The Food of the Cattle Egret
Author(s): W. R. Siegfried
Source: *Journal of Applied Ecology*, Vol. 8, No. 2 (Aug., 1971), pp. 447-468
Published by: British Ecological Society
Stable URL: https://www.jstor.org/stable/2402882

THE FOOD OF THE CATTLE EGRET

By W. R. Siegfried*

Percy FitzPatrick Institute, University of Cape Town, South Africa

INTRODUCTION

The cattle egret *Ardeola ibis* is common in agricultural, beef- and dairy-farming areas in many parts of the world. Most texts (e.g. Palmer 1962) indicate that it has a very varied diet, which reflects the species' general usefulness in the agro-economy.

While it is true that a fair knowledge has accumulated about what the bird eats, much of the information was gathered sporadically and, for the most part, is based on isolated incidents. Often it is based on descriptions of 'unusual' predatory behaviour, or of examination of numerically small and unrepresentative stomach-content samples. Exceptions were the investigations carried out in Egypt by Kirkpatrick (1925) who examined 139 stomachs, and Kadry Bey (1942) who examined 498.

This paper reports on the diet of cattle egrets feeding in man-made pastures in the south-western Cape Province, South Africa. The study-area was located near the town of Stellenbosch (33° 57′S, 18° 50′E).

MATERIAL AND METHODS

A total of 365 food samples was examined. Sampling took place in different ways and times.

For the evaluation of the food of independent, free-flying egrets, specimens were obtained by shooting. They were collected in 10 out of every 12 months over a period of 3 years, within a radius of about 30 km of Stellenbosch. No birds were collected in October and November because: (a) egrets were relatively scarce in and around Stellenbosch in those months; (b) the birds breed during those months and disturbance to breeders near their nesting colonies, and the imposed artificial mortality, would have affected the results of concurrent investigations, aimed at determining the species' reproductive success; and (c) stomach contents obtained from adult birds with young might have led to a distorted picture of the adults' true diet, since adults might have been purposely selecting food items particularly suitable for feeding to their nestlings.

Most of the samples were obtained from birds collected whilst feeding in one type of habitat, viz. dairy-cattle paddocks, primarily planted with kikuyu grass (*Pennesetum clandestinum*). These pastures are irrigated in summer, either by overhead sprinklers or by gravitational flooding, or both. The advantage of concentrating collection in this way was basically twofold. Firstly, irrigated pasture constitutes, by far, the species' most important feeding ground in the study-area. Secondly, a comparative analysis of the food resources of this habitat and the diet of the birds and their numbers could be studied (Siegfried, in preparation). A limited number of food samples were obtained from birds frequenting feeding places other than stock-grazing pastures.

* Present address: Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, U.S.A.

To standardize sampling further, specimens were collected only on days of uniform fine, relatively warm, weather which followed immediately on a minimum of 2 days of similar weather. With rare exceptions, each bird was kept under observation feeding undisturbed for at least 1 h before being shot. However, it is doubtful whether these precautions had much practical virtue, when measured against the many variables that influence hour-to-hour distribution, composition and abundance of the prey and their degree of availability to the bird.

Birds were collected at all times of the day, but collection was concentrated in the period between 2 and 8 h after sunrise. Birds collected earlier in the morning invariably had little food in their stomachs. Collection was not normally undertaken towards the end of the day at the end of the birds' feeding period. This was to avoid disturbing the species' pre-roosting and roosting social behaviour which was being investigated. In addition, the aggregation of birds, from a large area, towards dusk made control and identification of feeding place difficult.

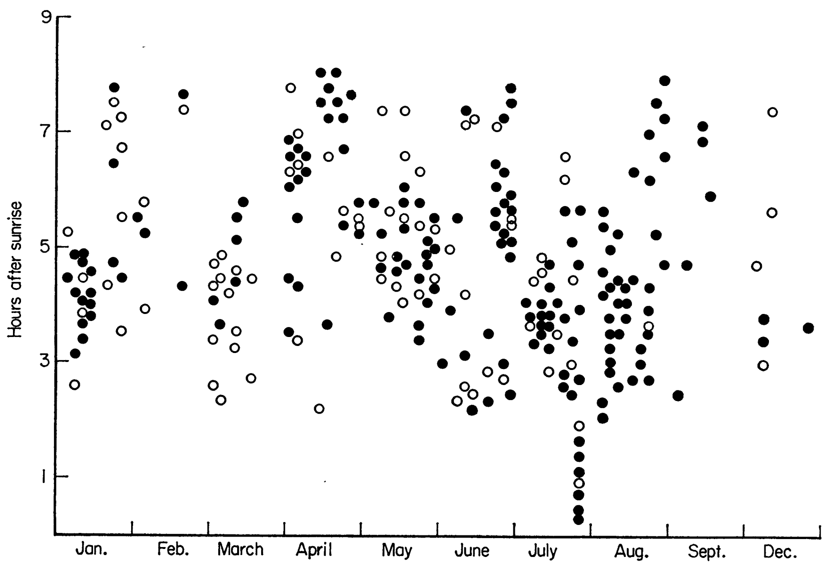

FIG. 1. Distribution of food-samples obtained from cattle egrets according to month and time of day that specimens were collected. ●, Adult birds; ○, juvenile birds.

A total of 265 independent, free-flying birds were collected, of which only two had completely empty stomachs. These yielded sufficient data to indicate reliably seasonal variation in diet and food preference, as well as providing information about changes in food according to time of day. Fig. 1 shows the temporal spread in the collection of these samples.

Food samples were obtained from nestlings and juveniles which were still dependent upon their parents for food, at a heronry during the period September to December; most of the sampling took place at weekly intervals during November. Young cattle egrets, like other members of the heron family (Kirkpatrick 1940; Owen 1955), readily regurgitate food when alarmed. Food samples, in the form of regurgitated boluses, were therefore obtained from nestlings and older, but still dependent, young. These larger young regurgitated food either of their own accord when alarmed, or when gently shaken and massaged on the abdominal region. This method was also applied to small chicks (1–8 days old), but with these, it was sometimes also possible to collect uneaten food directly off the nest. To obtain a true picture of the young cattle egret's diet, food samples were collected from birds of all ages, in many different nests and at various times of the day. All potential donors of food samples were watched closely prior to, and while, being fed and only sampled once, immediately after their parents had completed feeding them. In this way, fresh, undigested samples were obtained. A total of 100 food samples was examined in this stage of the study. In addition, samples from a previous collection (Siegfried 1966) were available.

Birds were weighed immediately after being shot. They were then opened and the contents of the stomach and oesophagus weighed. For nestlings, the procedure involved weighing the fresh food immediately after it had been regurgitated. After weighing, the sample from each bird was preserved separately in 70% alcohol. All preserved samples were labelled with an individually allocated number, date, time of day, locality, weights of food and bird. Samples were examined in the laboratory as soon after collection as possible, usually within 10 days.

In the laboratory, each sample was cleaned of sand and plant debris, before being spread between sheets of coarse blotting-paper for removal of surplus moisture. The entire sample was then re-weighed. Volume was then measured by water displacement in a graduated cylinder.

Identification of food objects was of necessity limited, most prey organisms being classified no further than family or ordinal level. The immature forms, pupae and larvae, were grouped separately. In certain instances, especially with the more agro-economically important invertebrates, food items were named specifically. Classification of the insects is based essentially on that given in Imms (1957).

