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A CRITICAL EVALUATION OF THE ROLE PLAYED BY THE RED-BILLED OXPECKER *BUPHAGUS ERYTHRORHYNCHUS* IN THE BIOLOGICAL CONTROL OF TICKS

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ABSTRACT

BEZUIDENHOUT, J. D. & STUTTERHEIM, C. J., 1980. A critical evaluation of the role played by the red-billed oxpecker *Buphagus erythrorhynchus* in the biological control of ticks. *Onderstepoort Journal of Veterinary Research*, 47, 51–75 (1980).

Buphagus erythrorhynchus uses 4 feeding methods—scissoring, plucking, pecking and insect catching. During the day the birds spend 68% of their time feeding, with peaks of activity during the early morning and late afternoon. A total of 21 641 ixodid ticks were found in 53 stomachs examined, with a range of between 16 and 1 665 per stomach. *Boophilus* and *Rhipicephalus* were the most important genera eaten. Thirty Diptera, also found in the stomachs, accounted for 0,4% of the diet by mass. The food of the nestlings consisted of 45,6% ticks, 19,4% Diptera and 35,0% hair and tissues.

When kept in captivity, *Buphagus* was able to account for an appreciable reduction in the numbers of *Boophilus* on cattle, reaching a figure of 95,7% reduction for adult ticks. In controlled experiments *Buphagus* showed the highest preference for *Boophilus decoloratus*, *Rhipicephalus appendiculatus* and *Hyalomma truncatum*. The daily food intake of a captive bird was 14,7 g, which is equivalent to 7 195 engorged *Amblyomma hebraeum* larvae. Three acaricides, namely, amitraz, chloromethiuron and DDT, did not cause any clinically detectable toxicity in captive birds during a 5-day period.

Résumé

UNE ÉVALUATION CRITIQUE DU RÔLE JOUÉ PAR L'OISEAU, BUPHAGUS ERYTHRORHYNCHUS, *DANS LE CONTRÔLE BIOLOGIQUE DES TIQUES*

Buphagus erythrorhynchus *utilise 4 méthodes d'alimentation: cisaillement, arrachement, becquetage et attrapage d'insectes en vol. Pendant la journée, les oiseaux passent 68% de leur temps à se nourrir avec des pointes plus actives très tôt le matin et dans la fin de l'après midi. Un total de 21 641 tiques ixodides fut trouvé dans 53 estomacs examinés, avec une variation de 16 à 1 665 par estomac.* Boophilus *et* Rhipicephalus *furent les genres les plus importants qui étaient mangés. Trente diptères également trouvés dans les estomacs constituaient 0,4% de la diète. L'alimentation des nichées constituait 45,6% de tiques, 19,4% de diptères et 35,0% de poils et tissus.*

Quand il est gardé en captivité, Buphagus *est capable de réduire d'une manière appréciable le nombre de* Boophilus *sur le bétail, atteignant un chiffre de réduction de 95,7% pour les tiques adultes. Dans des expériences contrôlées* Buphagus *montra la préférence la plus grande pour* Boophilus decoloratus, Rhipicephalus appendiculatus *et* Hyalomma truncatum. *L'absorption alimentaire quotidienne d'un oiseau captif fut de 14,7 g, soit un équivalent de 7 195 larves engorgées d'*Amblyomma hebraeum. *Trois acaricides, à savoir amitraz, chloromethiuron et DDT ne causèrent pas de toxicité cliniquement détectable chez les oiseaux captifs pendant une période de 5 jours.*

INTRODUCTION

Oxpeckers are specific predators of ticks and other ectoparasites of herbivorous animals (Moreau, 1933; Attwell, 1966). However, there has always been, and still is, much controversy regarding their effectiveness in controlling ticks. Some regard them as effective and beneficial, while others condemn them as ineffective and a pest in farming areas (Van Someren, 1951).

Although oxpeckers were once present in comparatively large numbers in most of South Africa's tick-infested regions, their numbers have markedly decreased in stock farming areas and they are now mainly concentrated in relatively undeveloped regions and in game parks (Stutterheim, 1979, unpublished data). The reasons for their near disappearance are

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obscure, but intensive dipping of livestock over the past 40 years or more and the reduction of game in farming areas are thought to have played major roles in the reduction of their numbers.

A critical evaluation of the role that oxpeckers can play in tick control became especially necessary in the light of the ever-increasing development of resistance to acaricides amongst tick populations (Whitehead, 1969; Whitnall, 1969). Although quantitative assessments of the food preferences of the red-billed oxpecker (*Buphagus erythrorhynchus*) have been made (Moreau, 1933; Van Someren, 1951), these have not been related to the actual availability of ticks, the number that can be consumed in a day and possible seasonal changes in food preferences. A study on this aspect of the birds' ecology depends not merely on analysing stomach contents in relation to the time of day and season during which they were collected, but also on obtaining some indication of the relative abundance of the different food items on which the birds feed (Siegfried, 1971). We thus decided to base this study on 5 sets of data, namely, the feeding methods, behaviour and daily activity patterns of the oxpeckers, stomach content analyses, variations in the abundance of Ixodoidea and Tabanidae and controlled studies with birds in captivity.

Feeding Ecology

Feeding methods, activity and behaviour

Previous publications on various aspects of the behaviour of the red-billed oxpecker have been reviewed by Attwell (1966), However, the feeding behaviour of this bird has not been studied in detail and it was therefore necessary to make a study of this aspect before investigating the ecology of this species.

Materials and methods

The behaviour and daily activity patterns of the red-billed oxpecker were studied from a vehicle with 7×50 binoculars in the Kruger National Park (KNP) from March 1973–December 1974. Feeding includes all the activities associated with the search for food, plus the activities of ingestion once food has been found. The mean diurnal time schedule was determined by using the instantaneous and scan-sampling method advocated by Altmann (1974). A total of 1 944 activity recordings on 12 different mammal species were made. No activity recording was made if the birds or mammals were disturbed by the observation vehicle. These data were then treated as if they had been obtained during a single day, although gathered over a 21-month period.

Experimental observations and discussions

Feeding methods

The methods used by each bird depend on the type of food being eaten. Among them, the following have been distinguished:

Scissoring: This method is used when the bird is feeding on ticks or wounds. The rapidly opening-and-closing bill is pushed through the hair or over any part of the mammalian symbiont's body. The angle of scissoring depends on the surface being operated on: in vertical scissoring, for example, the surface is usually nibbled with the tip of the bill, whereas in lateral scissoring the sharp cutting edges of the sides of the bill are used to collect food particles. As suggested by Van Someren (1951), scissoring is a feeding method based on touch, not sight, since indiscriminate surveys are made over any area of the hide, and any small object stuck in the hair is swallowed, before the birds move on to a new area. After every scissoring movement the head is lifted and the collected material swallowed, as indicated by a slight opening and closing of the bill. When scissoring, the bird's eyes are open and the tip of its tail is in contact with the body of the mammalian symbiont.

In lateral scissoring, one of the bird's legs is always directly underneath its body, with the tarsus/metatarsus pressed against the symbiont, and its other leg, usually at an angle of 45° with the longitudinal axis of its body, supports the bird on the symbiont. In vertical scissoring or nibbling both legs are directly underneath the bird's body. Ninety-four per cent of the total feeding behaviour consists of scissoring (Stutterheim, 1976).

Plucking: Sight is important in this method. The body of the mammalian symbiont is searched with the head turned sideways, and any visible ticks or loose pieces of skin are seized with the tip of the bill and pulled off with a backward turning movement of the head. During plucking, the bird's legs are directly underneath its body and the tip of its tail touches the body of the symbiont. Only 5 per cent of the total feeding behaviour consists of plucking (Stutterheim, 1976).

Pecking: This method is mainly used for feeding on sores and is a pickaxe-like action with either a slightly opened or a closed bill (Attwell, 1966). During pecking, the bird's legs are directly beneath its body and the tip of its tail touches the mammal's body. After a few pecking movements the bird usually stops to swallow any collected material. Pecking is usually followed by vertical scissoring when the bird is feeding on wounds in order to collect any free flowing serum or blood. No information is available on the percentage of time spent on pecking.

Insect catching: Three different methods are used for this:

(a) *Hawking:* The bird flies or jumps into the air to snap at an insect flying over the mammalian symbiont. Slow-moving insects are followed with a hovering flight. The bird always returns to the same mammal. Oxpeckers are not very adept at this aerial hunting and often seem to miss.

(b) *Random catching:* The bird suddenly stops what it is doing, snaps at any insect within reach on the animal and then returns to its previous occupation.

(c) *Stalking:* The bird lowers its body, points its bill at the insect, darts forward and shoots out its head to catch the insect on the body of the mammalian symbiont.

Very small insects are swallowed immediately, but most are killed first by being nipped. Larger insects are softened by being squeezed back and forth through the bill. Captive birds were seen softening hard insects by hitting them against a rigid surface. One per cent of the total feeding behaviour consists of insect catching (Stutterheim, 1976).

Feeding activity

The mean diurnal time spent feeding was calculated as 68% (n=1 944). Early morning (05h00–07h00) and late afternoon (16h00–18h00) peaks of feeding activity were observed. As ixodid ticks form the main food supply (see Stomach content analyses etc., p. 54) and are available throughout the day, the decline in feeding activity during the midday period can probably be linked with the rate of digestion and absorption of the food (Stutterheim, 1976). According to Hintz & Dyer (1970), who studied red-winged blackbirds (*Agelaius phoeniceus*), the early morning feeding serves to replenish reserves depleted during the night, and the late afternoon peak could be related to the rebuilding of energy reserves in preparation for the night. However, it must be remembered that the present data were collected in all seasons of the year but are treated as if they had been collected during one day. This could have biased the results, because no adjustment is made for the change in length of the diurnal period.

Feeding behaviour

Ixodoidea: Ticks are collected by scissoring and plucking. Scissoring, which accounted for 94% out of a total of 17 057 feedings observed, is used to collect ixodid larvae and probably also nymphae and small adults. Although larvae formed a considerable proportion (38%) of the total number of ticks in the stomach contents (see Stomach content analysis etc., p. 54), they constituted only 6,9% by mass of the ixodid part of the diet. Plucking accounted for 5% of the feedings observed and is used to collect the larger ticks. Unlike scissoring, every plucking movement appears to result in the capture of a tick. Within a given feeding niche an individual which can gather relatively large food items must have an advantage, because overall it will gain more energy than it has expended in gathering it (Siegfried, 1971). It can therefore be assumed that a bird gains more energy from plucking than from scissoring and it is still a mystery why *Buphagus* spends so much of its time scissoring, which is not always successful, rather than plucking. On impala (*Aepyceros melampus*), *Buphagus* frequently ignored ticks that were showing through the hair. Furthermore, during the breeding season, when the birds collect food for the chicks by plucking, they are able to collect large numbers of ticks in a short time.

Though giraffe (*Giraffa camelopardalis*) and buffalo (*Syncerus caffer*) in the KNP are usually infested with *Amblyomma* between the hind-legs, these ticks are seldom utilized. An engorged *Amblyomma* female has a mean mass of 2,74 g (n=100) and a captive bird was apparently unable to swallow a tick of this size. Furthermore, Attwell (1966) states that *Buphagus* is unable to dislodge adult *Amblyomma* females. These observations could explain the low number of adult *Amblyomma* females (n=13) found in the stomach analyses (see Stomach content analysis etc., p. 54).

Insects caught: Two tabanid species that *Buphagus* caught in the Satara area (KNP) were identified* as *Philoliche aethiopica* and *Tabanus minuscularis*. The mass of 1 specimen of *P. aethiopica* was 0,18 g and that of *T. minuscularis* 0,0329 g. Once, on a warthog (*Phacochoerus aethiopicus*), *Buphagus* caught and swallowed 3 *P. aethiopica* in succession. For a bird the size of an oxpecker, a fly of this size would contribute a large percentage of the food needed for any given day. From this it is obvious that the numbers of different food items eaten have little meaning when their contribution to the diet is determined.

On 3 occasions *Buphagus* caught and ate winged termites (Isoptera) on their nuptial flight. This behaviour was also observed by Mundy (personal correspondence, 1974), and Van Someren (1951) found 21 of these termites in a stomach examined in Kenya. The nuptial flight of the termite is an ephemeral event and, since most surviving alates disappear underground overnight, it is doubtful if they play an important role in the biology of *Buphagus*. Termites are caught by hawking, and the bird always returns to the same symbiont animal to swallow the captured insect. One specimen caught by the birds was identified as belonging to the genus *Microtermes*. Thorpe (1956, cited by Rowen, 1970) has pointed out that the appearance of unusual feeding behaviour patterns in birds are often associated with acute food shortages. The converse, however, is also true, and atypical foraging patterns are sometimes seen when an organism that the species does not normally eat is abundant.

Birds in captivity caught and swallowed any available insect. A bird was also seen catching a small moth (Lepidoptera) on a buffalo. On another occasion, a bird flew from an impala, disappeared into the grass and returned with a grasshopper (Acrididae) about 4 cm long, which was then consumed on the back of the antelope. Kemp (personal communication, 1973) observed birds in the KNP catching grasshoppers below their nest. From the number of observations and the number of specimens found in the stomachs examined, however, it is apparent that the Insecta (apart from Diptera) are of little significance in the diet of *Buphagus*.

Secretions of the nose and mouth: On the buffalo and white rhinoceros (*Diceros simus*), *Buphagus* was frequently observed collecting mucus from the nose by means of scissoring. This accounted for 1,3% of the total feeding behaviour patterns observed. It is doubtful whether the mucus has any nutritional value but it could contribute moisture. *Buphagus* has been observed swallowing saliva dripping from the mouth of a buffalo.

Lachrymal secretions: *Buphagus* was seen collecting lachrymal secretions from the eyes of impala, giraffe, buffalo, zebra (*Equus burchelli*), sable antelope (*Hippotragus niger*), nyala (*Nyala angasi*), white rhinoceros and domestic cattle by means of scissoring, and this accounted for 0,3% of the total feeding behaviour observed. Attwell (1966) likewise gives a record of *Buphagus* feeding at the eyes of a black rhinoceros (*Diceros bicornis*). The nutritional value of these secretions is not known.

