THE FOOD AND FEEDING HABITS OF THE STRAW-NECKED IBIS, *THRESKIORNIS SPINICOLLIS* (JAMESON), AND THE WHITE IBIS, *T. MOLUCCA* (CUVIER), IN AUSTRALIA

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Summary

A survey of the feeding habits of the straw-necked ibis, *Threskiornis spinicollis* (Jameson), and the white ibis, *T. molucca* (Cuvier), was made in eastern Australia during 1952–56. Analysis of the stomach contents of 162 straw-necked ibis and 202 white ibis reveals considerable overlap of food organisms, which are mainly aquatic and terrestrial invertebrates. The white ibis fed largely on freshwater crayfish and other aquatic foods, and made limited use of drier habitats; the straw-necked ibis used a wider range of habitats and food organisms. Plague locusts of all stages and densities were eaten by ibises, but the overall effect on locust numbers is slight.

I. INTRODUCTION

The three species of ibis in Australia—the straw-necked (popularly "black" or "black-and-white") ibis, *Threskiornis spinicollis* (Jameson); the white ibis, *T. molucca* (Cuvier); and the smaller and much less common glossy ibis, *Plegadis falcinellus* (L.)—appear to have, in general, similar feeding and breeding requirements. They occur principally in freshwater habitats, especially shallow marshes, which contain large breeding colonies during suitable flood conditions. They also range into drier country, and the straw-necked ibis in particular is highly regarded as a useful predator on the Australian plague locust, *Chortoicetes terminifera* Walker, and other agricultural pests. The development of dams on rivers flowing westward from the Great Dividing Range toward the drier interior, to control water flow in favour of irrigation areas, is a potential threat to successful breeding of ibises and other water-birds, especially in years of lower rainfall. The Burrendong Dam, now in course of construction on the Macquarie River near Wellington in central New South Wales, could prevent flooding of the extensive Macquarie Marshes, which are a noted breeding-place of water-birds and in 1955 were declared a sanctuary under the Fauna Protection Act, 1948, of New South Wales. Representations by pastoralists and naturalists have focused attention on the economic importance and general interest of these birds, especially the ibises, and on the measures necessary to ensure their continued breeding. Some of the latter are discussed in a mimeographed report of the Macquarie Marshes Investigation Committee, issued in 1951 by the Minister for Conservation, New South Wales. During 1952–56 a general survey of the feeding, breeding, and movements of the straw-necked ibis and the white ibis was made in order to obtain some idea of their actual economic value and of the measures which seem justified, on this or other grounds, for their conservation.

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Comparison of two closely related sympatric species of such similar size and apparently very similar ecology is of interest, for it may be possible to demonstrate the differences which enable them to coexist. Ecological distinction is most likely to appear in their food and feeding habits, the subject of this paper. A subsequent paper will deal with breeding, movements, and conservation.

II. Material and Methods

The collection of samples of adult ibises for examination of stomach contents was supplemented by observation of habitat preferences, available food supplies, and feeding behaviour. Much of the work was done at the Macquarie Marshes, especially in relation to predation on *Chortoicetes terminifera* adults at low densities and during mass hatchings of eggs in spring. Study of the possible relation between the abundance of locusts, as well as of other foods, and ibis breeding necessitated timely information on the latter. This was difficult to obtain, especially in regard to marshes and lakes in sparsely settled areas, and low aerial reconnaissance eventually economized greatly on the costs and limited time available for the study.

A total of 162 straw-necked ibises and 202 white ibises were collected throughout New South Wales at the Macquarie Marshes, Booligal on the Lachlan River, Griffith in the Murrumbidgee Irrigation Area, Pallamallawa near Moree on the Queensland border, and around Grafton on the north-east coast; in Victoria along the River Murray at Kiewa, Barmah, Kow, and Kerang swamps; and in south Queensland at Lake Bullawarra. These samples cover most months of the year and a wide range of habitats from flooded marshes to dry paddocks, as well as breeding and non-breeding situations. Only free-flying birds are included, for the crop of each adult when feeding young contains many—often several hundred—food items in excellent undigested condition for identification. Ibises are wary birds, and often fly far after being hit by shot or bullet, so that many specimens (apart from the small representative samples taken at breeding colonies) are the result of opportunist collecting; larger numbers would have been preferred. Only one bird was taken while feeding on a locust swarm (large nymphs of *Chortoicetes terminifera*), but several were collected where that locust was more sparse. The two species of ibis were frequently collected together, where they had equal opportunity to use the same feeding-places.