Judgement was to some degree arbitrary in determining the actual numbers of whole specimens represented by fragmented objects. Weights and volumes for each food category were determined separately for every food sample. Lengths of all objects were measured individually, and a mean value was calculated for each food category. Gravimetric and volumetric measurements were also made of the unrecognizable fragments and digested matter. However, in most instances, these items formed a small part of the entire sample and were not treated as a separate food class. Finally, selected samples of the food items representing the species' main diet were weighed while still fresh, and later weighed again after oven-drying to constant weight.

The difficulties inherent in undertaking quantitative analyses of diets have been stressed by many investigators. For bird foods in particular, Hartley (1948) and, more recently, Ashmole & Ashmole (1967) provide useful reviews and criticisms. Both studies conclude that it is essential to apply more than one method of analysis to obtain a valid picture of the diet of the animal concerned. Further, the use of several different types of analysis permits greater confidence when comparing the diets of species.

The main types of analysis are by number, weight or volume of the different food categories in each food sample; and by frequency of occurrence, which gives the proportion of food samples in which each food category is present, regardless of quantity. In the present study, I have used all these methods and have supplemented them by an analysis of the size frequency distributions of the prey in each food category.

In presenting the data, I have used only weight throughout. This is justified since the wet weight, expressed in grams, is about equal to its volume measured in millilitres, i.e. the specific gravity of the food is close to 1 (Fig. 2). All gravimetric data were converted to percentages and summarized by the 'aggregate–total–percentage method' (Martin, Gensch & Brown 1946). Frequency of occurrence of each food category is given as the percentage of food samples in which the category was recorded. The numbers of objects in each category of food are presented as percentages of the total number of objects represented in all food categories.

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). The same authors point out that considerable care should be taken when drawing conclusions from the results of food analyses and, furthermore, caution against applying statistical tests of significance to the data, which, generally, are not suitable for such treatment.

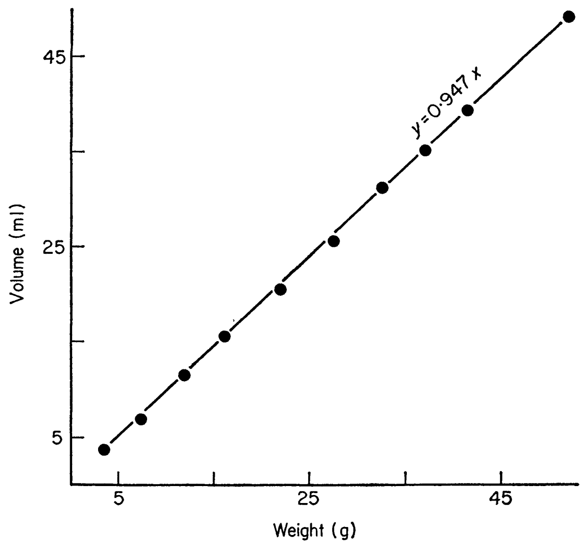

FIG. 2. Relationship between weight and volume of food samples in the diet of the cattle egret. Each solid circle represents the average of ten pairs of measurements.

RESULTS

In this type of study one has to contend with the problem of how best to present relatively long series of data representing different kinds of analysis, and how to interpret the relative importance of each. Ashmole & Ashmole (1967) employed a composite ranking system, which relies on a summation of the results from the different methods of analysis (Waldron & King 1962). I have not made use of this system nor others which employ composite indices (Hartley 1948; Reintjes & King 1953) for fear of obscuring any one set of results through combining basically different data. For the most part, the results have, however, been summarized and condensed, and are given in Tables 1 and 2 and Figs. 3–9. A measure of bias has perhaps been introduced in that I have most often concentrated on comparing the weights of food classes (though the results of all methods of analysis are given in the Tables and Figures). The prominence accorded to analysis-by-weight seems justified in this case, since it provides a basis for estimating absolute quantities of energy ingested by the birds (Siegfried 1969).

Table 1. *Composition of cattle egret diet* (*based on a total of* 250 *food samples*)

Food items	% occurrence (frequency)	% by weight	% by no.	Mean no. objects/ stomach	Max. no. objects in one stomach
	December–January				
ARTHROPODA					
INSECTA					
DICTYOPTERA					
Blattidae, Mantidae, Phasmidae	9·0	0·1	0·2	1	1
ORTHOPTERA					
Acrididae, Tettigonidae	70·6	8·4	10·9	7	27
Gryllidae	44·1	10·1	4·0	5	22
Gryllotalpidae	3·0	0·1	+	1	1
DERMAPTERA					
Forficulidae					
ISOPTERA					
Hodotermitidae					
ODONATA					
Libellulidae	6·0	2·4	1·0	9	16
HEMIPTERA					
Jassidae	9·0	0·1	0·7	4	7
Reduviidae	23·5	0·4	1·1	3	6
LEPIDOPTERA					
Nymphalidae	3·0	+	+	1	1
Pieridae	23·5	1·2	1·1	3	5
Geometridae larvae					
Sphingidae					
Noctuidae	29·4	1·3	1·8	3	7
larvae	91·2	33·6	46·4	26	68
Unidentified larvae and pupae	3·0	0·8	2·3	42	42
COLEOPTERA					
Cincindelidae	3·0	+	+	1	1
Carabidae	52·9	19·0	17·7	17	100
Lampyridae larvae					
Coccinellidae	3·0	+	+	1	1
Tenebrionidae	3·0	0·1	+	1	1
Chrysomelidae	6·0	0·1	0·1	1	2
larvae					
Scarabaeidae	20·6	0·4	0·4	1	2
larvae	3·0	0·1	+	1	1
Curculionidae pupae					
HYMENOPTERA					
Formicoidea	3·0	+	+	1	1
Sphecoidea					
Apodea					
Ichneumonoidea	3·0	+	+	1	

Food items	% occurrence (frequency)	% by weight	% by no.	Mean no. objects/ stomach	Max. no. objects in one stomach
DIPTERA					
Tipulidae					
Asilidae	3·0	0·1	0·1	3	3
Tabanidae					
Syrphidae	11·8	0·2	0·2	1	4
larvae					
Muscidae	14·7	0·2	0·4	2	3
larvae					
Tachinidae	11·8	0·1	0·2	1	1
Calliphoridae	11·8	0·1	0·5	2	4
Unidentified larvae and pupae					
ARACHNIDA					
ARANEIDA	23·5	0·4	1·3	4	6
ACARINA					
MYRIAPODA					
CHILOPODA					
CRUSTACEA					
ISOPODA	3·0	0·1	+	1	1
ANNELIDA					
OLIGOCHAETA					
MOLLUSCA					
GASTEROPODA					
VERTEBRATA					
AMPHIBIA					
ANURA	11·8	9·8	8·0	37	118
REPTILIA					
SQUAMATA					
SAURIA					
SERPENTES					
MAMMALIA					
INSECTIVORA					
RODENTIA	3·0	10·7	+	1	1
		February–March			
ARTHROPODA					
INSECTA					
DICTYOPTERA					
Blattidae					
Mantidae, Phasmidae					
ORTHOPTERA					
Acrididae, Tettigonidae	60·8	7·4	6·0	15	36
Gryllidae	34·8	7·8	1·7	7	16
Gryllotalpidae	4·3	+	+	1	1
DERMAPTERA					
Forficulidae					
ISOPTERA					
Hodotermitidae	4·3	+	0·1	5	5
ODANATA					
Libellulidae	8·7	0·1	+	1	1
HEMIPTERA					
Jassidae	17·4	0·3	1·4	12	28
Reduviidae	26·0	0·3	0·8	5	16