Leeches: On a hippopotamus (*Hippopotamus amphibius*) in the KNP, *Bughagus* was seen making plucking movements which accounted for 98,8% of the total feeding behaviour observed on this animal (n=166). Although ticks have been recorded from the hippopotamus, e.g. *Rhipicephalus simus, Amblyomma hebraeum* and *A. tholloni* (Theiler, 1962), none were found on 8 specimens examined from the Olifants River, but the animals were, however, heavily infested with leeches (Hirudinea), especially on the head, around the anus and between the hind legs. These were identified as *Placobdella jaegerskiondoli*, a species commonly found on the hippopotamus (Oosthuizen, personal communication, 1975). The birds may, therefore, have been feeding on leeches, but this is merely an unproven assumption as none were found in the stomach contents. The collection of oxpeckers from hippopotamus might provide some information in this respect.

Dung: At Skukuza, *Buphagus* was observed to fly from a captive buffalo and apparently collect and swallow small pieces of dung whilst sitting on the ground.

* Kindly identified by B. R. Stuckenberg, Natal Museum, Pietermaritzburg

Carrion feeding: There are several records of carrion feeding by the Buphaginae. Moreau (1933) records an instance of 4 oxpeckers feeding on drying impala meat in Tanzania, and Van Someren noted a flock of oxpeckers that frequented an abattoir and fed on the flayed carcasses hung up outside for inspection. Attwell (1966) mentions 5 birds eating strips of skin and meat from a hippopotamus which had been dead for at least 4 days. On 3 successive days in the KNP *Buphagus* was observed feeding on blood lying on the ground about 20 m from animal pens frequented by the birds. At the Orpen Dam, Marshall (personal communication, 1973) observed an oxpecker flying away from a dead giraffe which had an open wound behind its ear. This carrion feeding behaviour was investigated by hanging a strip of fresh meat near some captive buffalo at Skukuza. The birds, however, only visited this piece of meat and were not seen to feed on it. From these observations it is difficult to assess realistically the significance of carrion feeding in the biology of *Buphagus.*

Wound feeding: Pecking and scissoring are mainly used in wound feeding. A wound is opened by pecking and any free-flowing blood or serum is collected by vertical scissoring. Scabs are collected by plucking. Attwell (1966) summarized all the existing records of wound feeding and concluded that oxpeckers frequent domestic stock because of the availability of ticks rather than sores and felt that proof of deliberate injury to sound skin is still lacking. Observations on *Buphagus* in the KNP indicate that the birds are able to open partly healed wounds and show a strong preference for feeding on these wounds, as the degree of competition to feed at these sites indicates. From observations on a tame ox at Skukuza it is clear that the birds can also enlarge existing wounds. A bird was seen starting to peck on the forehead of an impala at the place from which a tick had been collected. It kept on pecking until a white spot appeared but was then chased away by the animal. The bird lost interest and started feeding on other impala standing nearby. Twice, on a zebra and a giraffe, birds were not allowed to feed on existing wounds. Birds in captivity show a high degree of preference for scab material and always return to the same spot even after being chased away. Goodwin (1963) offered an oxpecker a deliberately cut finger. The blood appeared to excite the bird more than the loose morsel of skin on which it had previously been feeding, and it fed on the blood.

Stomach content analysis and the seasonal variation in the availability of food items

Although quantitative assessments of the food preferences of *B. erythrorhynchus* have been made by Moreau (1933) and Van Someren (1951), their information was gathered sporadically and any possible seasonal changes in food preferences were not taken into account. Other studies are based on isolated incidents and on descriptions of "unusual" feeding behaviour (Prozesky, 1964; Attwell, 1966).

A report on the analysis of 53 stomachs collected in the KNP from culled oxpeckers over a 12-month period is given below.

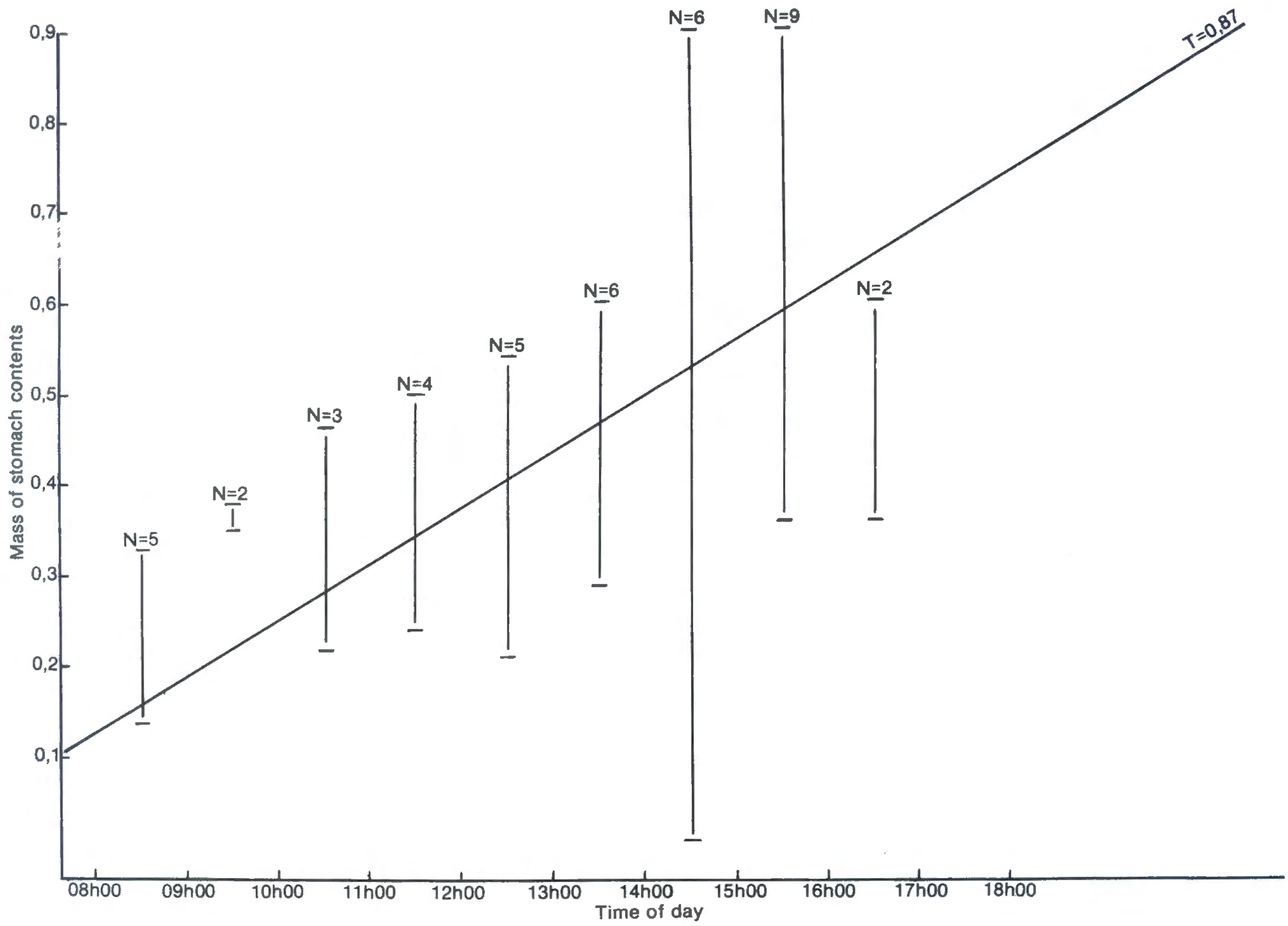

FIG. 1 The relationship between the mean mass of the stomach contents and the time of day

Materials and methods

Oxpeckers were shot for the analysis of stomach contents in the middle of each month in the vicinity of Renosterkoppies Dam, about 16 km south of Skukuza, KNP. The time of collection was not constant. Within 3 h of the birds being shot, the stomach of each was removed, preserved in 70% alcohol and labelled with a number, the date, time of day, locality, age and mass, and the name of the mammalian symbiont from which it had been collected. The mass of the stomach plus its contents was determined after it had been dried on 4 layers of blotting paper for 5 min at 37 °C. The stomach contents were then washed out, the stomach wall dried on 4 layers of blotting paper for 4 min at 36 °C and its mass determined.

A total of 53 stomachs were examined. The contents of each were washed into a Petri dish, examined under a stereoscopic microscope and analysed by the identification and removal of the 2 most important components, namely, the Ixodoidea and all other arthropods. The mass of each of these 2 components was determined after they had been dried for 10 min on 4 layers of blotting paper at 55 °C. The least digested contents of the stomach were identified as accurately as possible. However, some of the stomach contents were unidentifiable because of the fragmentary nature of the material. The adults and nymphae were identified generically, primarily by the structure of their scuta, and the adults were sexed. It proved impossible, however, to identify the larvae generically and these were divided into 2 groups: *Rhipicephalus* plus *Boophilus* and *Amblyomma*. It was assumed that *Hyalomma* larvae, which feed mostly on birds and some smaller mammals, such as hares, did not occur on the mammalian symbionts examined (Theiler, 1962). Any that were present would have been included with the count of *Amblycmma* larvae.

An indication of the seasonal variations in the biomass of Ixodidae in the KNP was obtained monthly from October 1973–December 1974 by culling an adult impala ram in the vicinity of Skukuza, combing its hair with a steel comb and collecting all the ticks that could be found. For comparison, total tick counts were also made on 4 buffalo, a zebra and a warthog. To determine the species of ticks found on the larger mammals that occur in the KNP, all the data collected by the National Parks Board research section and the Division of Veterinary Services at Skukuza were utilized. From January–December 1974 the biomass of the Tabanidae was determined by erecting a Harris fly-trap for 24 h once a month on the same site near Skukuza.

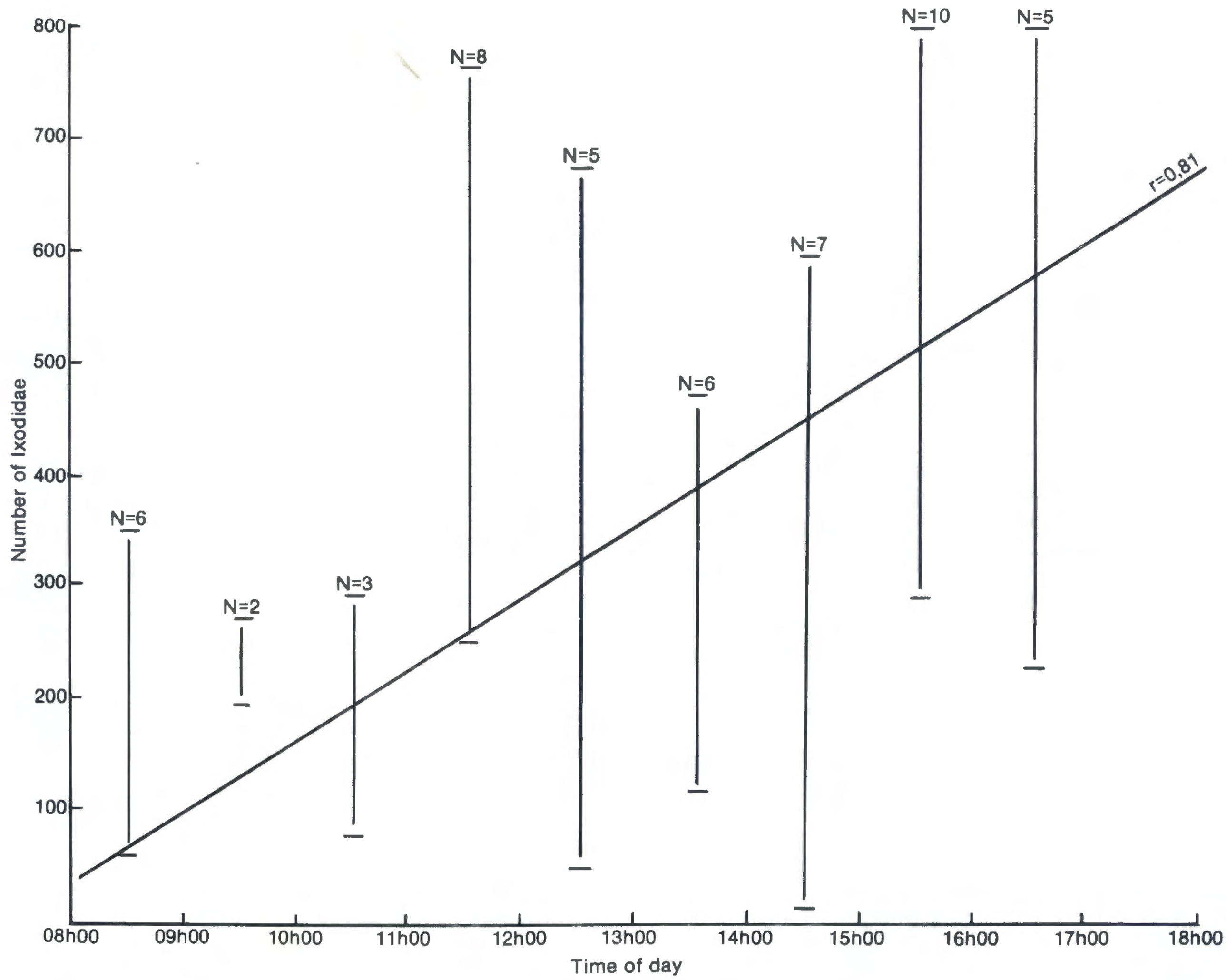

FIG. 2 The relationship between the number of Ixodoidea found in the stomach contents of 52 *B. erythrorhynchus* collected in the Skukuza area in the period July 1973–June 1974 and the time of day. Vertical lines give the range