Identification of food organisms from the stomachs and crops of these samples of ibises was taken only as far as necessary in each case. Locusts and grasshoppers (Acrididae) were named specifically, and adults and nymphs were counted separately. Other important species, such as the freshwater crayfish or "yabbie", *Cherax albidus* Clark, and the freshwater crab, *Paratelphusa leichardti* (Miers), were also named. Most invertebrates have been grouped at family or ordinal level, the aim being to classify them according to the degree of moisture of their usual habitat, and immature forms have been listed separately where this was necessary.

III. Food Samples

The wide range of food organisms in these samples is shown in Tables 1 and 2. The rate of digestion of different organisms, or parts of them, also varies widely,

TABLE 1

NUMBERS AND OCCURRENCE OF FOOD ORGANISMS IN STOMACHS OF 162 STRAW-NECKED IBIS AND 202 WHITE IBIS, AND RELATION OF FEEDING TO HABITAT

Numerals in ordinary type refer to straw-necked ibis, in *italics* to white ibis

Food Organisms*					Ibis	
Name		Total Number in Each Species of Ibis	Percentage of Total Number of Food Items	Maximum Number in One Bird	Number that Fed on Each Organism	Percentage of Total Sample
Annelida						
OLIGOCHAETA (earthworms)		90	0·5 *w*†	45	5	3·1
		272	*3·5 w*	*84*	*18*	*8·9*
HIRUDINEA (leeches)		3	‡ *aq*	2	2	1·2
		1	‡ *aq*	*1*	*1*	*0·5*
Arthropoda						
CRUSTACEA						
Cherax albidus ("yabbie")		268	1·5 *aq*	39	46	28·3
		810	*10·5 aq*	*25*	*134*	*66·3*
ISOPODA (slaters)		34	0·2 *av*	17	8	4·9
		2	‡ *av*	*1*	*2*	*1·0*
DECAPODA						
Paratelphusa leichardti (freshwater crab)		3	‡ *aq*	1	3	1·9
		114	*1·5 aq*	*27*	*10*	*5·0*
MYRIAPODA						
CHILOPODA (centipedes)		48	0·3 *av*	8	14	8·6
		23	*0·3 av*	*15*	*4*	*2·0*
DIPLOPODA (millipedes)		5	‡ *av*	2	4	2·5
		0	*0 av*	*0*	*0*	*0*
ARACHNIDA						
SCORPIONIDEA (scorpions)		18	0·1 *d*	12	5	3·1
		0	*0 d*	*0*	*0*	*0*
ARANEIDA (spiders)	adults	469	2·6 *av*	151	76	46·9
		31	*0·4 av*	*7*	*14*	*6·9*
	egg-sacs	24	0·1 *av*	3	17	10·5
		1	‡ *av*	*1*	*1*	*0·5*

*Adult form unless otherwise stated.

†Habitats: *d*, dry; *av*, average; *w*, wet; *aq*, aquatic. The habitat given for each item is the one most characteristic of the item concerned.

‡Very small percentages.

TABLE 1 (*Continued*)

Food Organisms					Ibis	
Name		Total Number in Each Species of Ibis	Percentage of Total Number of Food Items	Maximum Number in One Bird	Number that Fed on Each Organism	Percentage of Total Sample
INSECTA						
Odonata (dragonflies)						
Anisoptera	adults	5	‡ *aq*	2	4	2·5
		1	‡ *aq*	*1*	*1*	*0·5*
	nymphs	39	0·2 *aq*	13	11	6·8
		36	*0·5 aq*	*8*	*20*	*9·9*
Orthoptera						
Gryllacrididae (tree-crickets)		38	0·2 *av*	38	1	0·6
adults and large nymphs		*0*	*0 av*	*0*	*0*	*0*
Tettigoniidae (long-horned grasshoppers)		4	‡ *av*	2	3	1·9
		7	*0·1 av*	*7*	*1*	*0·5*
Gryllidae (crickets)		5674	31·9 *av*	443	66	40·7
adults and large nymphs		*3765*	*48·8 av*	*319*	*66*	*32·7*
Gryllotalpidae (mole-crickets)		18	0·1 *av*	12	4	2·5
		66	*0·9 av*	*29*	*13*	*6·4*
Acrididae (grasshoppers and locusts)	adults	1565	8·8 §	153	77	47·5
		901	*11·7* §	*129*	*29*	*14·3*
	nymphs	738	4·2 §	737	2	1·2
		3	‡ §	*3*	*1*	*0·5*
Dermaptera (earwigs)		23	0·1 *av*	10	8	4·9
		5	‡ *av*	*1*	*5*	*2·5*
Dictyoptera (cockroaches)		185	1·0 *av*	79	23	14·2
		13	*0·2 av*	*10*	*4*	*2·0*
Hemiptera						
Cicadidae (cicadas)	adults	35	0·2 *av*	35	1	0·6
		0	*0 av*	*0*	*0*	*0*
	nymphs	0	0 *av*	0	0	0
		26	*0·3 av*	*26*	*1*	*0·5*