Food items	% occurrence (frequency)	% by weight	% by no.	Mean no. objects/ stomach	Max. no. objects/ in one stomach
LEPIDOPTERA					
Nymphalidae					
Pieridae	13·0	0·3	0·2	3	5
Geometridae	30·4	15·2	19·2	96	215
larvae					
Sphingidae	4·3	+	+	1	1
Noctuidae	34·8	0·3	0·4	1	4
larvae	100·0	51·5	50·8	77	236
Unidentified	4·3	+	+	1	1
larvae and pupae					
COLEÓPTERA					
Cincindelidae					
Carabidae	34·8	2·0	3·2	14	44
Lampyridae larvae	8·7	+	+	1	2
Coccinellidae					
Tenebrionidae	17·4	1·3	1·1	10	15
Chrysomelidae					
larvae					
Scarabaeidae	56·5	7·6	2·5	7	15
larvae					
Curculionidae	30·4	0·3	0·3	2	4
pupae					
HYMENOPTERA					
Formicoidea	30·4	0·3	2·8	13	27
Sphecoidea					
Apodea					
Ichneumonoidea					
DIPTERA					
Tipulidae					
Asilidae	8·7	+	0·2	3	5
Tabanidae	4·3	+	+	1	1
Syrphidae	30·4	+	0·3	2	5
larvae					
Muscidae	47·8	0·7	1·2	4	13
larvae					
Tachinidae	8·7	3·0	5·0	86	172
Calliphoridae	8·7	0·3	1·4	24	47
Unidentified					
larvae and pupae					
ARACHNIDA					
ARANEIDA	34·8	0·5	1·1	5	14
ACARINA					
MYRIAPODA					
CHILOPODA					
CRUSTACEA					
ISOPODA					
ANNELIDA					
OLIGOCHAETA	4·3	0·4	0·1	3	3
MOLLUSCA					
GASTEROPODA					
VERTEBRATA					
AMPHIBIA					
ANURA					

Food items	% occurrence frequency)	% by weight	% by no.	Mean no. objects/ stomach	Max. no. objects in one stomach
REPTILIA					
SQUAMATA					
SAURIA					
SERPENTES					
MAMMALIA					
INSECTIVORA					
RODENTIA					
			April–May		
ARTHROPODA INSECTA					
DICTYOPTERA					
Blattidae	5·6	0·1	0·2	5	10
Mantidae, Phasmidae	9·8	0·4	0·5	5	6
ORTHOPTERA					
Acrididae, Tettigonidae	56·1	12·6	17·4	35	340
Gryllidae	38·3	2·9	2·5	7	90
Gryllotalpidae	1·4	+	+	1	1
DERMAPTERA					
Forficulidae	4·2	+	+	2	4
ISOPTERA					
Hodotermitidae	9·8	+	0·4	4	8
ODONATA					
Libellulidae	1·4	+	+	1	1
HEMIPTERA					
Jassidae	8·4	+	0·2	3	9
Reduviidae	26·8	0·5	1·2	5	24
LEPIDOPTERA					
Nymphalidae					
Pieridae	7·0	+	0·1	1	2
Geometridae	5·6	+	+	1	3
larvae					
Sphingidae					
Noctuidae	9·8	0·1	0·1	1	2
larvae	76·0	13·1	19·6	29	528
Unidentified larvae and pupae	9·8	0·1	0·1	1	3
COLEOPTERA					
Cincindelidae					
Carabidae	39·4	0·7	0·8	3	10
Lampyridae larvae	7·0	+	0·1	2	4
Coccinellidae					
Tenebrionidae	7·0	0·1	0·2	2	8
Chrysomelidae					
larvae					
Scarabaeidae	46·4	3·5	1·8	4	58
larvae	2·8	+	+	1	2
Curculionidae	4·2	+	+	1	1
pupae	1·4	+	0·2	16	16
HYMENOPTERA					
Formicoidea	2·8	+	+	2	4
Sphecoidea	1·4	+	+	5	5
Apodea	1·4	+	+	1	1
Ichneumonoidea					

Food items	% occurrence (frequency)	% by weight	% by no.	Mean no. objects/ stomach	Max. no. objects in one stomach
DIPTERA					
Tipulidae	2·8	+	+	1	2
Asilidae	32·4	0·7	1·9	2	44
Tabanidae					
Syrphidae	21·1	2·0	7·5	40	97
larvae	18·3	0·9	2·4	15	42
Muscidae	29·7	2·9	10·1	42	237
larvae					
Tachinidae					
Calliphoridae	21·1	0·9	2·2	12	67
Unidentified	19·7	0·1	0·5	8	33
larvae and pupae	2·8	+	+	1	2
ARACHNIDA					
ARANEIDA	35·2	1·0	2·5	13	66
ACARINA	4·2	0·1	0·2	5	13
MYRIAPODA					
CHILOPODA	1·4	+	+	1	1
CRUSTACEA					
ISOPODA	2·8	+	+	1	3
ANNELIDA					
OLIGOCHAETA	36·4	44·5	14·8	45	90
MOLLUSCA					
GASTEROPODA					
VERTEBRATA					
AMPHIBIA					
ANURA	12·9	7·6	9·6	56	220
REPTILIA					
SQUAMATA					
SAURIA	8·4	2·6	0·1	1	3
SERPENTES					
MAMMALIA					
INSECTIVORA	1·4	0·5	+	1	1
RODENTIA					
			June–July		
ARTHROPODA					
INSECTA					
DICTYOPTERA					
Blattidae	2·5	0·1	0·4	4	20
Mantidae } Phasmidae }	1·2	+	+	1	1
ORTHOPTERA					
Acrididae } Tettigonidae }	36·2	9·3	28·9	70	682
Gryllidae	37·5	3·0	1·8	4	20
Gryllotalpidae					
DERMAPTERA					
Forficulidae					
ISOPTERA					
Hodotermitidae	3·7	+	+	1	1
ODONATA					
Libellulidae	1·2	+	+	1	1
HEMIPTERA					
Jassidae	1·2	+	+	2	2
Reduviidae	16·3	0·3	0·9	4	29