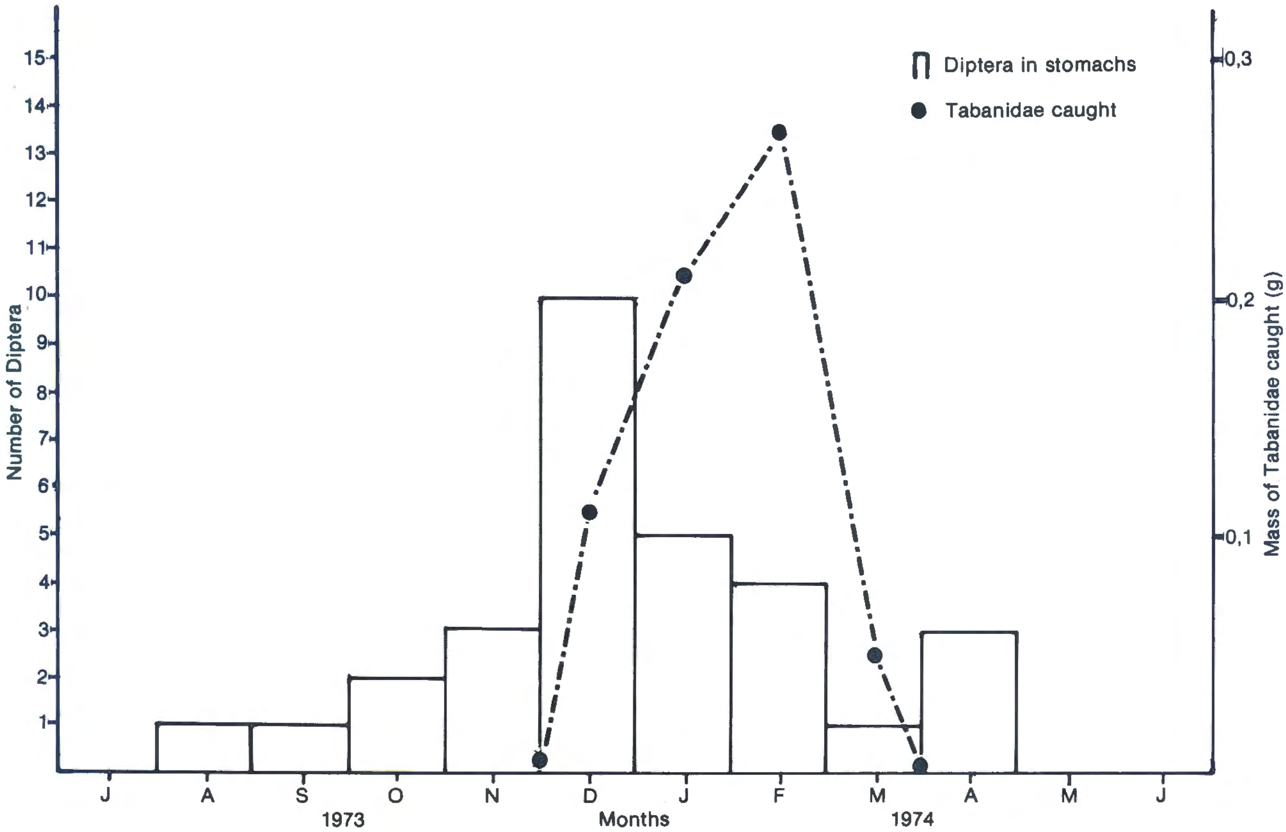

FIG. 3 The number of Diptera found in 53 stomachs of *B. erythrorhynchus* as related to the mass of Tabanidae caught in a Harris fly trap in the Skukuza area during the period July 1973–June 1974

Experimental observations and discussion

Before the results are considered in detail, the shortcomings of the study should be mentioned. Results based on an analysis of stomach contents have inherent errors. Since the rate at which the different food items digest varies, the number of hard items in the stomach is likely to be higher than that of soft items (Kemp, 1972). The energy expended in obtaining food, the degree of its digestion and the different nutritional values of foods are not considered, but are taken as being constant. Slobodkin (1961) found that different insect tissues are very similar in terms of joules per ash-free gram, and consequently the mass of the food items was used in the present survey, as it was considered the best parameter for field studies. Moreover, some fats were probably removed from the stomach wall and stomach contents while they were stored in alcohol, but the effects would be approximately the same for all specimens (Johnston, 1967).

Because it was difficult to collect sufficient oxpeckers in a single day, the method of collection was not standardized and the birds were not all shot at the same time of the day. A significant relationship (r=0,87) was found between the mean mass of the stomach contents and the time of day (Fig. 1), and also between the number of ticks in the stomach and the time of day (r=0,81) (Fig. 2). It can therefore be concluded that in the course of a day the amount of food in the stomach increases with time, also that an analysis of stomach contents cannot be used to calculate the total amount of food consumed by an oxpecker in a given day.

The number of Ixodidae was determined by the number of scuta found in the stomach. It was impossible, however, to do a quantitative study on the amount of scurf cells, hair and epidermal tissue found in the stomach, as no method is available for the separation of these components. They could only be classified by the frequency of their occurrence in the samples, given as the percentage of food samples in which each item was recorded (Siegfried, 1971). It was thought unpractical to perform volumetric determinations because some components occurred in quantities too small for accurate determination. For the purpose of the present study, however, the methods used are considered sufficiently precise.

Siegfried (personal communication, 1975) stressed that the actual numbers of different food items eaten have little meaning when their contributions to the diet are assessed and that the mass of each food item must be used to estimate this factor. This was impossible for the Diptera (especially the Tabanidae) as the fragmented specimens could not be identified below the ordinal level (Stuckenberg, personal communication, 1974). An attempt was made to correlate the number of tabanids that were available to *B. erythrorhynchus* in a particular area with the number that the birds consumed (Fig. 3). However, even using the mass of a food item to indicate its contribution to the diet is only an approximation (Kemp, 1972).

Ixodoidea

The consumption of ticks was not restricted to any particular season of the year as they were found in all 53 of the stomachs examined at various times during the year and formed 52,3% by mass of the recognizable stomach contents (Table 1). A total of 21 641 ticks were found altogether, with a mean per stomach of 408,3 and a range of 16–1 665 (Table 2). Moreau (1933) found a mean of 41 ticks per bird in 58 stomachs analysed in Tanzania, while Van Someren (1951) found a mean of 16 ticks per bird in 12 stomachs analysed in Kenya. However, Moreau and Van Someren counted only the undigested or partly digested ticks, which probably explains why their figures are so much lower. In the present study the number of scuta found in the stomach was used as an indication of the number of ticks ingested. It must be remembered that the oxpeckers studied by the various authors were not collected in the same area or from the same species of mammal.

The ixodid genera identified from the stomach contents were *Boophilus, Rhipicephalus, Amblyomma* and *Hyalomma* (Table 1). It was also impracticable to separate *Amblyomma* and *Hyalomma* larvae morphologically, but it was assumed that *Hyalomma* larvae, which feed mostly on birds and some smaller mammals such as hares, did not occur on the mammalian symbionts examined (Theiler, 1962). These larvae were therefore classified as *Amblyomma.*

Only 2 specimens of the family Argasidae were found, namely, 2 *Ornithodoros* nymphae. *Boophilus* was clearly the most important ixodid utilized by *Buphagus,* since the adults and nymphae of this species constituted 50,8% (n=11 003) of the total number of ticks eaten. Significant difference (t=test, P<0,05) between the number of *Boophilus* males and females consumed, indicated a preference for females. The genus *Rhipicephalus* was numerically next in importance, and the genera *Boophilus* and *Rhipicephalus* together accounted for 89,8% (n=19 429) of the ixodid ticks recovered. Very few (n=36) adult *Amblyomma* and *Hyalomma* ticks were found in the 53 stomachs examined and these accounted for only 0,18% of the total number of ticks consumed. However, *Amblyomma* nymphae and larvae made up 10,1% (n=2 174) of the total number of ticks recovered. It is also evident (Table 1) that ixodid larvae in general were a numerically important constituent of the stomach contents (38%) (n=8 404).

Moreau (1933) and Van Someren (1951) recorded a low incidence of *Boophilus* (6% and 20%, respectively), and a high incidence of *Rhipicephalus* (67% and 73%, respectively). In addition, *Amblyomma variegatum* accounted for 23% and 6%, respectively, of the total number of ixodid ticks identified. The difference in generic composition between their findings and those in the present study could be a reflection of the different ixodid species found on the mammalian symbionts. Walker (1974) rarely recorded *Boophilus* from wild animals in Kenya, which may explain the low percentage (6%) of this genus found in the stomach contents of *Buphagus* from Kenya.

Figures obtained for the mean mass of different ixodids as determined by Londt & Arthur (1975) and from further mass measurements made in this laboratory were used to calculate the total contribution in mass to the diet made by the 4 genera of Ixodidae found in the stomach contents examined. A comparison between the number of ticks recovered and their mass (Table 4) shows that adult *Boophilus* females were the most important ixodids utilized by mass (38,2%), followed by adult *Boophilus* males, and these 2 food components contributed 59,2% by mass of the ixodid ticks recovered. Moreover, although the ixodid larvae appeared to be a numerically important food component, they contributed only 5,9% of the total mass of ixodid ticks consumed.

Furthermore, adult *Rhipicephalus* females contributed only 1,3% to the diet by number but 14,4% by mass, while *Boophilus* nymphae contributed 18,3% by number but only 4,4% by mass. *Rhipicephalus* plus *Boophilus* comprised 89,4% of the mass of the ticks found in the stomachs. No significant correlation (r=0,37) was found between the number of ticks in the stomach contents and the percentage by mass of the stomach contents that consisted of ticks. This again emphasized the fact that the numbers of different food items eaten have little meaning when their contribution to the diet is assessed.

A significant difference (t=test, P<0,05) was found between the mean total numbers of ticks and of the different developmental stages found in the stomachs of adult male and female birds, the females containing greater numbers than the males (Table 5). The reason for this is obscure. The stomachs of only 2 immature free-flying birds less than 8 months old were examined, consequently no comparison can be made with the adult birds.

Lice and mites

Moreau (1933) found 7 lice and Van Someren (1951) 29 lice and 2 mites in the stomachs they examined. In the present study 3 lice and 2 mites were found.

Diptera

Thirty Diptera, found in 13 of the 53 stomachs examined, comprised 0,4% of the diet by mass (Tables 2 & 3). From the analysis of the stomach contents, it appears that flies were a source of food during the rainy months from November–March. This corresponds to the number of Tabanidae caught in a Harris fly-trap during the summer months of November–March (Fig. 3).

Moreau (1933) and Van Someren (1951) recorded a mean of 7,3 and 13,5 flies per stomach, respectively, compared with 0,6 flies per stomach in the present study. Moreau (1933) found that Diptera were eaten by 76% of the birds and 2 stomachs contained flies only. The reason for the differences between their findings and ours is unknown.

No dipteran maggots were found in the stomachs examined. Van Someren (1958, cited by Attwell, 1966), recorded maggots and fly eggs as food material but none were recorded by Moreau (1933) and Van Someren (1951). Attwell (1966) speculates that rapid digestion makes their detection difficult. In captivity, birds were also given blowfly larvae, *Lucilia* spp., which they ate eagerly.

Two specimens of Hippoboscidae found in the stomachs were identified as *Hippobosca fulva,* a species that was collected from impala in the Skukuza area. Oxpeckers apparently have a low preference for these flies, since direct observations suggested that the birds completely ignored them on impala, and Moreau (1933) found only 2 hippoboscid flies in 58 stomachs examined. These could have been accidentally picked up while the birds were scissoring through the hair. The way that hippoboscids move beneath the hair may make them difficult to catch.

TABLE 1 Members and species of Ixodoidea recorded during an analysis of the stomach contents of 53 *Buphagus erythrorhynchus* collected in the Skukuza area from July 1973–June 1974

Date collected	Time collec-ted	Age and sex of birds	*Boophilus*			*Rhipicephalus*			*Boophilus* and *Rhipiceph.* LL	*Amblyomma*			*Am-blyomma* LL	*Hyalomma*			Totals of different stages				Grand totals
			♂♂	♀♀	NN	♂♂	♀♀	NN		♂♂	♀♀	NN		♂♂	♀♀	NN	♂♂	♀♀	NN	LL	
18/7/73............	13h00	Ad ♂	39	33	20		1	3	5			14	7				39	34	37	12	122
18/7/73............	14h10	Ad ♂	11	113	64		1	4	29		1	9	8				11	115	77	37	240
18/7/73............	15h20	Ad ♀	87	76	70	1	5	6	23			18	52	1	1		89	82	94	75	340
19/7/73............	12h10	Ad ♀	66	79	129	3	2	9	24			11	23				69	81	149	47	346
19/7/73............	12h40	Ad ♂	110	93	102	1	1	154	65			19	65				111	94	275	130	610
19/7/73............	13h50	Ad ♂	81	107	84	1	1	10	7			8	11				82	108	102	18	310
19/7/73............	13h50	Ad ♂	61	85	100			4	51			11	58				61	85	115	109	370
30/8/73............	11h15	Ad ♂	120	70	125	1		13	26			18	85				121	70	156	111	458
30/8/73............	12h45	Ad ♀	16	6	4	2	1		23			1					18	7	5	23	53
30/8/73............	13h05	Ad ♀	63	230	74							22					63	230	96	0	389
31/8/73............	08h20	Ad ♂	67	16	72		1		32	1		1	5				68	17	73	37	195
17/9/73............	10h05	Ad ♂	43	53	101			7	80		2	4	5				43	55	112	85	295
17/9/73............	11h00	Ad ♂	91	83	120	4		27	35			10	5	1	2		96	85	157	40	378
17/9/73............	14h30	Ad ♀	130	111	104		2	3	46		4						130	117	107	46	400
17/9/73............	14h30	Ad ♀	94	90	111		1	68	53			18	10				94	91	197	63	445
17/9/73............	14h30	Ad ♀	137	120	118	1		41	85			9	24				138	120	168	109	535
17/9/73............	14h35	Ad ♂	130	92	60			13	5			16	34				130	92	89	39	350
10/10/73...........	17h45	Ad ♂	93	136	54	2	1	33	78		1	68	22				95	138	155	100	488
18/10/73...........	14h10	Ad ♂	5	3	5			2	1								5	3	7	1	16
18/10/73...........	14h10	Ad ♀	142	142	195	1	2	58	34			11	14				143	144	264	48	599
18/10/73...........	15h00	Ad ♀	67	70	92			27	103			14	11				67	70	133	114	384
13/11/73...........	08h00	Ad ♂	31	15	67			10	85			16	25				31	15	93	110	249
13/11/73...........	08h00	Ad ♂	34	30	81	3	1		183		1	9	6				37	32	90	189	348
13/11/73...........	08h00	Ad ♀	22	27	34			2	13		1	7	10				22	28	43	23	116
13/11/73...........	09h30	Ad ♀	42	54	53		1	11	62			13	37				42	55	77	99	273
26/11/73...........	12h00	Ad ♂	48	71	76	1	2	2	19			2	10				49	73	80	29	231
26/12/73...........	16h30	Ad ♀	72	106	104			7	18			1	2				72	106	112	20	310
26/12/73...........	16h50	Ad ♀	20	29	54			24	95			3	5				20	29	81	100	230
27/12/73...........	11h35	Ad ♂	36	44	45	2	1	29	587	3	2	8	8				41	47	82	595	766
24/1/74............	16h30	Ad ♀	42	131	23		4	42	453			6					42	135	71	453	701
25/1/74............	11h25	Ad ♀	36	50	52	1	3	18	338				1				37	53	70	339	499
25/1/74............	16h00	Juv ♀	39	58	48	10	5	94	1 400			7	4				49	63	149	1 404	1 665
25/1/74............	16h00	Ad ♂	84	223	70				18	3							87	223	70	18	398
19/2/74............	15h00	Ad ♀	13	29	50	4	22	18	235			20	20				17	51	88	255	411
19/2/74............	15h40	Ad ♀	10	34	140	1	21	20	486			40	38				11	55	200	524	790
19/2/74............	15h40	Ad ♀	39	74	124	60	70	37	396			53	96				99	144	214	492	949
19/2/74............	15h40	Ad ♀	18	15	101	4	20	7	199			11	10				22	35	119	209	385
20/3/74............	10h30	Ad ♂	13	23	12	2	2	3	4			3	4				15	25	18	8	66
20/3/74............	10h40	Ad ♀	3	7	8	10	22	46	85			3	46				13	29	57	131	230