§The percentage of Acrididae has been subdivided according to the habitat of each species (see Table 2) as follows:

adults: straw-necked ibis, 1·3 *d*, 3·6 *av*, 3·9 *w*; white ibis, *0 d*, *5·0 av*, *6·7 w*.

nymphs: straw-necked ibis, 4·2 *d*, 0 *av*; white ibis, *0 d*, ‡ *av*.

TABLE 1 (*Continued*)

Food Organisms					Ibis	
Name		Total Number in Each Species of Ibis	Percentage of Total Number of Food Items	Maximum Number in One Bird	Number that Fed on Each Organism	Percentage of Total Sample
INSECTA (*continued*)						
Nepidae (water-scorpions)		0	0 *aq*	0	0	0
		10	*0·1 aq*	*10*	*1*	*0·5*
Notonectidae (water-bugs) and Corixidae		337	1·9 *aq*	316	12	7·4
		32	*0·4 aq*	*6*	*20*	*9·9*
Pentatomidae (shield-bugs)		108	0·6 *av*	47	12	7·4
		2	‡ *av*	*1*	*2*	*1·0*
Neuroptera						
Myrmeleontidae (ant-lions)	larvae	3	‡ *d*	1	3	1·9
		1	‡ *d*	*1*	*1*	*0·5*
Lepidoptera						
Noctuidae (moths)	adults	368	2·1 *av*	362	4	2·5
		1	‡ *av*	*1*	*1*	*0·5*
	pupae	43	0·2 *av*	24	8	5·0
		3	‡ *av*	*3*	*1*	*0·5*
	larvae (caterpillars)	3127	17·6 *av*	442	56	34·6
		263	*3·4 av*	*195*	*14*	*6·9*
Diptera						
Tipulidae (crane-flies)	larvae	112	0·6 *av*	107	3	1·9
		0	*0 av*	*0*	*0*	*0*
Syrphidae (hover-flies)	pupae	0	0 *aq*	0	0	0
		3	‡ *aq*	*3*	*1*	*0·5*
	larvae	276	1·6 *aq*	276	1	0·6
		365	*4·7 aq*	*189*	*2*	*1·0*
Other flies	adults	6	‡ *av*	2	5	3·1
		10	*0·1 av*	*4*	*7*	*3·5*
	larvae	5	‡ *av*	4	2	1·2
		2	‡ *av*	*1*	*2*	*1·0*
Hymenoptera						
Tenthredinidae (sawflies)	pupae	3	‡ *av*	2	2	1·2
		20	*0·3 av*	*18*	*3*	*1·5*

TABLE 1 (*Continued*)