Food items	% occurrence (frequency)	% by weight	% by no.	Mean no. objects/ stomach	Max. no. objects in one stomach
LEPIDOPTERA					
Nymphalidae					
Pieridae	7·5	0·2	0·7	8	20
Geometridae	11·2	0·1	0·2	1	2
larvae					
Sphingidae					
Noctuidae	7·5	0·2	0·2	3	12
larvae	75·0	6·6	10·2	12	178
Unidentified larvae and pupae	12·5	0·5	0·9	6	29
COLEOPTERA					
Cincindelidae					
Carabidae	40·0	1·1	1·8	4	14
Lampyridae larvae					
Coccinellidae					
Tenebrionidae	1·2	0·5	0·7	55	55
Chrysomelidae	12·7	0·2	0·9	6	37
larvae					
Scarabaeidae	37·5	1·2	0·9	2	7
larvae	3·7	0·2	0·1	2	3
Curculionidae	3·7	+	+	1	2
pupae					
HYMENOPTERA					
Formicoidea	5·0	+	0·1	2	7
Sphecoidea	1·2	+	+	1	1
Apodea					
Ichneumonoidea					
DIPTERA					
Tipulidae	1·2	+	+	6	6
Asilidae					
Tabanidae					
Syrphidae	8·7	0·3	2·0	20	78
larvae	8·7	0·3	1·3	13	30
Muscidae	40·0	1·8	5·7	12	67
larvae	3·7	0·1	0·3	6	10
Tachinidae	40·0	2·0	6·2	13	130
Calliphoridae	26·2	0·9	1·9	7	28
Unidentified larvae and pupae	6·2	+	0·2	3	9
ARACHNIDA					
ARANEIDA	71·2	3·3	11·7	14	132
ACARINA	1·2	+	+	1	1
MYRIAPODA					
CHILOPODA	3·7	+	+	1	2
CRUSTACEA					
ISOPODA	3·7	0·3	0·3	7	2
ANNELIDA					
OLIGOCHAETA	72·5	56·8	20·4	24	110
MOLLUSCA					
GASTEROPODA	1·2	0·2	0·1	9	9
VERTEBRATA					
AMPHIBIA					
ANURA	6·2	1·3	0·2	3	3

Food items	% occurrence (frequency)	% by weight	% by no.	Mean no. objects/ stomach	Max. no. objects in one stomach
REPTILIA					
SQUAMATA					
SAURIA	5·0	3·0	+	1	2
SERPENTES	2·4	1·1	+	1	2
MAMMALIA					
INSECTIVORA	1·2	1·9	+	1	1
RODENTIA	1·2	1·8	+	1	1
		August–September			
ARTHROPODA					
INSECTA					
DICTYOPTERA					
Blattidae					
Mantidae } Phasmidae }	2·3	+	+	1	1
ORTHOPTERA					
Acrididae } Tettigonidae }	31·8	8·2	23·3	76	457
Gryllidae	20·4	4·1	2·1	10	38
Gryllotalpidae					
DERMAPTERA					
Forficulidae					
ISOPTERA					
Hodotermitidae	2·3	+	+	1	1
ODONATA					
Libellulidae					
HEMIPTERA					
Jassidae					
Reduviidae	2·3	+	+	1	1
LEPIDOPTERA					
Nymphalidae					
Pieridae	4·5	+	+	1	1
Geometridae					
larvae					
Sphingidae					
Noctuidae	9·1	0·1	0·1	1	2
larvae	54·5	1·5	2·0	4	24
Unidentified larvae and pupae	6·8	+	0·1	2	2
COLEOPTERA					
Cincindelidae	4·6	+	0·2	5	10
Carabidae	40·9	0·4	0·1	2	8
Lamypyridae larvae					
Coccinellidae					
Tenebrionidae	16·0	2·7	2·4	15	38
Chrysomelidae	16·0	0·1	0·5	4	14
larvae					
Scarabaeidae	45·4	1·5	1·1	3	16
larvae	7·0	1·0	0·3	7	11
Curculionidae	2·3	+	+	1	1
pupae					
HYMENOPTERA					
Formicoidea	4·6	+	+	1	1
Sphecoidea					
Apodea					
Ichneumonoidea					

Food items	% occurrence (frequency)	% by weight	% by no.	Mean no. objects/ stomach	Max. no. objects in one stomach
DIPTERA					
Tipulidae	2·3	+	0·2	14	14
Asilidae					
Tabanidae					
Syrphidae	9·1	+	0·1	1	2
larvae	4·6	+	+	1	2
Muscidae	43·2	3·5	14·4	35	460
larvae	2·3	+	0·2	9	9
Tachinidae	34·1	0·7	2·1	6	52
Calliphoridae	29·5	3·4	10·4	35	361
Unidentified larvae and pupae	6·8	+	0·1	2	3
ARACHNIDA					
ARANEIDA	59·1	1·9	5·9	10	64
ACARINA					
MYRIAPODA					
CHILOPODA	9·1	+	0·1	1	3
CRUSTACEA					
ISOPODA	4·6	+	0·2	3	6
ANNELIDA					
OLIGOCHAETA	65·9	67·5	32·2		88
MOLLUSCA					
GASTEROPODA					
VERTEBRATA					
AMPHIBIA					
ANURA	6·9	0·9	0·1	4	6
REPTILIA					
SQUAMATA					
SAURIA					
SERPENTES	2·3	0·6	+	1	1
MAMMALIA					
INSECTIVORA					
RODENTIA					

+, Values smaller than 0·1.

The diet of independent, free-flying birds

For *Ardeola ibis* feeding in pasture-lands, it is evident that the diet embraces a wide range of food organisms (Table 1). The most important constituent by bulk, measured on an annual basis, was insect material (Figs. 3–5). The major insect groups in order of importance by weights were: Lepidoptera, Orthoptera, Coleoptera and Diptera. Earthworms (Annelida—*Lumbricus* sp.) were second in importance, and the two groups together accounted for almost 90% of the diet, both by weight and number. Most of the remaining 10% was made up by arachnids and vertebrate animals.

Information on the diet of cattle egrets feeding in habitats other than pasture, is meagre. Apart from information gathered through direct observation, the only other data derive from an examination of the stomach contents of six specimens which were collected in a newly ploughed field. All six birds were shot in the same field at the same time of day (11.00 hours local time) in June. Eighty-five per cent by weight of the total stomach contents, consisted of earthworms (100% frequency-of-occurrence) and the balance was insect material: mainly larvae and pupae of Lepidoptera and Coleoptera.

Figs. 6 and 7 and Table 1 show the seasonal variation in the food taken by *Ardeola ibis* when feeding in pasture lands. The most obvious and important change involved

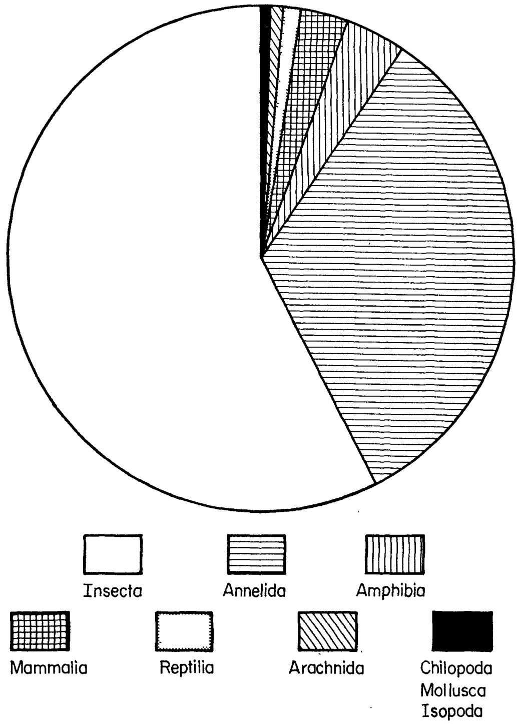

FIG. 3. Percentage composition by weight of the major food categories in the diet of the cattle egret. The complete circle represents 100%.