TABLE 1 (*continued*)

Date collected	Time collected	Age and sex of birds	*Boophilus*			*Rhipicephalus*			*Boophilus* and *Rhipiceph.*	*Amblyomma*			*Amblyomma*	*Hyalomma*			Totals of different stages				Grand totals
			♂♂	♀♀	NN	♂♂	♀♀	NN	LL	♂♂	♀♀	NN	LL	♂♂	♀♀	NN	♂♂	♀♀	NN	LL	
20/3/74	11h20	Ad ♂	21	32	51	8	25	14	34			18	50				29	57	83	84	253
20/3/74	12h45	Ad ♂	35	50	111		15	13	150			30	272				35	65	154	422	676
10/4/74	08h45	Ad ♂	7	17	13			1	16			2	6				7	17	16	22	63
10/4/74	08h55	Ad ♂	14	13	24	1		9	60				11				15	13	33	71	132
10/4/74	09h35	Ad ♂	17	19	28	4	26	17	68			9	10				21	45	54	78	198
16/4/74	15h20	Ad ♀	103	407	67	3			44			6					106	407	73	44	630
21/5/74	13h35	Ad ♂	65	58	47		3	7	23			13	9				65	61	67	32	225
21/5/74	15h15	Ad ♂	140	142	150	1	5	39	167			12	45				141	147	201	212	701
21/5/74	15h15	Ad ♀	106	83	78	2	1	28	92			14	39				108	84	120	131	443
21/5/74	15h15	Juv ♂	49	33	46	2	2	4	122			19	6	11			62	35	69	128	294
15/6/74	11h35	Ad ♂	73	69	157	1		29	202			1	130				74	69	187	332	662
18/6/74	13h55	Ad ♂	90	99	67	4	3	32	102		1	7	69				94	103	106	171	474
18/6/74	11h55	Ad ♀	29	46	42		1	50	155			16	38				29	47	108	193	377
18/6/74	11h55	Ad ♀	65	88	123			43	157			12	85				65	88	178	242	573
			3069	3984	3950	141	274	1138	6873	7	13	643	1531	13	3		3230	4274	5731	8404	21641
		$\overline{X}$	57,9	75,2	74,5	4,7	8,1	24,2	132,2	2,33	1,61	13,4	33,3	4,2	1,5		60,9	80,6	108,1	161,6	408,3
		SD	39,4	60,4	49,4	6,14	7,6	17,6	109,6	0,3	0,3	6,7	19,4	0,6	0,5		40,0	50,2	65,9	102,4	166,5
		Range	3–142	3–407	4–195	0–60	0–70	0–154	0–1400	0–3	0–4	0–68	0–272	0–11	0–2		5–143	3–407	5–275	0–1404	16–1665
		% of total	14,18	18,40	18,25	0,65	1,26	5,25	31,75	0,03	0,06	2,97	7,07	0,06	0,01		14,93	19,75	26,48	38,83	

Ad =Adult birds or birds older than 8 months

Juv =Free-flying birds younger than 8 months

Ad ♂ =Adult male

Ad ♀ =Adult female

Juv ♂ =Juvenile male

Juv ♀ =Juvenile female

NN =Nymphae

LL =Larvae

$\overline{X}$ =Mean

SD =Standard deviation

TABLE 2 Mass and numbers of food items identified during an analysis of the stomach contents of 53 *Buphagus erythrorhynchus* collected in the Skukuza area from July 1973–June 1974

Date collected	Time collected	Age and sex of bird	Mammalian symbiont from which collected	Mass of stomach contents (g)	Ixodoidea			Insecta			
					Total numbers	Mass (g)	Stomach contents (%)	Mass (g)	Stomach contents (%)	Number	
										Diptera	Other
18/7/73......	13h00	Ad ♂	Impala	0,3101	122	0,0593	19,1				
18/7/73......	14h10	Ad ♂	Giraffe	0,6705	240	0,1503	22,4				
18/7/73......	15h20	Ad ♀	Impala	0,8696	340	0,1295	14,9				
19/7/73......	12h10	Ad ♀	Impala	0,4599	346	0,0905	17,5				
19/7/73......	12h40	Ad ♂	Impala	—	610	0,3100	—				
19/7/73......	13h50	Ad ♀	Impala	0,5406	310	0,1095	20,3				
19/7/73......	13h50	Ad ♂	Impala	0,7000	370	0,1902	27,2	0,0009	0,13		1
30/8/73......	11h15	Ad ♂	Impala	0,4501	458	0,2204	49,0	0,0043	0,96	1	
30/8/73......	12h45	Ad ♀	Kudu	0,2100	53	0,0093	4,4				
30/8/73......	13h05	Ad ♀	Kudu	0,5599	389	0,5098	91,1				
31/8/73......	08h20	Ad ♂	Impala	0,3915	195	0,3745	95,7				
17/9/73......	10h05	Ad ♂	Impala	0,4605	295	0,4590	99,7				
17/9/73......	11h00	Ad ♀	Impala	0,4805	378	0,1197	24,9	0,0008	0,17	1	
17/9/73......	14h30	Ad ♀	—	0,4165	400	0,3120	74,9				
17/9/73......	14h30	Ad ♀	—	0,3502	445	0,1000	28,6	0,0001	0,03		1
17/9/73......	14h30	Ad ♀	—	0,5075	535	0,4545	89,6				
17/9/73......	14h35	Ad ♂	—	—	350	0,1296	—				
10/10/73.....	17h45	Ad ♂	—	0,8455	488	0,7375	87,2				
18/10/73.....	14h10	Ad ♂	Giraffe	0,0695	16	0,0100	14,4				
18/10/73.....	14h10	Ad ♀	Giraffe	1,2659	599	0,8659	68,4				
18/10/73.....	15h00	Ad ♀	Giraffe	0,7195	384	0,2396	33,3	0,0062	0,86	2	
13/11/73.....	08h00	Ad ♂	Impala	0,1403	249	0,1207	86,0				
13/11/73.....	08h00	Ad ♂	Impala	0,2900	348	0,1275	44,0	0,0022	0,76	1	
13/11/73.....	08h00	Ad ♀	Impala	0,1498	116	0,0497	33,2	0,0014	0,93	1	
13/11/73.....	09h30	Ad ♀	—	0,3500	273	0,0294	8,4	0,0003	0,09	1	
26/11/73.....	12h00	Ad ♂	Impala	0,4799	231	0,0296	6,2				
26/12/73.....	16h30	Ad ♀	Impala	1,0120	310	0,6580	65,0	0,0109	1,08	9	
26/12/73.....	16h50	Ad ♀	Giraffe	0,3602	230	0,0406	11,3				
27/12/73.....	11h35	Ad ♂	Zebra	0,5096	766	0,0999	19,6	0,0093	1,82	1	
24/1/74......	16h30	Ad ♂	Zebra	0,8950	701	0,7355	82,2	0,0024	0,27	5	
25/1/74......	11h25	Ad ♀	Zebra	0,3025	499	0,1200	39,7				
25/1/74......	16h00	Juv ♀	Zebra	0,5006	1665	0,2307	38,5	0,0095	1,58		1
25/1/74......	16h00	Ad ♂	Giraffe	—	398	—	—				
19/2/74......	15h40	Ad ♀	Impala	0,6492	411	0,4199	64,7	0,0006	0,09	2	
19/2/74......	15h40	Ad ♀	Impala	1,5855	790	1,2440	78,5				
19/2/74......	15h40	Ad ♀	Impala	0,6707	949	0,2807	41,9	0,0090	1,34	2	
19/2/74......	15h40	Ad ♀	Impala	0,5370	385	0,4875	90,8				
20/3/74......	10h35	Ad ♂	Impala	0,3704	66	0,0698	18,9	0,0186	4,86		1
20/3/74......	10h40	Ad ♀	Impala	0,2204	230	0,2093	95,0				
20/3/74......	11h20	Ad ♂	Impala	0,2407	253	0,0204	8,5				
20/3/74......	12h45	Ad ♂	Impala	0,5403	676	0,2204	40,8	0,0213	5,60	1	
10/4/74......	08h45	Ad ♂	—	0,3256	63	0,0304	9,3				
10/4/74......	08h55	Ad ♂	—	0,3597	132	0,0305	8,5				
10/4/74......	09h35	Ad ♂	—	0,3803	198	0,1399	36,8	0,0041	1,08	3	
16/4/74......	15h20	Ad ♀	Impala	0,3604	630	0,2700	75,0				
21/4/74......	13h45	Ad ♂	Impala	0,4302	225	0,1399	32,5				
21/5/74......	15h15	Ad ♂	Impala	0,4369	701	0,4014	91,9				
21/5/74......	15h15	Ad ♀	Impala	0,7198	443	0,2704	37,6				
21/5/74......	15h15	Juv ♂	Impala	0,5870	294	0,3939	67,0				
15/6/74......	11h35	Ad ♂	Impala	0,3594	662	0,0397	11,0				
15/6/74......	13h55	Ad ♂	Impala	0,2935	474	0,2235	76,1				
18/6/74......	11h55	Ad ♀	Impala	0,2601	377	0,0901	34,6				
18/6/74......	11h55	Ad ♀	Impala	0,3650	573	0,3215	88,0				
Σ...............		53		25,0588	21641	13,1150		0,1010		30	4
X̄...............				0,5012	408,3	0,2522	52,3		0,40		
SD...............					166,5						
Range............					16–1665						

Σ =Total

X̄ =Mean

SD =Standard deviation

Ad ♂ =Adult male

Ad ♀ =Adult female

Juv ♂ =Juvenile male

Juv ♀ =Juvenile female

TABLE 3 Frequency of occurrence of items recorded in 53 stomachs of *Buphagus erythrorhynchus* collected in the Skukuza area from July 1973–June 1974

Item	Frequency of occurrence
	%
Ixodoidea	100
Diptera	25
Homoptera	2
Formicidae	2
Orthoptera	2
Hemiptera	2
Scurf cells	100
Epidermal tissue	100
Hair	100
Grit	100
Leaves	36
Grass seeds	30
Grass stems	47
Thorns	33
Pieces of thorn	2

TABLE 4 A comparison between the contribution of the number of the different ixodid species and their calculated mass to the diet of *Buphagus erythrorhynchus* at Skukuza from July 1973–June 1974

Species of ixodid	Age and sex of ixodid	Total number identified in stomachs of *Buphagus*	% of total number identified	Mean mass of unengorged specimen (mg)	Total mass (g)	% of total mass
Boophilus	Adult ♂	3 069	14,18	0,98	3,01	21,0
	Adult ♀	3 984	18,40	1,37	5,46	38,2
	Nymphae	3 950	18,25	0,16	0,63	4,4
Rhipicephalus	Adult ♂	141	0,65	7,00	0,99	6,9
	Adult ♀	274	1,26	7,50	2,06	14,4
	Nymphae	1 138	5,25	0,40	0,46	3,2
Boophilus & Rhipicephalus	Larvae	6 873	31,75	0,03	0,19	1,3
Amblyomma	Adult ♂	7	0,03	21,00	0,15	1,0
	Adult ♀	13	0,06	25,23	0,33	2,3
	Nymphae	643	2,97	0,40	0,26	1,8
	Larvae	1 531	7,07	0,43	0,66	4,6
Hyalomma	Adult ♂	13	0,06	5,80	0,08	0,5
	Adult ♀	3	0,01	9,60	0,03	0,2
					14,31	49,8

TABLE 5 A comparison between the number of Ixodoidea found in the stomachs of 25 male and 26 female *Buphagus erythrorhynchus* collected in the Skukuza area from July 1973–June 1974

	Adult female oxpeckers (26)	Adult male oxpeckers (25)
Total number of ticks	11 096	8 537
Mean number of ticks per stomach	426,8	341,5
Number of male ticks Σ	1 704	1 365
X̄	65,5	54,6
Number of female ticks Σ	2 477	1 695
X̄	95,3	67,8
Number of nymphae Σ	3 087	2 458
X̄	118,7	98,3
Number of larvae Σ	3 838	3 019
X̄	147,6	120,8

Other insects

Only 1 specimen of the Acrididae (Orthoptera) was found in the stomachs examined. Other insects found were a small ant (Formicidae), 1 hemipteran and 1 homopteran (Table 2). As these organisms contributed only 0,12% of the total diet, they are merely incidental items (See section under Feeding methods, activity and behaviour, p. 52).