Food Organisms				Ibis	
Name	Total Number in Each Species of Ibis	Percentage of Total Number of Food Items	Maximum Number in One Bird	Number that Fed on Each Organism	Percentage of Total Sample
INSECTA (*continued*)					
Ichneumonidae (parasitic wasps)	2	‡ *av*	1	2	1·2
	0	*0 av*	*0*	*0*	*0*
Formicoidae (ants)	30	0·2 *d*	12	10	6·2
	1	‡ *d*	*1*	*1*	*0·5*
Apidae (bees)	5	‡ *av*	3	3	1·9
	1	‡ *av*	*1*	*1*	*0·5*
Coleoptera					
Carabidae (ground-beetles)	710	4·0 *av*	200	87	53·7
	144	*1·9 av*	*18*	*58*	*28·7*
Dytiscidae, Gyrinidae, and Hydrophilidae (water-beetles)					
adults	119	0·7 *aq*	17	38	23·5
	60	*0·8 aq*	*9*	*35*	*17·3*
larvae	426	2·4 *aq*	181	25	15·4
	122	*1·6 aq*	*58*	*19*	*9·4*
Lucanidae (stag-beetles)	1	‡ *av*	1	1	0·6
	0	*0 av*	*0*	*0*	*0*
Scarabaeidae (chafer-beetles, Christmas beetle, dung-beetles)	345	1·9 *av*	97	24	14·8
	76	*1·0 av*	*26*	*16*	*7·9*
Elateridae (click-beetles) and Tenebrionidae (tenebrio-beetles)					
adults	82	0·5 *av*	11	33	20·4
	49	*0·6 av*	*6*	*34*	*16·8*
larvae	958	5·4 *av*	432	21	12·4
	42	*0·5 av*	*27*	*5*	*2·5*
Coccinellidae (ladybird-beetles)	5	‡ *av*	1	5	3·1
	0	*0 av*	*0*	*0*	*0*
Curculionidae (weevils)	353	2·0 *av*	87	52	32·1
	27	*0·4 av*	*18*	*8*	*4·0*

TABLE 1 (*Continued*)

Food Organisms				Ibis	
Name	Total Number in Each Species of Ibis	Percentage of Total Number of Food Items	Maximum Number in One Bird	Number that Fed on Each Organism	Percentage of Total Sample
Mollusca					
LAMELLIBRANCHIATA (freshwater mussels)	8	‡ *aq*	1	8	5·0
	34	*0·4 aq*	*25*	*5*	*2·5*
GASTEROPODA (water-snails)	464	2·6 *aq*	92	28	17·3
	190	*2·5 aq*	*87*	*37*	*18·3*
Chordata					
ACTINOPTERYGII (bony fish)	26	0·2 *aq*	12	8	5·0
	73	*0·9 aq*	*10*	*25*	*12·4*
AMPHIBIA (frogs)	520	2·9 *aq*	38	60	37·0
	99	*1·3 aq*	*22*	*40*	*19·8*
REPTILIA					
LACERTILIA (lizards)	18	0·1 *d*	6	6	3·7
	1	‡ *d*	*1*	*1*	*0·5*
OPHIDIA (snakes)	7	‡ *av*	4	4	2·5
	1	‡ *av*	*1*	*1*	*0·5*
MAMMALIA					
Muridae (rats and mice)	3	‡ *av*	2	2	1·2
	2	‡ *av*	*1*	*2*	*1·0*
Totals 54 { 51 / *46*	17756 / *7712*			162 / *202*	

Incidence of Feeding in Relation to Habitat

	Dry (%)	Average (%)	Wet (%)	Aquatic (%)
Straw-necked ibis	5·9	75·2	4·4	14·0
White ibis	‡	64·2	10·2	25·2

TABLE 2

NUMBERS AND OCCURRENCE OF GRASSHOPPERS AND LOCUSTS (ACRIDIDAE) IN STOMACHS OF 77 STRAW-NECKED IBIS AND 30 WHITE IBIS, AND RELATION OF FEEDING TO HABITAT

Numerals in ordinary type refer to straw-necked ibis, in *italics* to white ibis

Species		Acrididae: Total Number in Each Species of Ibis	Acrididae: Percentage of Total Acrididae	Acrididae: Maximum Number in One Bird	Ibis: Number that Fed on Each Acridid	Ibis: Percentage of Sample
SPECIES OF ECONOMIC IMPORTANCE						
Chortoicetes terminifera						
Australian plague locust	adults	88	3·8 *d**	39	15	19·5
		0	*0 d*	*0*	*0*	*0*
	nymphs	737	32·0 *d*	737	1	1·3
		0	*0 d*	*0*	*0*	*0*
Austroicetes cruciata						
Small plague grasshopper	adults	39	1·7 *d*	27	4	5·2
		0	*0 d*	*0*	*0*	*0*
	nymphs	1	‡ *d*	1	1	1·3
		0	*0 d*	*0*	*0*	*0*
Phaulacridium vittatum						
Wingless grasshopper	adults	59	2·6 *av*	26	7	9·1
		34	*3·8 av*	*31*	*2*	*6·7*
Gastrimargus musicus						
Yellow-winged locust	adults	3	0·1 *av*	1	3	3·9
		0	*0 av*	*0*	*0*	*0*
	nymphs	0	0 *av*	0	0	0
		3	*0·3 av*	*3*	*1*	*3·3*
Austracris guttulosa						
Spur-throated locust	adults	699	30·4	73	44	57·1
		516	*57·0*	*86*	*24*	*79·2*
Totals for five economic species		1626	70·6		61	
		553	*61·1*		*26*	

*Habitats: *d*, dry; *av*, average; *w*, wet. The habitat given for each item is the one most characteristic of the item concerned.