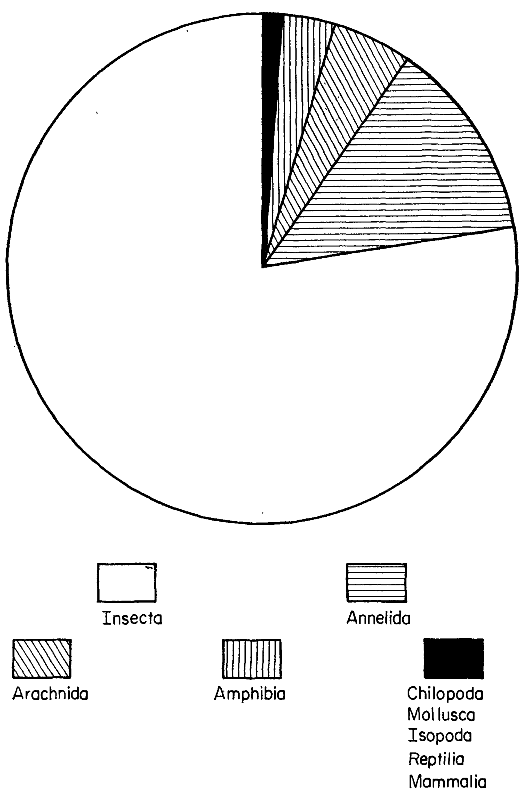

FIG. 4. Percentage composition by number of the major food categories in the diet of the cattle egret. The complete circle represents 100%.

earthworms. These accounted for about 60%, by weight, of the total food taken during the period April–October (the rainy season) and were virtually absent (in nestling stomach contents too) at other times of the year. It is evident, from the frequency-of-occurrence analysis (Fig. 7), that earthworms were a consistently abundant source of food during the

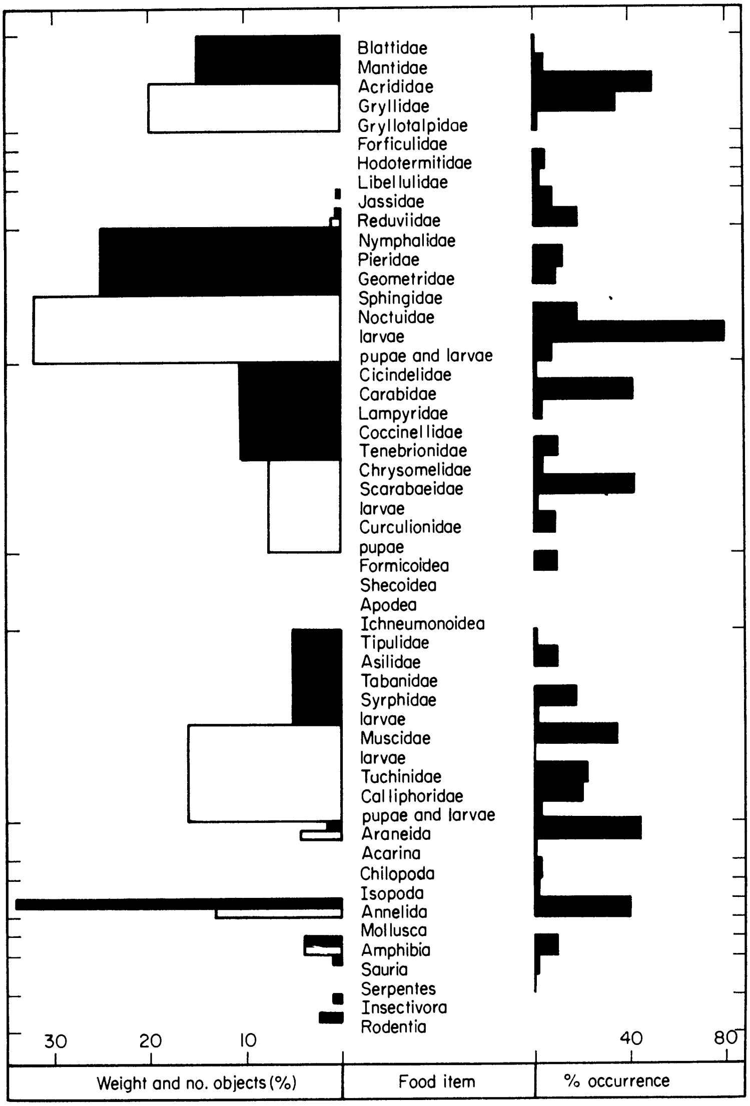

FIG. 5. Percentage frequency of occurrence in food organisms and relative weight and number of food items in the diet of the cattle egret. The histograms on the right indicate the average percentage of samples (stomachs) in which each food item was represented; those on the left, the average representation of each food class by weight (closed columns) and number (open columns). Absence of a column indicates a percentage value smaller than 1·0.

rainy months and apparently were most readily available from June to July, which is the wettest time of the year. Lepidoptera figured sparsely, by weight, during the period April–October.

Another consistent, though less well marked, seasonal dietary change was a progressive

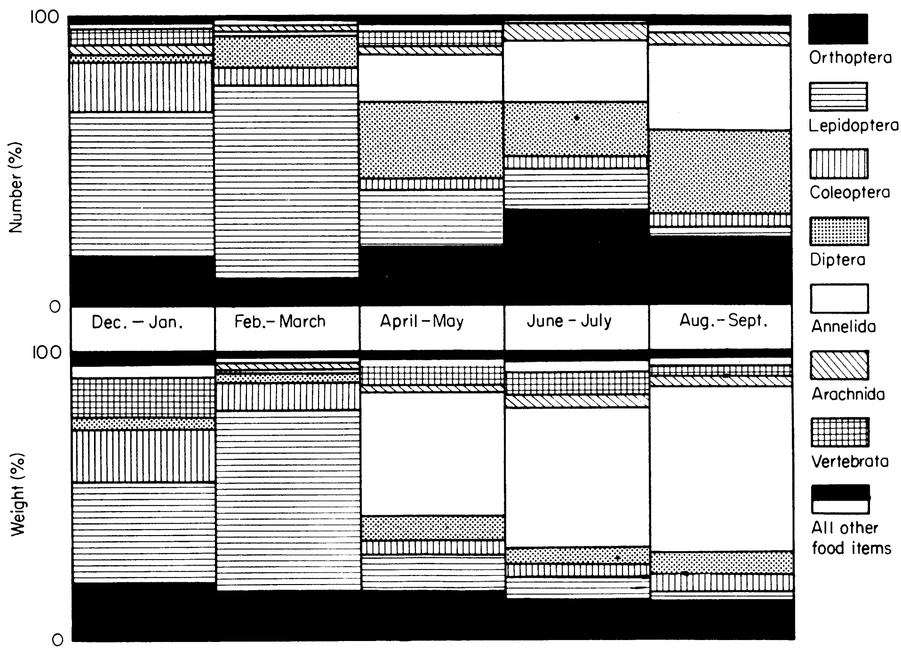

FIG. 6. Percentage composition by weight and by number of objects of major insect orders and other taxa in the diet of the cattle egret.