Hair

Hair was found in varying quantities in all the stomachs examined (Table 3). Many contained what was practically a bolus of hair and from field observations it is clear that hair is accidentally ingested because of the feeding methods employed. It is not known whether it has any nutritional value, but from microscopic examinations the hair follicles are obviously digested. Moreau (1933) speculates that the fatty exudations of the sebaceous glands that are found attached to the base of the hair could be a supplementary source of food. The fact that no hair was found in the intestines or in the faeces supports the suggestion by Van Someren (1951) that it is regurgitated in the form of pellets. However, this behaviour was not observed during our 2-year study period, nor in birds kept in captivity for 6 months.

Scurf cells

Scurf cells were found in all the stomachs examined (Table 3), but their nutritional value is unknown. At Skukuza birds visited tick-free buffalo kept in pens for experimental work and were observed swallowing something after every scissoring movement. Skin scrapings made on these buffalo revealed large numbers of scurf cells which are possibly a supplementary source of food.

Epidermal tissue

Varying quantities were found in all the stomachs examined (Table 3). Pieces are often pulled off with the ticks and these can be identified by the round holes piercing them. Some may also have been collected during wound feeding (see Feeding methods, activity and behaviour, p. 52).

Vegetable matter

The various items found are listed in Table 3.

The leaves recovered were identified as belonging to the genus *Acacia*. It is doubtful whether these items have any nutritional value and they are probably collected accidentally during scissoring, when the birds are feeding by touch and not by sight, and when any small objects stuck in the hair are swallowed. Bolster (1935) reported that *B. erythrorhynchus* had been seen to "eat fruit from the garden". However, the accuracy of this record is doubtful.

Grit

According to Prozesky (1964), the young birds are fed with pieces of quartz to aid their digestion. Grit was found in all the stomachs examined and the biggest particle measured 0,8 × 0,4 mm. Van Someren (1951) suggested that grit is swallowed accidentally during scissoring, and the size of the grit particles found in the stomachs suggests that this is probably the case in the KNP birds.

Species of Ixodoidea found on the larger mammalian species and seasonal variations in their numbers compared with the results of the stomach content analysis

The seasonal variations in the numbers of ticks found in the stomachs are influenced by various factors. Firstly, since the ixodid ticks were identified by means of their scuta, only those on which the birds had fed on that specific day would be recorded. Secondly, the birds were collected at different times and those shot during the early hours would have fewer ticks in their stomachs than those collected later in the day. Furthermore, since only 53 stomachs were examined, that is, about 4 stomachs per month, such a small sample could give biased results.

Lengthy speculation on the significance of various points noted in the seasonal variation of ixodid ticks recovered from the stomachs is unwarranted, but the principal questions can be pin-pointed, some of which can perhaps be resolved by further research.

According to Siegfried (1971), the diet of any animal is influenced by the relative abundance of its various food items in the habitat. To check whether the ixodid ticks that were apparently preferred did not merely reflect the dominance of these particular species in the KNP, 3 sets of data were used, namely, a check list of the Ixodidae found on the larger mammals (Table 6), total tick-counts from 4 different mammals (Table 7) and monthly total tick-counts from impala over a 15-month period in the KNP (Table 8). The numbers of ticks recorded undoubtedly fell far short of the true totals, because of the difficulty of collecting the larval and nymphal stages (Spinage, 1969). As the collection method was standardized, however, it should show general trends and indicate any seasonal variations in the biomass of the ixodid ticks. The majority of Ixodidae found on the larger mammal species are not host-specific (Zumpt, 1964), although some do show pronounced preferences (Table 6).

TABLE 6 Ixodidae found on some of the larger mammal species in the Game Parks in the RSA according to the unpublished records of the National Parks Board and the Division of Veterinary Services, Skukuza, Kruger National Park

Mammal species	Ixodidae											
	Rhipicephalus tricuspis	*Rhipicephalus evertsi*	*Rhipicephalus simus*	*Rhipicephalus sulcatus*	*Rhipicephalus appendiculatus*	*Rhipicephalus maculatus*	*Rhipicephalus sanguineus*	*Hyalomma truncatum*	*Hyalomma rufipes*	*Amblyomma hebraeum*	*Amblyomma tholloni*	*Boophilus decoloratus*
Black rhinoceros			X		X	X		X	X	X	X	
Square-lipped rhinoceros			X			X				X		
Zebra	X	X	X	X	X	X	X	X		X		X
Warthog	X	X	X		X	X	X	X		X		
Hippopotamus			X							X	X	
Giraffe	X	X	X		X		X	X	X	X		X
Oribi	X	X	X	X		X	X					
Klipspringer		X			X		X					
Reedbuck	X	X	X		X	X		X		X		X
Waterbuck	X		X		X	X	X					X
Impala	X	X	X		X		X	X		X		X
Roan antelope		X	X		X		X	X	X			X
Sable antelope	X	X	X		X	X	X	X	X			
Tsessebe		X										X
Blue wildebeest	X	X	X		X			X		X		X
Nyala		X	X		X	X	X			X		X
Bushbuck	X	X	X		X	X	X	X		X		X
Kudu	X	X	X		X	X	X	X	X	X		X
Eland		X	X		X	X	X	X	X	X		X
Buffalo	X	X	X		X	X	X		X	X	X	X
% of occurrence (frequency)	62	75	91	12	83	66	70	58	29	70	20	58

TABLE 7 Ixodidae occurring on culled specimens of 4 species of mammals in the vicinity of Skukuza, Kruger National Park, during 1974

Species of mammal	*Boophilus*					*Rhipicephalus*					*Boophilus and Rhipicephalus*		*Amblyomma*						*Hyalomma*				Other species	Total	Number of specimens
	♂♂	♀♀	NN	Total	% occurrence	♂♂	♀♀	NN	Total	% occurrence	LL	% occurrence	♂♂	♀♀	NN	LL	Total	% occurrence	♂♂	♀♀	Total	% occurrence			
Impala.......	75	70	143	288	64	26	12	7	45	89	59	13	2	4	24	28	30	12					1	451	15
Buffalo.......						23	5		28	29			53	7	1		61	64	4	1	5	5		94	4
Warthog......						55	12		67	48			35	21	2		58	42	13		13	9		138	1
Zebra........						55	5		60	83			5		2		7	9	4	1	5	6		72	1

♂♂ =Adult male
♀♀ =Adult female
NN =Nymphae
LL =Larvae

TABLE 8 List of Ixodidae collected monthly from 15 impala rams in the Skukuza area during the period October 1973–December 1974

Date collected	*Boophilus*			*Rhipicephalus*			*Boophilus* and *Rhipicephalus*	*Amblyomma*			*Amblyomma*	Other species	Total
	♂♂	♀♀	NN	♂♂	♀♀	NN	LL	♂♂	♀♀	NN	LL		
22/10/73......	73	52	78	2	1	6		1		1			214
12/11/73......	49	44	250	1	1	11	114			13		2	485
14/12/73......	75	114	85	109	32		39			38	1		493
29/1/74.......	46	56	67	67	19		1			15	9		280
19/2/74.......	30	29	11	155	77		14			10	14		340
21/3/74.......	56	51	113	26	17		15			28	69		375
16/4/74.......	66	79	46	3	28		8			57	134		421
19/5/74.......	63	37	83	3			2			28	2		218
18/6/74.......	59	41	111			13	8	4		48	41		325
12/7/74.......	41	44	39	2		39	39			35	32		271
21/8/74.......	155	165	248			27	18	1		30			644
24/9/74.......	96	77	56	3		21	2	2		29			286
21/10/74......	89	80	362			9	285			86	17	15	943
18/11/74......	135	98	488	4			320			8	100	1	1 154
20/12/74......	83	93	106	12	6		9			21			330
Total..........	1 116	1 060	2 143	387	181	126	874	8	0	447	419	18	6 779
Mean.........	74,4	70,6	142,8	25,8	12,0	8,4	58,2	0,53	0	29,8	27,9	1,2	451,9
Incidence (%)..	16,4	15,6	31,6	5,7	2,6	1,8	12,8	0,11	0	6,5	6,1	0,26	

♂♂ =Adult male
♀♀ =Adult female
NN =Nymphae
LL =Larvae

Boophilus occurs on a wide variety of mammals but, apart from the buffalo, shows a marked preference for the Bovidae (Tables 6 & 7). Although *Boophilus* have been recorded elsewhere on buffalo, none were found on 4 buffalo examined in the KNP, and Carmichael (1976) found only 1 specimen of *B. decoloratus* in a total of 100 buffalo examined in Botswana. *Boophilus* was the dominant species (incidence 64%) on 15 impala examined over a 15-month period and *Rhipicephalus, Amblyomma* and *Hyalomma* species were found in smaller numbers (Table 7). Species belonging to the genus *Rhipicephalus* feed on all the larger mammals found in the KNP (Table 6) and appear to be the commonest ticks on warthog and zebra (Table 7). *Amblyomma* spp. were found on 72% of the larger mammals (Table 6) and appeared to be the dominant ticks on buffalo (Table 7). Although *Hyalomma* species are found on 60% of the larger mammals (Table 6), their numbers are much smaller than those of the other 3 important genera (Table 7).

Buphagus utilizes 15 different mammalian species in the KNP (Stutterheim, 1976). If there was no species preference for ixodid ticks, the ticks found in the stomachs would reflect those species found on the mammal on which the bird was feeding. From Table 1, in which a very low incidence of *Amblyomma* and *Hyalomma* adults and nymphae in the stomachs is indicated, it can be deduced that a preference for certain ixodid species does indeed exist (see Controlled Experiments with Oxpeckers in Captivity, p. 70). Furthermore, there is evidence that *Buphagus* prefers to feed on certain mammals and this could be because certain tick species feed on these mammals (Stutterheim, 1979, unpublished data).

When discussing seasonal changes or any other differences in food composition, the relative abundance of the various foods and the preferences of the animal concerned must also be taken into account (Brown 1969, cited by Siegfried 1971). The seasonal variations in the genera *Boophilus* and *Rhipicephalus* found on impala in the Skukuza area are given in Fig. 4 & 5. *Boophilus* adults and nymphae were found on all the animals examined, with mean totals of 145 and 143 respectively (Table 8). No definite seasonal pattern of variation in the numbers of *Boophilus* adults and nymphae is evident though (Fig. 4), and no significant relationship was found between the monthly rainfall and the number of *Boophilus* adults found on the impala ($r=0,22$). Apparently, though, an increase in the number of *Boophilus* nymphae was reflected subsequently in an increase in the number of adults ($r=0,72$) (Fig. 4). In Fig. 6 a comparison of the seasonal variations in the numbers of adult *Boophilus* found on the impala and in the 53 stomachs of *Buphagus* does indicate some correlation, although for some unknown reason the peak in *Boophilus* utilization by *Buphagus* appear to be a month later than the peak on the impala. In Fig. 7 a comparison of the seasonal variations in the numbers of *Boophilus* and *Rhipicephalus* larvae found on impala and in the stomachs of the birds shows that on impala peak numbers of larvae were found between October and December, but this pattern is not reflected in the stomach contents of *Buphagus*, in which most larvae were present between December and March.

In Fig. 6 the seasonal variations of *Rhipicephalus* adults and nymphae found on impala are compared with those in the stomachs examined. On impala, the peak in the number of *Rhipicephalus* adults between December and March is reflected also in the *Buphagus* stomachs, with the highest number in February ($r=0,66$). No correlation was found between the number of *Rhipicephalus* nymphae and the number in the stomachs examined ($r=0,18$).

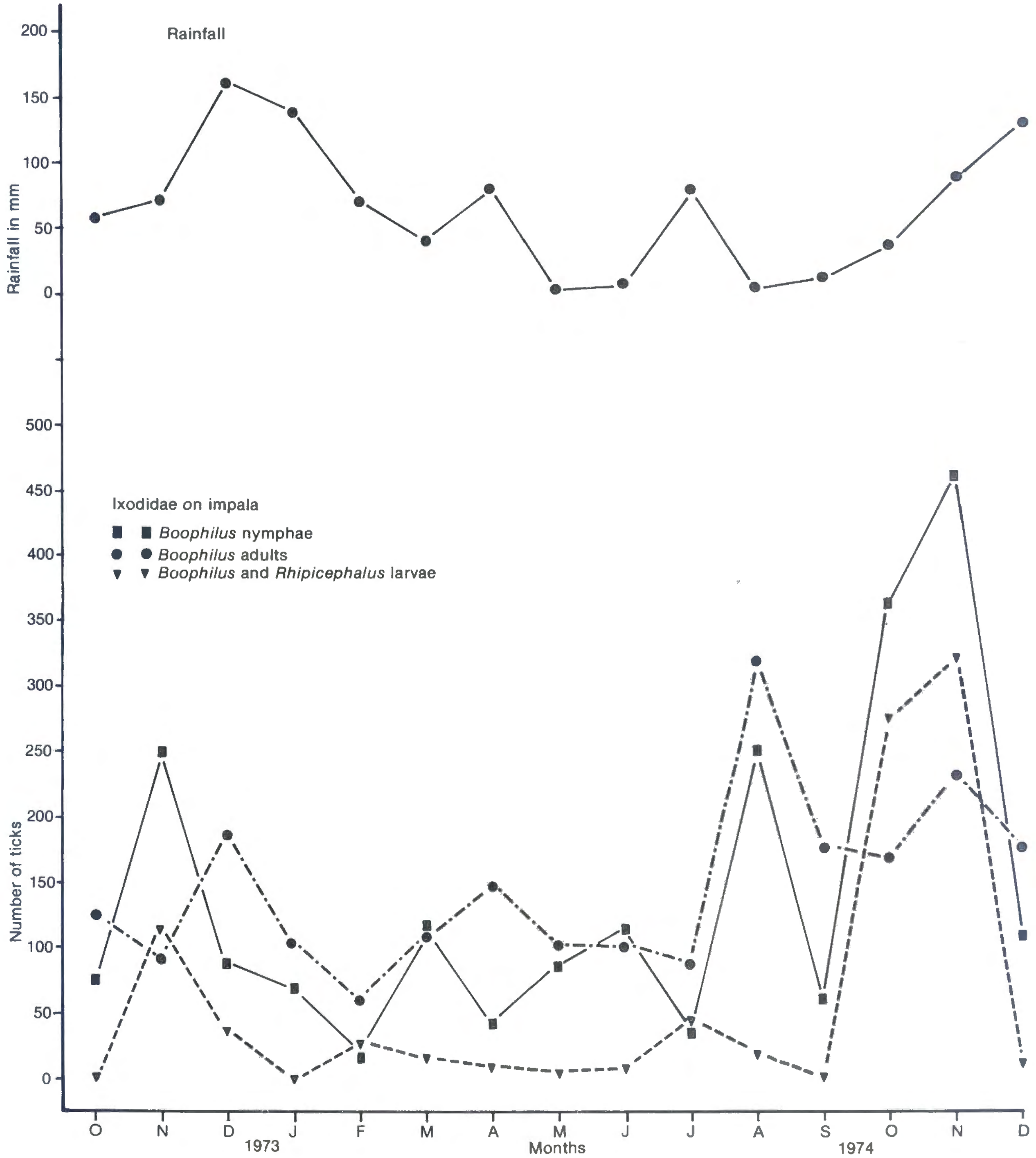

FIG. 4 Seasonal variation in rainfall and in the numbers of *Boophilus* adults and nymphae and *Rhipicephalus* and *Boophilus* larvae collected from 15 impala shot at monthly intervals in the Skukuza area during the period October 1973–December 1974.