‡Very small percentages.

TABLE 2 (*Continued*)

Species	Acrididae: Total Number in Each Species of Ibis	Acrididae: Percentage of Total Acrididae	Acrididae: Maximum Number in One Bird	Ibis: Number that Fed on Each Acridid	Ibis: Percentage of Sample
OTHER SPECIES (all adults)					
Aiolopus tamulus	40	1·7 *av*	9	14	18·2
	0	*0 av*	*0*	*0*	*0*
Austroicetes vulgaris	13	0·6 *av*	8	3	3·9
	0	*0 av*	*0*	*0*	*0*
Brachyexarna lobipennis	100	4·3 *av*	42	6	7·8
	52	*5·7 av*	*50*	*2*	*6·7*
Coryphistes sp.	1	‡ *av*	1	1	1·3
	0	*0 av*	*0*	*0*	*0*
Cratilopus sp.	3	0·1 *d*	3	1	1·3
	0	*0 d*	*0*	*0*	*0*
Ecphantus quadrilobus	1	‡ *av*	1	1	1·3
	0	*0 av*	*0*	*0*	*0*
Monistria pustilifera	1	‡ *av*	1	1	1·3
	0	*0 av*	*0*	*0*	*0*
Oedaleus australis	19	0·8 *av*	10	8	10·4
	0	*0 av*	*0*	*0*	*0*
Peakesia fuscomaculata	121	5·3 *av*	58	13	16·9
	0	*0 av*	*0*	*0*	*0*
Perelytrana rana	7	0·3 *d*	7	1	1·3
	0	*0 d*	*0*	*0*	*0*
Perelytrana sp. nov.	53	2·3 *d*	14	9	11·7
	0	*0 d*	*0*	*0*	*0*
Praxibulus sp.	205	8·9 *av*	92	10	13·0
	208	*23·0 av*	*182*	*4*	*13·3*
Pycnostictus seriatus	1	‡ *d*	1	1	1·3
	0	*0 d*	*0*	*0*	*0*
Schizobothrus flavovittatus	7	0·3 *w*	2	4	5·2
	2	*0·2 w*	*1*	*2*	*6·7*

TABLE 2 (*Continued*)

Species	Acrididae: Total Number in Each Species of Ibis	Acrididae: Percentage of Total Acrididae	Acrididae: Maximum Number in One Bird	Ibis: Number that Fed on Each Acridid	Ibis: Percentage of Sample
OTHER SPECIES (*continued*)					
Zabrala sp.	32 *0*	1·4 *d* *0 d*	17 *0*	5 *0*	6·5 *0*
Undeterminable items, mostly mandibles§	73 *89*	3·2 *av* *9·8 av*	33 *24*	11 *10*	14·3 *33·3*
Totals 24{23 / *8*	2303 *904*			77 *30*	

Incidence of Feeding in Relation to Habitat

	Dry (%)	Average (%)	Wet (%)	Aquatic (%)
Five economic species only				
Straw-necked ibis	37·5	2·7	30·4	
White ibis	0	4·1	57·0	
Total Acrididae species				
Straw-necked ibis	41·6	27·5	30·7	
White ibis	0	42·6	57·2	

§These include species other than *Austracris guttulosa*, the mandibles of which are identifiable.

e.g. in the cases of earthworms and heavily chitinised insects. Unknown errors of some magnitude are introduced when food samples of this kind are presented by weight or volume as representing the diet of the bird (Hartley 1948), and in this study, which is concerned more with the effects which feeding might exert on the numbers of the prey, the data are treated numerically in terms of the relative abundance of each food organism and its frequency of occurrence in each species of ibis. A food item may be the entire individual recently ingested, or the remnant, such as insect mandibles, of one taken some time previously; all are equated regardless of relative size or the period of time during which they may have been collected by the bird. An indication of the extent to which each ibis species feeds in dry or wet situations is obtained by assigning food organisms to four broad categories of habitat in which they would normally occur.