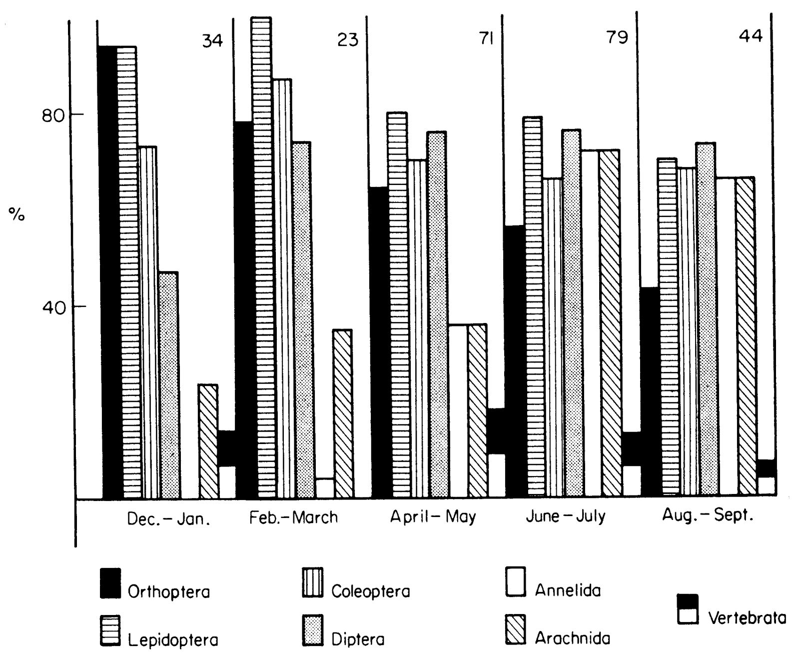

FIG. 7. Percentage frequency of occurrence of major insect orders and other taxa in the diet of the cattle egret. Figures at the top right indicate the number of food-samples on which each group of histograms is based.

drop in the overall mass of Orthoptera, taken over the 10-month period, December–September (Fig. 6), and there was a similar steady decrease in their frequency of occurrence (Fig. 7). On the other hand, analysis by number places orthopterans at their highest level in June and July (Fig. 6). Possibly two factors, acting singly, or in combination, are important here. Firstly, a decrease in the average size (length) of the orthopteran prey and, secondly, the suspected specialized feeding habits of individual birds.

Like earthworms, Diptera and Arachnida were at their highest levels by weight and numbers as dietary items during the April–September wet period (Fig. 6). Like Lepidoptera, Coleoptera declined during this period. The reason for the ascendency of dipterans in the diet at this time of the year is somewhat obscure. From Fig. 7, it appears that Arachnida were about twice as available from June to September as at other times of the year. Spiders were seemingly more abundant in pasture in winter, but why this should have been, I am unable to say. Vertebrates, also varied seasonally, by weight and numbers in the diet. There are indications that they were consistently more available in the wet months than in the dry ones (Fig. 7).

In summary, it may be said that insects and earthworms constituted the main food of *A. ibis*, when feeding in pastures in the south-western Cape. The consumption of earthworms was virtually restricted to the wet period of the year (April–October). During this period the diet (by weight) was dominated by earthworms. However, Diptera and Arachnida also featured more prominently then than at other times. In the dry months (November–March) the diet consisted predominantly of Orthoptera, Lepidoptera and Coleoptera. Comparatively smaller quantities (by weight) of each of these three food classes were consumed by the birds during the period April–October.

Diversity of food by individual birds and time of day

Marked individual variations in stomach contents sometimes occurred among birds collected together. For instance, a group of three adults collected at the same place and time contained major food categories in the following proportions. These birds had equal opportunity to forage at length in the same habitat.

Analysis by number:

Bird A: grasshoppers—60%; crickets—5%; caterpillars—30%.
Bird B: grasshoppers—10%; crickets—50%; caterpillars—35%.
Bird C: grasshoppers—15%; crickets—0%; caterpillars—70%.

No special attempt was made to investigate this diversity in feeding, but possibly it was due to specialized feeding by individual birds or concentrated availability of particular food resources.

To illustrate variation in diet according to the time of day, the following example is given. Eight birds were collected on the same day and at the same place. Four of these were shot in the morning, 4 h after sunrise, and four in the afternoon, 4 h before sunset. Each of these birds had been given equal opportunity (3 h) to forage in the same habitat. The pre-noon stomachs contained, by weight, 85% earthworms and the balance insects. The post-noon stomach contents consisted of 75% insects and 14% earthworms. It is hard to evaluate differences of this kind with any accuracy, since rates of digestion vary for the different food organisms. In this case, digestion is rapid for soft earthworms and relatively slow for chitinized insects (the microscopical examination of stomach contents for indigestible chaetae of earthworms proved impracticable). The introduction of errors, sometimes of considerable magnitude, of this kind bedevils investigations aimed at determining the actual food of an animal, and limits the accurate assessment of the value

Table 2. *Composition of the diet of nestling cattle egrets (based on a total of 98 food samples)*

Food items	% occurrence (frequency)	% by weight	% by no.	Mean no. objects/ stomach	Max. no. objects in one stomach
ARTHROPODA					
INSECTA					
DICTYOPTERA					
Mantidae } Phasmidae }	9·0	0·3	0·3	1	3
ORTHOPTERA					
Acrididae } Tettigonidae }	79·2	34·3	35·0	20	90
Gryllidae	10·1	1·7	0·7	3	13
Gryllotalpidae	2·5	0·1	0·1	1	2
DERMAPTERA					
Forficulidae	1·2	+	+	1	1
ISOPTERA					
Hodotermitidae	2·5	1·0	3·0	69	132
ODONATA					
Libellulidae	3·8	+	+	1	1
HEMIPTERA					
Jassidae	1·2	+	+	1	1
Reduviidae	3·8	+	0·1	1	3
LEPIDOPTERA					
Nymphalidae larvae	1·2	0·1	0·2	7	7
Pieridae	17·7	0·5	0·8	2	12
Geometridae larvae	7·6	0·2	0·6	2	5
Sphingidae larvae	1·2	0·2	+	2	2
Noctuidae	34·2	5·5	6·0	7	57
larvae	60·7	16·6	17·0	30	50
Unidentified pupae	19·0	9·2	12·2	30	135
COLEOPTERA					
Carabidae	29·0	1·0	1·7	4	10
Lampyridae larvae	3·8	+	0·1	1	2
Coccinellidae	1·2	+	+	1	1
Tenebrionidae	16·4	0·8	0·7	2	4
Chrysomelidae larvae	1·2	+	0·3	13	13
Scarabaeidae	17·7	0·8	1·1	3	10
larvae	2·5	0·5	0·3	5	5
Curculionidae	2·5	0·1	1·2	30	31
HYMENOPTERA					
Formicoidea	1·2	+	+	3	3
DIPTERA					
Asilidae	6·3	+	0·3	2	2
Syrphidae	10·0	+	0·3	1	2
larvae	2·5	0·8	1·0	15	26
Muscidae	16·4	0·2	1·6	5	24
larvae	5·0	1·7	6·5	70	159
Tachinidae	5·0	+	0·1	1	1
Calliphoridae	17·7	1·7	4·0	10	53
ARACHNIDA					
SCORPIONIDAE	1·2	0·2	+	1	1
ARANEIDA	24·0	0·2	1·4	4	20
ACARINA	1·2	+	+	1	1
MYRIOPODA					
CHILOPODA	1·2	+	+	1	1

Food items	% occurrence (frequency)	% by weight	% by no.	Mean uo. objects/ stomach	Max. no. objects in one stomach
ANNELIDA					
OLIGOCHAETA	1·2	+	+	1	1
VERTEBRATA					
AMPHIBIA					
ANURA	31·6	12·7	2·9	6	20
REPTILIA					
SQUAMATA					
SAURIA	5·5	3·0	0·1	1	3
AVES	2·6	3·8	+	1	1

+, Values smaller than 0·1.

to be attached to the diet's component parts. Nevertheless, the difference between pre- and post-noon diet in *A. ibis* is a very real one, especially during the wet months, and it probably reflects the relative availability of particular food organisms.