Too few adult *Amblyomma* and *Hyalomma* ticks were found for comparison on the impala and in the stomachs, respectively, and no significant relationship was found between the number of *Amblyomma* nymphae found on the impala and those found in the stomachs ($r=0$). However, the large number of *Amblyomma* larvae utilized by *Buphagus* during March 1974 corresponded with the large number of larvae found on impala (Table 8). This is probably because larvae are obtained by means of scissoring, where eyesight does not play a role. An increase in the number of larvae on the animals would thus be reflected in the stomachs of the birds.

The food given to the nestlings

To date, the few original descriptions of the food given to nestling oxpeckers have suggested that it may be different from that of the adults (Attwell, 1966). Jackson (1938) records that food resembling caterpillars or grubs was brought to a nesting hole, while Dowsett (1965) found much hair, an unidentified seed, apparent beetle remains and apparent blood, but no ticks, in the stomach of a fledgling yellow-billed oxpecker (*B. africanus*). The analysis of 15 food samples fed to nestling oxpeckers by their parents forms the basis of this section of the investigation.

Materials and methods

As part of an intensive study on the breeding biology of *B. erythrorhynchus* in the Satara area, KNP, a total of 15 food samples fed to nestlings were collected during March–December 1974. Developmental studies were conducted at 6 nests and at each a small door, measuring 10 cm × 8 cm, was cut in the trunk near the bottom of the nesting holes. The nestlings were removed through this door every 2nd day for examination. To collect the food samples a 1,0 cm strip of "Safflag" was tied around the neck of each experimental nestling so that the bird could breathe but not swallow. The food was then collected from the mouth and throat as soon as the nestling had been fed.

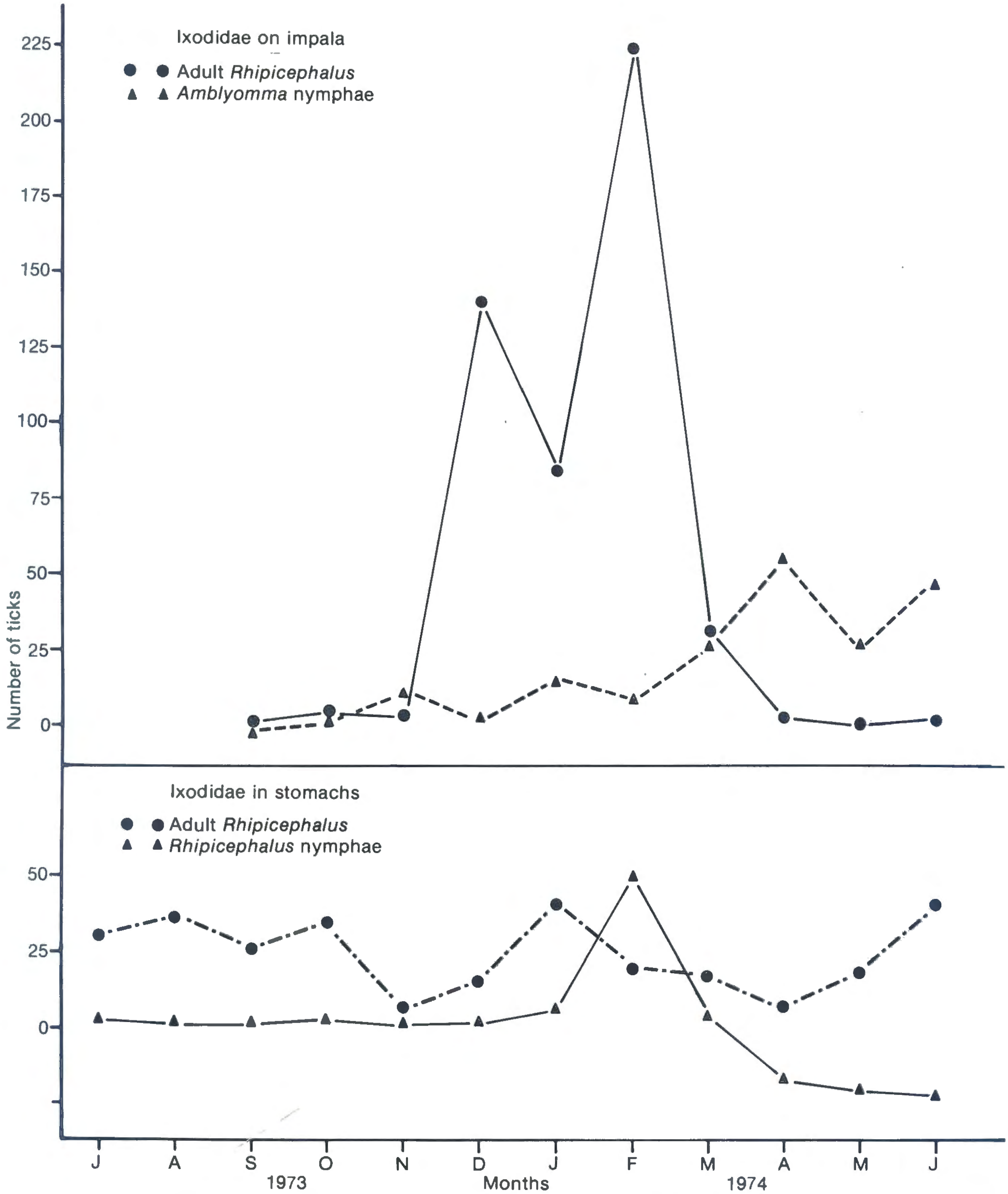

FIG. 5 A comparison between the seasonal variation in the numbers of *Rhipicephalus* adults and nymphae and *Amblyomma* nymphae found on 15 impala and 53 stomachs of *B. erythrorhynchus* collected in the Skukuza area during the period July 1973–June 1974

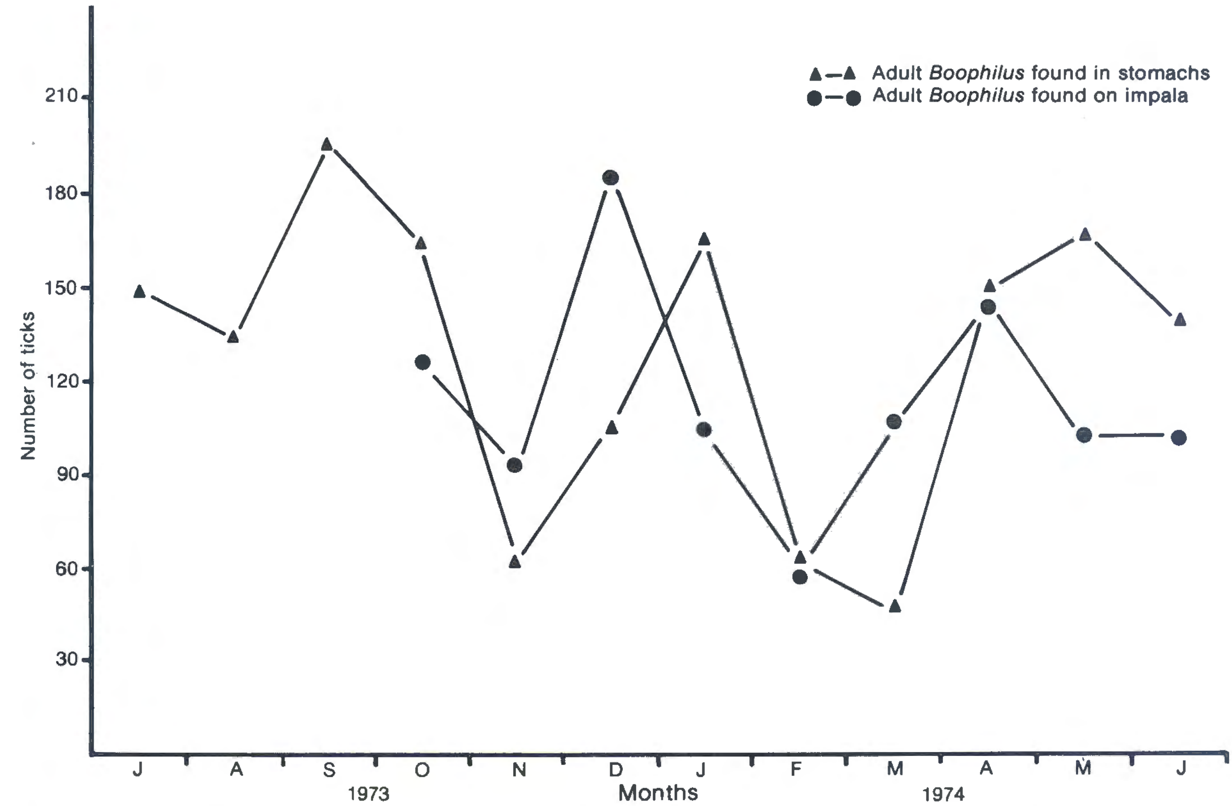

FIG. 6 Seasonal variation in the numbers of adult *Boophilus* found on 15 impala and in 53 stomachs of *B. erythrorhynchus* collected in the Skukuza area during the period July 1973–June 1974

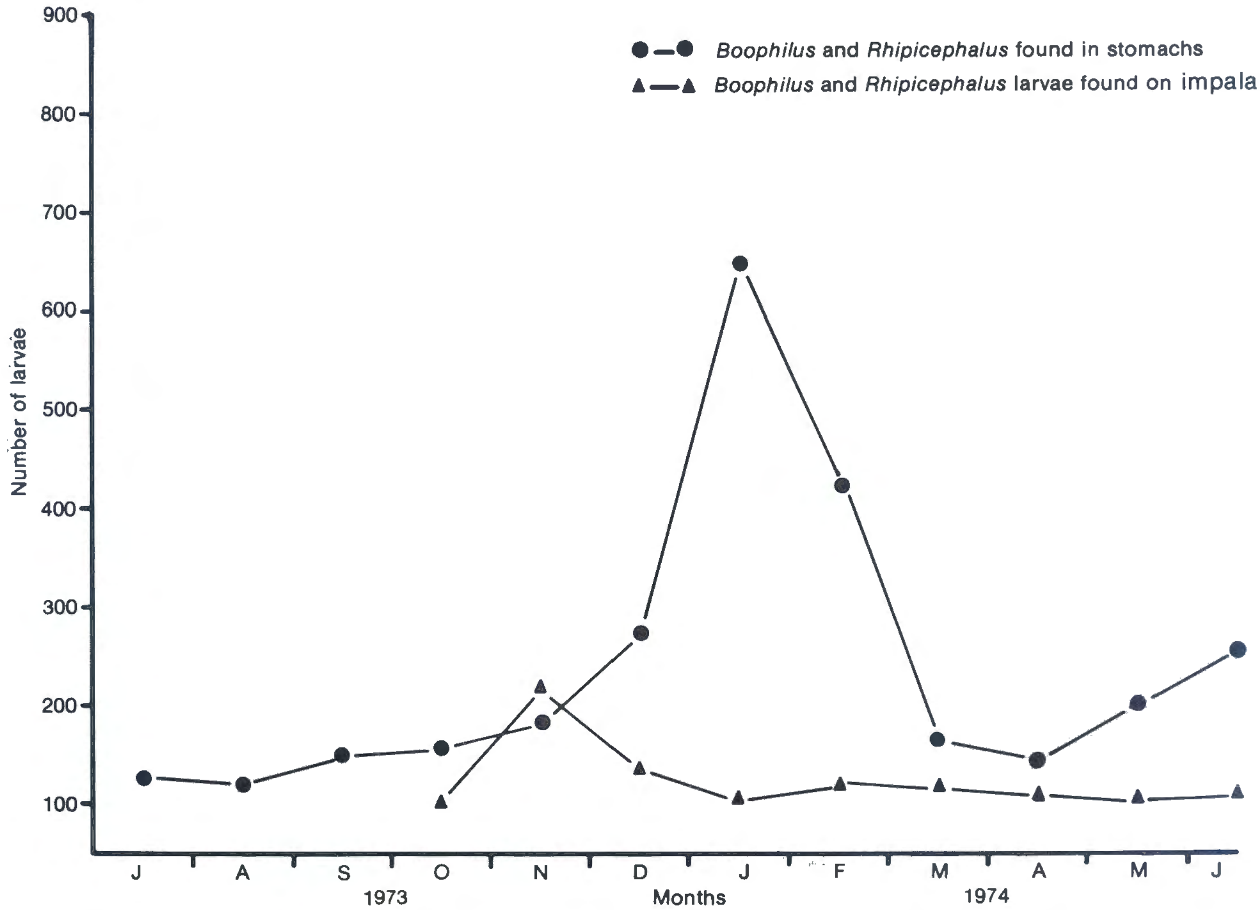

FIG. 7 Seasonal variation in the numbers of *Boophilus* and *Rhipicephalus* larvae found on 15 impala and in 53 stomachs of *B. erythrorhynchus* collected in the Skukuza area during the period June 1973–July 1974