The diet of nestling birds

As with the food taken by free-flying birds, the diet of nestlings consisted predominantly of insects: primarily grasshoppers (Orthoptera) and caterpillars (Lepidoptera) (Table 2, Figs. 8 and 9). Vertebrates, principally frogs, featured quite prominently, while earthworms were of no importance. Taken on balance, the composition of the nestling diet closely resembled that of free-flying birds during the spring season as a whole. However, in terms of relative quantities, nestlings contained a much bigger proportion of grasshoppers (by number and weight, more than one-third of the total diet) than did adults (cf. Tables 1 and 2).

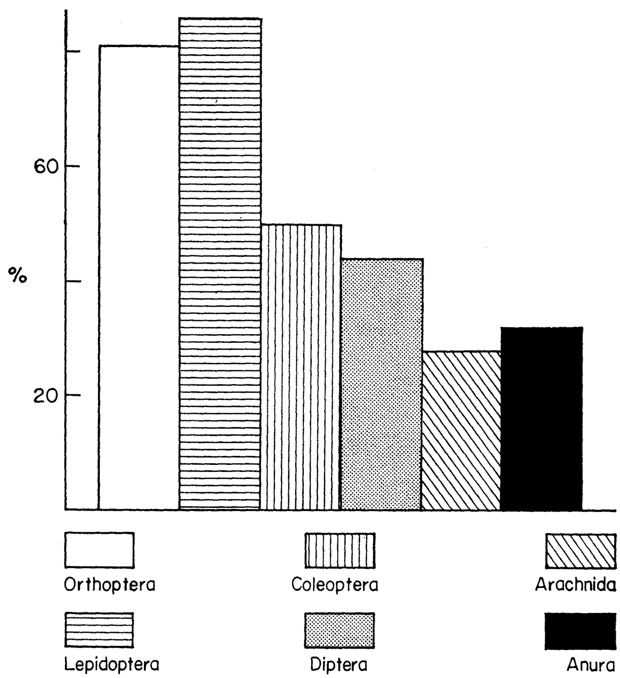

FIG. 8. Percentage frequency of occurrence of major insect orders and other taxa in the diet of nestling cattle egrets.

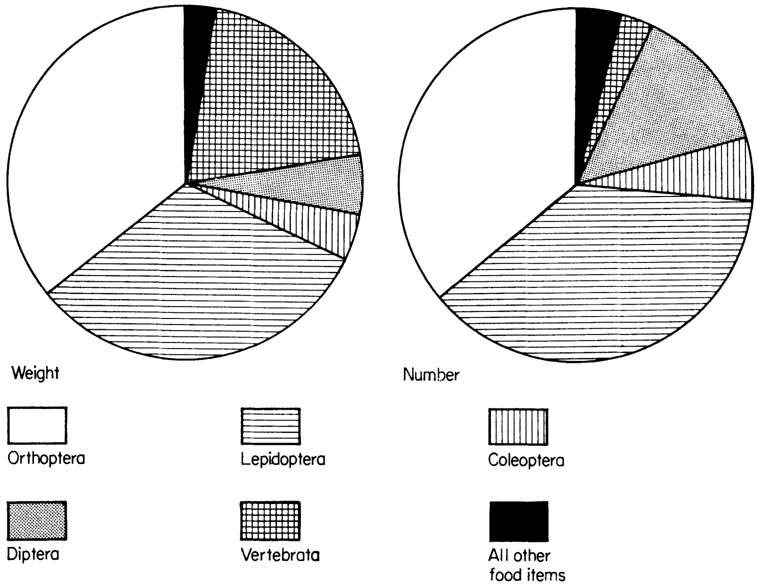

FIG. 9. Percentage composition by weight and number of the major food categories in the diet of nestling cattle egrets.

DISCUSSION

Many variables affect the diet of *Ardeola ibis*. Further, it must be admitted that, even with the relatively large number of stomachs examined during this study, the techniques and methods of analysis available were not sufficiently refined to yield precise data. However, the results do give general estimates, qualitative and quantitative, of the species' diet.

Marked seasonal variation attended the diet of *A. ibis* in the south-western Cape. Apparently, a considerable measure of flexibility in the selection of food items is required, so that the bird may obtain an adequate supply of food. The diet of any animal is influenced by changes in the abundance of different food items available in its habitat. When discussing seasonal changes, or any other variation, it is necessary to consider at the same time the two governing and correlated factors, viz. the available abundance of food and food-preference of the animal concerned (cf. Brown 1969). Included, too, are auxiliary factors, such as the status of the animal population being sampled. Ideally one needs to evaluate changes in diet in terms of the amount of available food, both in quantity and variety, as well as nutritive quality. A comparison of the frequency of occurrence of a particular food class in the diet, with the frequency of occurrence of that class in a given time and space, is required to indicate preferential feeding.

In the late part of the wet season and the early part of the dry season (when young are in the nest) the diet of the cattle egret is not as diverse as late in the dry season. Then, the wide variety of food taken by juvenile egrets (Siegfried in prep.) is typical of many species and is apparently due to an initial responsiveness to generalised stimuli eliciting a variety of feeding responses (Kear 1962, 1964; Hinde 1966). Learning later limits the effective stimuli. In this connexion, the diversity of stomach contents of individual egrets, when collected at the same time and place, is interesting. Carrick (1959) has recorded similar differences in feeding performance by individuals in the strawnecked ibis (*Threskiornis* *spinicollis*) and white ibis (*T. mollucca*). Whether preference in *Ardeola ibis* was due to individual bias towards food selection, or differing availability of foods within a relatively small feeding area that appeared uniform, is difficult to say. In pasture certain food items are distributed patchily. For instance, crickets tend to be more available in the immediate vicinity of water furrows, since gravitational irrigation disturbs and flushes these insects from hiding. In a compact flock of egrets, feeding as a group over pasture, certain individuals were commonly observed deliberately restricting their feeding to the proximity of furrows. Often, individuals were recorded along furrows actually waiting for irrigation to start. This in itself, of course, implies learned ability as a result of successful past experiences which perhaps originated from, and became firmly established during, initial trial-and-error, when the birds were first learning to feed independently. On the other hand, selection of particular food items could have been due to temporary learning, described by Tinbergen's (1960) theory of 'specific search images.' On balance, it seems most likely that in *A. ibis* differences in the diet of individual birds, feeding in the same flock and habitat, are determined by a number of components (e.g. internal physiological state, refined behavioural patterns and food availability).

Within a feeding niche, an advantage must accrue to an individual who can gather relatively large food items. In this way it stands to gain more energy from the food than is expended on gathering it. Vertebrates featured more prominently as dietary items in the wet months, and early in the dry season, than late in the dry season. On the other hand, 10% of adult and 43% of juvenile cattle egrets sampled at the end of the dry season had been eating ants 2–3 mm in length. At other times of the year ants feature in comparatively fewer stomachs and in smaller quantities in the diet.

Finally, it is clear that the diet of the cattle egret in the south-western Cape depends heavily on grasshoppers, caterpillars and earthworms, though a wide range of other food items is taken. On the whole, the diet indicates considerable diversity and suggests a wide degree of adaptability; an important factor in the species' success.