TABLE 9 Food collected from nestling *Buphagus erythrorhynchus* in the Satara area, Kruger National Park, during March and December 1974

Date collected	Time collected	*Boophilus* and *Rhipicephalus* spp.						*Amblyomma*			Total number of Ixodidae	Mass of Ixodidae (g)	Number of Diptera	Mass of Diptera (g)	Mass of hair and tissue (g)	Total mass of sample
		Boophilus			*Rhipicephalus*		LL									
		♂♂	♀♀	NN	♀♀	NN		♂♂	NN	LL						
11/3/74	16h25		6		3						9	0,2628			0,0329	0,2957
14/3/74	16h30	1	2								3	0,0439			0	0,0439
17/3/74	11h05		1							1	2	0,0051			0	0,0051
18/3/74	09h17	1	3	2				1	1		8	0,1937			0,0899	0,2836
19/3/74	10h00		2		3					2	7	0,2438			0,0151	0,2589
22/3/74	12h05		5			1	1			12	19	0,1344	3	0,0258	0,0407	0,2009
26/3/74	08h30								2	9	11	0,0660	3	0,0030	0,1887	0,2577
26/3/74	09h55		2	9	1	74	133			1	220	0,3743			0,1847	0,5590
27/3/74	09h22					38	195				233	0,4085			0,0678	0,4673
29/3/74	07h43	4	8	4	1	1	1			1	20	0,3555			0,0330	0,3885
3/12/74	09h45	3	8	10		2	9		5	4	41	0,2322			0,0803	0,3125
7/12/74	13h45	1	15	2	1				4	12	35	0,1529	28	0,2521	0,5901	0,9951
9/12/74	16h30	4	2	2	1				8	20	37	0,1406	1	0,0913	0,5638	0,7957
10/12/74	11h00										0	0	9	0,4102	0,1046	0,5148
10/12/74	15h30		1		1				7		9	0,1458	3	0,3958	0,1319	0,6735
	Σ	14	55	29	11	116	339	1	27	62	654	2,7595	47	1,1782	2,1235	6,0612
	%	2,1	8,4	4,4	1,7	17,7	51,8	0,2	4,1	9,5		45,6		19,4	35,0	
	$\bar{X}$										43,6					
	Range										0–233					

♂♂ =Adult male
♀♀ =Adult female
NN =Nymphae
LL =Larvae
Σ =Total
X =Mean

Experimental observations and discussion

At the outset it must be stressed that the samples only give an indication of the type of food that is fed to the nestlings. They do not constitute the total food given at any one time because, despite precautions, some was swallowed before collection. Moreover, since the ages of the chicks were not known, the samples would not indicate any changes that took place in their diet during their development.

The analysis of the 15 samples collected is shown in Table 9. Ixodid ticks accounted for 45,6% of the total mass compared with Diptera (19,4%) and hair and tissue (35,0%). *Boophilus* and *Rhipicephalus* larvae were numerically by far the most important ixodids utilized and accounted for 51,8% of the total number of ticks found in the samples. *Rhipicephalus* nymphae were numerically next in importance and the two genera, *Boophilus* and *Rhipicephalus*, together accounted for 86,1% of the ixodid ticks utilized. A significant difference (t=test, $P<0,05$) was found in the utilization of adult *Boophilus* males and females, the latter being preferred. Although only 1 adult *Amblyomma* and no adult *Hyalomma* ticks were found in the samples analysed, *Amblyomma* nymphae and *Amblyomma* larvae made up 13,6% of the total number of ticks utilized.

A total of 47 Diptera were found in the 15 samples analysed and were identified as belonging to the families Muscidae (n=13), Tabanidae (n=9) and Simuliidae (n=25). Epidermal tissue was found in varying quantities in 86,6% of the samples examined, but hair was present in only 60%.

Controlled Experiments with Oxpeckers in Captivity

Since in any ecological study there are numerous variables, most of which detract from the precision of the results, only in controlled studies is it possible to limit the number of these variables. It was decided therefore to try to answer some of the questions that had arisen from the stomach content analyses by carrying out controlled experiments on birds in captivity.

The capture of wild oxpeckers and their maintenance in the laboratory

The birds used for this study were trapped by 1 of 2 methods in the vicinity of Skukuza, KNP.

Mist nets at animal pens: At the animal-holding pens of the Veterinary Division near Skukuza, oxpeckers were attracted by buffalo, wildebeest (*Connochaetes taurinus*) and cattle kept in 3 adjacent open pens. By erecting two 20 m×2,6 m nylon mist nets with a 36 mm mesh in these pens 9 oxpeckers were caught in 27 trapping hours. The birds were usually caught while they were flying from 1 group of animals to another in an adjacent pen. Very few were caught while settling on the animals or flying away.

Mist nets at water reservoirs: In the KNP oxpeckers drink from open cement water reservoirs. By erecting two 12 m×2,4 m nylon mist nets with a 36 mm mesh over a reservoir at Nwatimhiri windmill, 11 oxpeckers were caught in a 3-hour trapping period.

Immediately after capture, the oxpeckers were transported in a dark box to Skukuza where they were kept in quarantine for 7 days in accordance with veterinary regulations. Here they were released into a fly-free room measuring 7 m×10 m×10 m with a donkey which had been artificially infested with about 8 000 *Boophilus* larvae. Their diet was supplemented with an ample supply of engorged *Boophilus* females, *Stomoxys* flies and a mixture of minced meat, "Pronutro" and egg yolk provided in a Petri dish. Water was supplied *ad lib.*

Four nestlings, approximately 20 days old, were also collected and hand-raised until fledged on a diet consisting of ticks, flies and a mixture of minced meat, "Pronutro" and egg yolk.

At the expiry of the quarantine period at Skukuza, the birds were transported in dark boxes by air to the Veterinary Research Institute, Onderstepoort. There they were released as soon as possible onto a mammalian symbiont in one of 2 adjacent cages, each measuring 9 m×3 m×3 m, and kept for this purpose, a procedure which reduced stress to a minimum. At different times during the course of the experiments, donkeys, cattle, goats and haired sheep were kept in the cages with the birds. A shallow tray filled with clean sand was provided for the birds for sand-bathing and water was supplied *ad lib.*

The birds in each cage were fed as follows:

(a) *B. decoloratus* and *B. microplus* ticks, supplied by infesting the cattle or donkeys that were kept with the oxpeckers with larvae.

(b) Engorged *Boophilus* females and/or engorged *Amblyomma* larvae and nymphae supplied in Petri dishes. These ticks had been fed on cattle and sheep before being offered to the birds.

(c) Live *Stomoxys calcitrans* or *Musca domestica* flies, when the tick supply was inadequate.

(d) A mixture of minced meat, egg yolk and "Pronutro" as a supplement to their diet.

When required, the birds were caught by being chased into a mist net held across the width of the cage. For controlled experiments, when 1 or 2 birds only were required, small commercially available bird cages with trays filled with sand were used. These methods of trapping, transporting and confining proved to be successful, as no birds were lost.

The control of ticks on cattle

Materials and Methods

This experiment was planned to obtain information on the level of tick control that can be obtained with the use of oxpeckers. The fact that relatively large numbers of ticks were found in the stomachs of these birds does not necessarily mean that oxpeckers can effectively control ticks on animals.

Two series of experiments were carried out, the second experiment a year after the first. In each series 6 cattle, divided into 3 groups (A, B and C) containing 2 animals each, were used. Prior to the experiments these animals were infested with *B. microplus* larvae. To ensure that approximately equal numbers of larvae were put onto each animal, the tick eggs were divided into batches of equal mass before they hatched.

In each group one animal, which acted as the control, was kept in a separate cage so that all the engorged female ticks that developed on it could be collected and counted. The second experimental animal was introduced at the appropriate time into a cage with 2–4 oxpeckers for 6–10 days, thereafter removed and caged alone so that the remaining ticks could complete their development. The engorged females were allowed to drop, and were then collected and counted for comparison with the numbers obtained from the control. In Group A the oxpeckers were allowed to feed on the experimental animal when the ticks were still in the larval stage, in Group B when the ticks had developed into nymphae, and in Group C when the ticks had developed into adults.

Experiments on Group C in the first series and on all groups in the second series of the experiments were repeated once. The same pairs of animals were used but their roles were reversed, i.e. the original controls became the experimental animals and the original experimental animals were used as controls. This was done to rule out possible differences in susceptibility to tick infestation in the animals used.

Experimental observations and discussion

The birds in Series I died before the end of the experiment. However, the incomplete results obtained are included in Table 10, as they support those of Series II.

In Series I, the highest level of control (99,9%) was obtained when the birds were forced to eat adults, compared with 88,9% for nymphae and 21,0% for larvae. In the latter case, however, 2 birds only were present and this could have accounted for the lower level of control.

In Series II, similar results were obtained for the adult stage, namely, 95,7% control. Only 30,7% of the nymphs were controlled, but a surprisingly high level of control (52,9%) was obtained for the larval stage. The reason for this decrease in nymphal control is not clear.

From the results summarized in Table 10 it is clear that the oxpeckers appreciably reduced the numbers of *B. microplus* on the animals. Although numbers of engorged female ticks were used for comparison only, males present with them were obviously also eaten because very few males could be found on those cattle that the birds were on when adult ticks were present. Males are most probably consumed with the females while in the process of mating. Only *Boophilus* females were counted because there is no valid technique for counting the smaller, less conspicuous males on live animals.

A significantly higher level (t=test, $P<0,05$) of control was obtained when birds were kept with animals infested with the adult stage of *B. microplus* than when larvae or nymphae only were present. This is probably because individual adult ticks are more easily visible or are picked up during feeding.

Tick species preference

Materials and Methods

Six linen bags were secured by means of "Genkem" glue onto the back of an 18-month-old ox. On the following day larvae of *Boophilus decoloratus*, a one-host species, were put into 1 of these isolation chambers.

Groups of 25 male and 25 female ticks of the other tick species used, namely, *Amblyomma hebraeum, Hyalomma marginatum rufipes, H. truncatum, Rhipicephalus appendiculatus* and *R. evertsi evertsi*, were each put into separate bags at appropriate intervals to ensure that they all became engorged at approximately the same time.

The bags were removed to expose the ticks just before they started to become engorged, and 2 oxpeckers were placed with the animal in a bird cage. The ticks were counted on the first day immediately before the birds and the ox were put together and subsequently at 1–3 hour intervals for the remainder of the day. Thereafter ticks were only counted at the beginning of each day for 7 days. Only females of *Boophilus* were counted, not the males.

TABLE 10 The control of *Boophilus microplus* on cattle by the red-billed oxpecker *Buphagus erythrorhynchus* at Onderstepoort

Series 1

Groups	Developmental stage of ticks when birds introduced	Bovine No.	No. of birds	No. of days with animals	No. of engorged females collected	% control
A	Larvae	757	2	7	1 290	21,0
		759 Control	0	0	1 632	
B	Nymphae	420	3	7	609	88,9
		342 Control	0	0	5 485	
C	Adults	322	4	10	9	99,9
		334 Control	0	0	3 929	
		334	3	10	7	99,7
		322 Control	0	0	2 668	

Series 2

Groups	Developmental stage of ticks when birds introduced	Bovine No.	No. of birds	No. of days with animals	No. of engorged females collected	% control	
A	Larvae	1305	4	7	1 124	52,6	52,9
		1056 Control	0	0	2 369		
		1056	2	7	1 509	53,2	
		1305 Control	0	0	3 227		
B	Nymphae	1030	4	6	521	52,9	30,7
		802 Control	0	0	1 107		
		802	2	7	1 775	8,6	
		1030 Control	0	0	1 943		
C	Adults	1975	3	7	99	96,2	95,7
		1974 Control	0	0	2 577		
		1974	2	7	175	95,3	
		1975 Control	0	0	3 699		

TABLE 11 Preferences shown by 2 adult captive red-billed oxpeckers *Buphagus erythrorhynchus* for 7 different species of ixodid ticks on cattle at Onderstepoort during June 1977

Tick species		Number of ticks on cattle											
		Day 1 09h20	Day 1 10h20	Day 1 12h00	Day 1 13h30	Day 1 15h30	Day 2 08h00	Day 3 08h00	Day 4 08h00	Day 5 08h00	Day 6 08h00	Day 7 08h00	Day 8 08h00
Boophilus decoloratus.................	♀	50	10	10	7	4	0	0	0	0	0	0	0
Rhipicephalus appendiculatus...........	♀	10	6	1	1	0	0	0	0	0	0	0	0
	♂	11	8	2	1	1	1	1	0	0	0	0	0
Hyalomma truncatum.................	♀	18	5	5	3	3	1	0	0	0	0	0	0
	♂	23	18	15	10	7	6	0	0	0	0	0	0
Hyalomma rufipes....................	♀	18	14	4	4	3	3	0	0	0	0	0	0
	♂	22	22	21	17	14	11	0	0	0	0	0	0
Rhipicephalus e. evertsi................	♀	20	18	18	18	18	14	13	0	0	0	0	0
	♂	15	13	13	13	9	8	8	0	0	0	0	0
Amblyomma hebraeum................	♀	18	18	18	18	18	8	1	0	0	0	0	0
	♂	25	25	25	25	25	25	25	25	25	25	25	25

♀=Female
♂=Male

TABLE 12 The daily food intake of a month-old captive red-billed oxpecker *Buphagus erythrorhynchus* at Onderstepoort during May 1977

Day	Food intake						
	Ticks (*Amblyomma*)			Flies (*Musca*)		Artificial food*	Total food intake per day (g)
	No. of nymphs	No. of larvae	Mass (g)	No.	Mass (g)	Mass (g)	
1...........	20	290	1,36	104	0,79	2,2	4,35
2...........	130		3,80	139	1,32	7,4	12,52
3...........	119		5,0	72	0,40	7,83	13,43
4...........	105		4,77	145	0,87	13,82	19,46
5...........	64	1 333	5,14	65	0,47	14,33	19,94
6...........	115		4,01	270	3,12	7,45	14,58
7...........	70		2,11	173	1,34	15,48	18,93
Total.........	613	1 623	26,19	968	8,31	68,51	103,21
Mean........	87,6	231,9	3,7	138,3	1,2	9,8	14,7

* Mixture of mincemeat, "Pronutro" and egg yolk

Experimental observations and discussion

From the results of this experiment (Table 11) it appears that the highest preference was shown for *B. decoloratus*, *Rhipicephalus appendiculatus* males and females and *H. truncatum* females, since there was a sharp decrease in the numbers of these species within the first hour of their exposure. The number of *Hyalomma marginatum rufipes* females started to decrease rapidly from the second hour and these were followed by *H. truncatum* males. A very low preference was shown for *Hyalomma marginatum rufipes* males and females and *Amblyomma hebraeum* females. No *Amblyomma hebraeum* males were utilized, even in the absence of any other ticks. These results show a marked difference between the preference for *Rhipicephalus appendiculatus* and that for *R. evertsi evertsi*, a phenomenon also noted by Van Someren (1951). This is possibly because, under natural conditions, *R. evertsi evertsi* attaches round the host's anus (Baker & Ducasse, 1967).