The studies reported by Kirkpatrick (1925) and Kadry Bey (1942) were undertaken primarily to ascertain the economic value of *A. ibis* in relation to agriculture in Egypt. Although relying on the stomach-contents of only thirty-six specimens, Saayman (1966) oriented his conclusions towards an evaluation of the species' economic importance in farming areas of the eastern Cape Province. The evidence gathered by these three investigators led them to claim that the feeding habits of *A. ibis* are highly beneficial to agriculture. According to Saayman (1966), 'strict protection of *A. ibis* should be regarded as vital to South African agriculture and that the value of this egret cannot be overemphasised.'

While in no way refuting the claims of these workers, I must point out that my data make it difficult to assess realistically the economic value of the bird in relation to agriculture in the south-western Cape. This difficulty is caused, firstly by the relatively high proportion of earthworms in the diet (earthworms are generally regarded as highly beneficial to agriculture); and, secondly, by lack of proper knowledge about the roles played by individual food organisms in different habitats. Certainly, unlike Saayman (1966), I am reluctant to classify all food organisms into rigid compartments according to economically indifferent, injurious or beneficial influences to the agro-potential. Hartley (1948) has stressed the complications attending any pronouncement upon the economic status of birds on the basis of their diets. Another point is that I did not identify all prey organisms to species level, the main aim having been to name specifically only those food organisms which were readily recognizable, or of particular importance, and only when this did not pose special problems in the treatment of the samples. For instance, to sort and separate large aggregates of grasshoppers, firstly, as adults and nymphs and, secondly, to species was impracticable in this study. In spite of these shortcomings, however, it is correct to say that on balance the insect material, examined for this study, exerts a deleterious effect on the agro-potential. Among Lepidoptera in the egret's diet, immature forms, chiefly caterpillars, were dominant throughout the year; adult lepidopterans were of comparative minor importance. Caterpillars of the moths *Heliothis armigera* (known locally and erroneously as the American Bollworm) and *Argrotis* sp. were prominent; the lucerne butterfly (*Colias electo*), larvae and adults, occurred regularly in fair numbers. According to Smit (1964) all of these forms are responsible for damage to pasture and other crops. Among Coleoptera, the potentially harmful *Heteronychus sanctaehelenae* featured very prominently in the bird's diet. Crickets, chiefly *Gryllus bimaculatus*, and grasshoppers can rightly be regarded as potentially injurious to most crops; these insects are especially common in mixed pasture in the south-western Cape. MacFadyen (1967) has calculated that under English conditions about one-third of the net production (energy/unit of time) of grass meadows grazed by cattle, is eaten by herbivores and half of this goes to insects, leaving only about one-sixth for the cattle. Of course, it is not known whether the European situation is applicable to the south-western Cape, but, in any event, cattle egrets contribute towards lowering the grass-eating orthopteran populations.

ACKNOWLEDGMENTS

The study was financed in part by the Cape Department of Nature Conservation and the Percy FitzPatrick Institute of African Ornithology.

SUMMARY

(1) Cattle egrets (*Ardeola ibis*) feeding in dairy-cattle pastures in the south-western Cape, South Africa, ate mainly grasshoppers, caterpillars and earthworms, though a wide range of other food categories was taken.

(2) The most obvious seasonal change in diet involved earthworms: these accounted for about 60%, by weight, of the total food taken during the rainy season (April to October) and were virtually absent (in the birds' stomach contents) at other times of the year.

(3) The diet of nestlings resembled that of the independent birds. Grasshoppers and caterpillars were the most important food items.

(4) The cattle egret's diet generally is reviewed, chiefly in relation to the agro-economy.

REFERENCES

Ashmole, N. P. & Ashmole, M. J. (1967). Comparative feeding ecology of sea birds of a tropical oceanic island. *Bull. Peabody Mus. nat. Hist.* **24,** 1–131.

Brown, R. G. B. (1969). Seed selection by pigeons. *Behaviour*, **34,** 115–31.

Carrick, R. (1959). The food and feeding habits of the Straw-necked Ibis, *Threskiornis spinicollis* (Jameson), and the White Ibis, *T. molucca* (Cuvier), in Australia. *C.S.I.R.O. Wildl. Res.* **4,** 59–92.

Hartley, P. H. T. (1948). The assessment of the food of birds. *Ibis*, **90,** 361–81.

Hinde, R. A. (1966). *Animal Behaviour—A Synthesis of Ethology and Comparative Psychology.* McGraw-Hill, New York.

Imms, A. D. (1957). *A General Textbook of Entomology*. Methuen, London.

Kadry Bey, I. (1942). The economic importance of the Buff-backed Egret (*Ardea ibis* L.) to Egyptian agriculture. *Bull. zool. Soc. Egypt*. **4,** 20–6.

Kear, J. (1962). Food selection in finches with special reference to interspecific differences. *Proc. zool. Soc. Lond*. **138,** 163–204.

Kear, J. (1964). Food selection. *A New Dictionary of Birds* (Ed. by A. L. Thomson), pp. 319–21. Nelson, London.

King, J. E. & Ikehara, I. I. (1956). Comparative study of food of Bigeye and Yellowfin tuna in the Central Pacific. *Fish. Bull. U.S. Fish. Wildl. Serv*. **57** (108), 61–85.

Kirkpatrick, C. M. (1940). Some foods of young Great Blue Herons. *Am. Mid. Nat*. **24,** 594–601.

Kirkpatrick, T. W. (1925). The Buff-backed Egret (*Ardea ibis*, L. Arabic: Abu-Querdan) as a factor in Egyptian agriculture. *Bull. Min. Agric*. **56,** 1–28.

MacFadyen, A. (1967). Population dynamics. Discussion Leader's address at Symposium on Terrestrial Animal Ecology. *News Bull. zool. Soc. sth. Afr*. **9,** 15–7.

Martin, A. C., Gensch, R. H. & Brown, C. P. (1946). Alternate methods in upland game bird food analysis. *J. Wildl. Mgmt*, **10**(1), 8–12.

Owen, D. F. (1955). The food of the Heron *Ardea cinerea* in the breeding season. *Ibis*, **97,** 276–95.

Palmer, R. S. (Ed.) **(1962).** *Handbook of North American Birds*, Vol. 1. Yale University Press, Yale, Connecticut.

Reintjes, J. W. & King, J. E. (1953). Food of the Yellowfish Tuna in the Central Pacific. *Fish. Bull. U.S. Fish. Wildl. Serv*. **54**(81), 91–110.

Saayman, J. E. (1966). *A study of the diet and parasites of* Ardeola (Bubulcus) ibis, Numida meleagris *and* Gallus domesticus *from the eastern Cape Province, South Africa*. Unpublished Ph.D. thesis, University of South Africa.

Siegfried, W. R. (1966). On the food of nestling Cattle egrets. *Ostrich*, **37,** 291–20.

Siegfried, W. R. (1969). Energy metabolism of the Cattle Egret. *Zoologica Africana*, **4,** 265–73.

Smit, B. (1964). *Insects in Southern Africa: How to Control Them*. Oxford University Press, Cape Town.

Tinbergen, L. (1960). The dynamics of insect and bird populations in pine woods. *Archs néerl. Zool*. **13,** 259–472.

Waldron, K. D. & King, J. E. (1962). Food of Skipjack in the Central Pacific. World Scientific Meeting on the Biology of Tunas and Related Species. Sect. No. 5, Experience Paper 26, pp. 1–28.

(*Received* 15 *June* 1970; *revision received* 10 *August* 1970)