Daily food intake

Materials and Methods

In this experiment a 1-month-old oxpecker, taken from the nest 2 weeks previously, was used. Its mass was determined on Day 1 and Day 8 with a Mettler K7 top loading balance, which was also used to determine the mass of the food that the bird consumed. For 7 days it was fed at 08h00, 10h00, 14h00 and 16h00 on ticks, flies and a mixture of "Pronutro", minced meat and egg. Before and after each meal the mass of the food was determined and the ticks and flies were counted.

Experimental observations and discussion

The results of this experiment are given in Table 12. The bird had a mass of 39,5 g before the experiment started and 8 days later its mass was 41,0 g. Although the 3 food components (tick larvae and nymphae, flies and artificial food) varied from day to day, they

TABLE 13 The effect of acaricides on captive red-billed oxpeckers *Buphagus erythrorhynchus* at Onderstepoort during July 1977

Compound	Concentration ppm	No. of birds in experiment	Affinity for dipped animals	Affinity for dipped ticks		Observation period in days
Control (water)...........		1	+++	+++	No effect........................	50
Chloromethiuron.........	1 800	2	+++	+++	No effect........................	50
Amitraz.................	250	2	+++	+++	No effect........................	50
Dioxathion/Chlorfenvinphos	250	2	+++	+	One died after being on the animal for 1 hour, while the other bird died 10 minutes after it had been dosed	
Chlorfenvinphos..........	500	2	+++	+	One bird died after 3 days and the other after 5 days on the animal	
Quinthiophos............	300	1	+++	++	Died 1 day after dosing	
Camphechlor.............	2 500	1	+++	+	Died after 2 days on animal	
Arsenic trioxide..........	1 600	1	not tested	++	Died after 2 days on animal	
DDT....................	1 375	1	+++	+++	No effect........................	50

\+ — reluctant
++ — low affinity
+++ — normal affinity

give an indication of the daily requirements of an oxpecker. This was calculated as 14,7 g with a range between 4,35–19,94 g. The mean number of ticks consumed daily was 320, i.e. 25,2% of the mean daily food intake. The maximum number of ticks (engorged *Amblyomma hebraeum* larvae) this bird was able to consume in a 24-hour period was 7 195 larvae with a mass of 14,2 g. The total mass of these larvae is thus about the same as the calculated mean total food intake per day. The mean number of flies that were consumed in a day was calculated at 138. These, however, contributed only 8,1% of the total food intake. The maximum number of flies (*Musca domestica*) that a 6-month-old bird could eat in a 24-hour day was 790.

The effect of dipping materials on the red-billed oxpecker in captivity

Once it had been established that red-billed oxpeckers are highly effective in the control of ticks, ways to re-introduce them into farming areas were considered. It was then realised that it would be extremely difficult, if not impossible, to propagate oxpeckers in areas where intensive dipping is practised as this would limit the number of ticks available to the birds. It is equally unrealistic to discourage dipping in areas where insufficient numbers of oxpeckers are present to take over the control of ticks.

An ideal situation, therefore, would be to use dips that control ticks, but are non-toxic to oxpeckers. If this could be done, the oxpeckers would have a chance of becoming established and multiplying, while the dipping compounds could be used to control tick numbers during certain peak periods.

A study was undertaken, therefore, to test the effect of representative dipping compounds, taken from all the important groups of acaricides used on cattle in this country, on the feeding habits and survival of the red-billed oxpecker.

Materials and Methods

The dipping compounds listed in Table 13 were prepared as recommended by the manufacturers. Because only a limited number of birds were available, 2 birds per test were used for 4 compounds and only 1 bird for the other 4 compounds.

Cattle, infested with *B. decoloratus* approximately 18 days beforehand, were hand-sprayed with the test acaricide diluted in 10 ℓ of water. Each animal was then introduced into a cage with 1 or 2 oxpeckers. The birds were carefully observed to see whether they would settle on the dipped animal and whether they would eat the ticks on it.

They were also supplied with ticks which had been dipped in acaricide in Petri dishes and the number eaten was recorded daily. If the birds did not eat the treated ticks, or if they did not show any symptoms of toxicity within 3 days, they were dosed orally with 1,0 mℓ of the diluted dipping material. This is equal to the volume that will adhere to ± 60 engorged *B. decoloratus* females and thus represents the amount of material that could be ingested by an adult bird during 1 day. The dosing of birds was done with a 1 mℓ plastic syringe, the needle of which was replaced with a plastic tube or needle cover. After dosing, the birds were kept in a small cage for about 4 h and, if no symptoms of toxicity were observed, they were released into the larger cage together with cattle where regular observations could be made.

Experimental observations and discussion

The effect of the 8 acaricides tested on oxpeckers in captivity is shown in Table 13. Three dips, namely, chloromethiuron, amitraz and DDT, did not cause any clinically detectable signs of toxicity during an observation period of 50 days. Birds, however, died when they were allowed to eat ticks from animals dipped either in camphechlor, chlorfenvinphos, arsenic trioxide or a combination of chlorfenvinphos and dioxathion, or ticks dipped in these compounds.

In 2 other tests, where quinthiophos and a combination of chlorfenvinphos and dioxathion were used, the birds died only after they had been orally dosed with these dipping materials.

Observations showed that birds will go onto freshly sprayed animals and will immediately start searching for ticks. Birds eagerly fed on ticks dipped in water, chloromethiuron, amitraz and DDT, but not so eagerly when they were dipped in quinthiophos and arsenic trioxide. They were reluctant to eat ticks dipped in camphechlor, chlorfenvinphos and a combination of chlorfenvinphos and dioxathion.

This was, of course, a preliminary experiment. One could argue, with justification, that more birds, not necessarily oxpeckers, should be used to determine the effect of dips on birds. It was reasoned, however, that a practical answer to the problem could only be obtained if the oxpeckers ate dipped ticks on a dipped animal.

When these results are being evaluated, it should be remembered that these birds were forced to stay with the dipped animals and that they were given freshly dipped ticks to feed on. In nature the birds could possibly have avoided intoxication by spending time on game or undipped animals.

These preliminary experiments have shown, however, that most of the dipping materials used in the past were toxic for the red-billed oxpecker, and therefore support the view that intensive dipping could have played a major role in the disappearance of oxpeckers from farming areas (Van Someren, 1951).

General Discussion

Regardless of the method or methods of analysis used, there are many uncontrollable variables inherent in food studies which detract from the precision of the results (King & Ikehara, 1956, cited by Siegfried, 1971). The same authors point out that great care should be taken when drawing conclusions from the results of food analyses and, furthermore, caution is necessary when applying statistical tests of significance to the data, since these are generally unsuitable for such treatment. In the absence of other data on the feeding biology of oxpeckers, however, some discussion that will serve to identify the principal issues is warranted.

From the behavioural and activity studies on *Buphagus* it is evident that these birds spend a large part of the day (68%) feeding. Captive birds have a mean daily food intake of 14,7 g, which is equivalent to about 7 195 engorged *A. hebraeum* larvae or 60 engorged *Boophilus* females. The number of ticks consumed in a day would thus depend on the species and developmental stages available. Data from the stomach content analyses of free-living birds indicate that ixodid ticks form the major food component by mass (52,3%), and that a mean of 408 ticks is consumed daily. The latter statement is supported by data from controlled studies on captive birds which show that all traces of tick material are digested and disappear from the stomach within 24 hours; thus any ticks recovered from stomach contents would have been ingested that day. Even the figure of 408 ticks per day is probably an underestimate, because a stomach content analysis obviously indicates the number of food items consumed prior to collection of the bird and not the total amount of food that would be eaten during a whole day.

From the stomach content analyses it appears that the genera *Boophilus* and *Rhipicephalus* were the most important ixodid utilized by *Buphagus*, although *Amblyomma* nymphae and larvae also accounted for a substantial percentage (10%) (n=2 174) of the total. The nymphae and larvae were probably picked up by scissoring, which is a feeding method based on touch and not sight. Consequently, the species and numbers of immature ticks collected probably merely depend on what is present on the animal, and not on the choice by the bird. However, the adult ticks are probably collected by plucking, and the numbers found in the stomachs could be influenced by the birds' preference for certain species. The preference for adult *Boophilus* ticks was reflected in the controlled experiments with birds in captivity. The captive birds also had a greater preference for *R. appendiculatus* than for *R. evertsi evertsi,* but this preference could not be confirmed in the stomach content analyses because the ticks were not specifically identified. Moreover, only 16 adult *Hyalomma* were found in all the stomach contents examined, although birds in captivity had a high preference for this genus. This may be because *Hyalomma* apparently do not occur in large numbers in nature (Baker & Ducasse, 1967, and Table 7).

The experiments on birds in captivity suggest that *B. erythrorhynchus* is reluctant to feed on the adults of *H. m. rufipes, R. evertsi evertsi* and *Amblyomma hebraeum* and, consequently, the adult stages of these species would not be controlled under natural conditions if adequate numbers of the preferred species are available. It is doubtful, however, if a preference exists for any particular species in their larval and nymphal stages because of the uniformity of their size. In captivity, a mean level of control of 59,8% and 36,9% for *Boophilus* nymphae and larvae was obtained, respectively. This would mean that the numbers of some unpreferred species would be substantially reduced before they reached the adult stage. The level of control, however, would depend on the number of oxpeckers and ixodid ticks on the symbionts.

From the experiments with captive oxpeckers it is evident that a high level of tick control can be obtained in the laboratory. It is difficult, however, to assess realistically the possible economic value of the bird under natural conditions in relation to agriculture in southern Africa, largely because adequate information is lacking on the number of ticks found on animals in different habitats and the control of ticks under natural conditions. Nevertheless, it seems likely that, because the birds can consume so many ticks each day and achieve a high level of tick control on animals in captivity, they could contribute towards the reduction of ixodid tick populations on free-living animals.

From the observations, it is evident that oxpeckers utilize available wounds and, furthermore, are able to enlarge existing wounds. In the controlled experiments in captivity, where the oxpeckers subjected cattle to a high level of utilization in conditions where food for the birds was limited periodically, they were able to remove hair by scissoring on a specific site. The birds did not damage the skin, however, and apparently utilize only existing wounds. This feeding behaviour can thus be described as "opportunist", as the presence of wounds result in their being utilized, and not vice versa.

Out of a total of 17 057 feedings observed in the KNP, the utilization of wounds on game comprised only 0,4%. In comparison, observations on 1 044 feedings on domesticated animals showed a 2,8% utilization of wounds on donkeys and 1,9% on cattle. In these observations, the origins of the wounds were unknown, as *Buphagus* had been feeding on them when observations commenced. The high percentage of wounds on donkeys that were utilized is directly related to the high numbers of wounds on the animals. In Botswana, where these observations were made, 12 out of 41 donkeys (29,3%) had saddle sores that could be attacked by the birds (Stutterheim, unpublished data, 1979).

Undoubtedly, the utilization of wounds can sometimes have an adverse effect on domestic animals, especially when the birds are able to locate the animals daily and feed on the wounds to such an extent that they cannot heal. To date, no research has been undertaken to solve this problem, with say, the use of a repellant spray or ointment on such wounds. It should be noted, however, that, from an economic point of view, the advantages of biological control of ticks would be far greater than the disadvantages stemming from the utilization of wounds on a few animals.

The results of experiments conducted in captivity suggest that ticks treated with the pesticides, chloromethiuron, amitraz and DDT, did not have an adverse effect on the birds. It must be remembered, however, that the birds were dosed only once, thus any long term effects would not show. In Botswana, oxpeckers were able to rear chicks successfully for 2 weeks on ticks that had been treated with amitraz weekly (Stutterheim, unpublished data, 1979), so these acaricides may not have an adverse effect on *Buphagus*. It is also clear, however, that these chemicals should necessarily also be tested under natural conditions, before concise deductions can be made. In the case of DDT, however, because of the accumulative potential of this dipping chemical, it is likely that it would have an adverse effect on the birds in the long run.

The experiments on birds in captivity indicated that they do not readily accept ticks treated with either camphechlor, chlorfenvinphos or a combination of chlorfenvinphos and dioxathion. Thus, although these acaricides are toxic for the birds, under normal circumstances free-living birds would probably refrain from eating them. In one instance, an oxpecker died a few hours after it had merely been in contact with an animal dipped in chlorfenvinphos and dioxathion. There were no ticks on this animal at the time. It must be remembered that when the birds were dosed with a chemical, the effect that exposure of the chemical on the animal might have on its toxic potential was not taken into account. Under natural conditions, the ticks would probably not be ingested by the birds shortly after treatment of the symbiont with an acaricide and this cannot be equated with dosing the acaricide directly to *Buphagus*. In controlled experiments, however, the symbionts were utilized by the birds directly after they had been treated.

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