Entirely animal food, mostly invertebrate, is taken by both straw-necked ibis and white ibis, as shown in Tables 1 and 2 and Figure 1. There is considerable

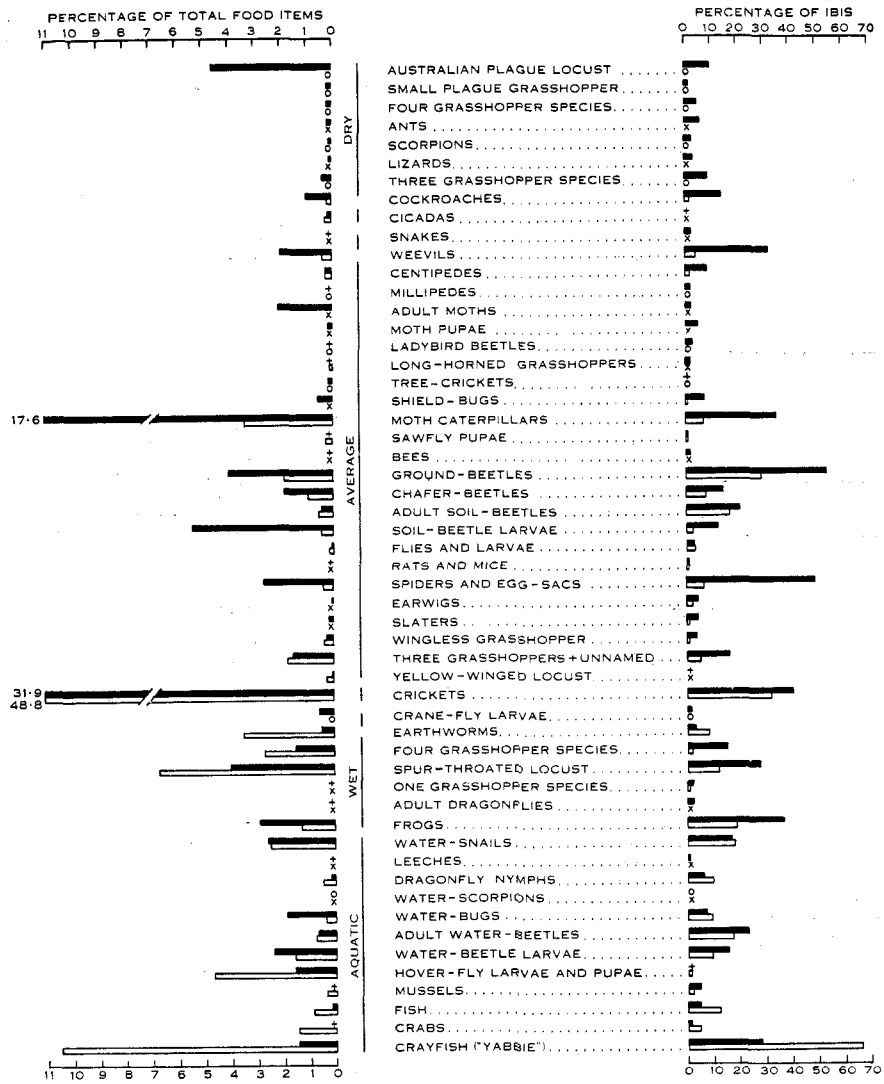

Fig. 1.—Occurrence of food organisms in stomachs of 162 straw-necked ibis and 202 white ibis. Organisms are arranged in series according to habitat. Histograms on the left show the percentage of each food organism in the total number of food items; those on the right show the percentage of each species of ibis that contained each food organism. Solid columns refer to straw-necked ibis, and open columns to white ibis; + (straw-necked ibis) and × (white ibis) represent small percentages, and ○ indicates none.

overlap, the former species taking 51 of the 54 categories listed and the latter taking 46. The straw-necked ibis sample covers all types of habitat, and the proportion of food organisms from dry situations is much lower than opportunity offered

because only one individual among many feeding on swarms of *Chortoicetes terminifera* was collected. The white ibis sample contained relatively more food items from wet and aquatic situations, and many of the latter were large freshwater crayfish and crabs, which were fed upon by more than twice as many white ibis as straw-necked ibis. More than half the Acrididae taken by the white ibis were large adults of the spur-throated locust, *Austracris guttulosa* Walker, which was abundant around the margins of marshes after flooding. The average numbers of all food items

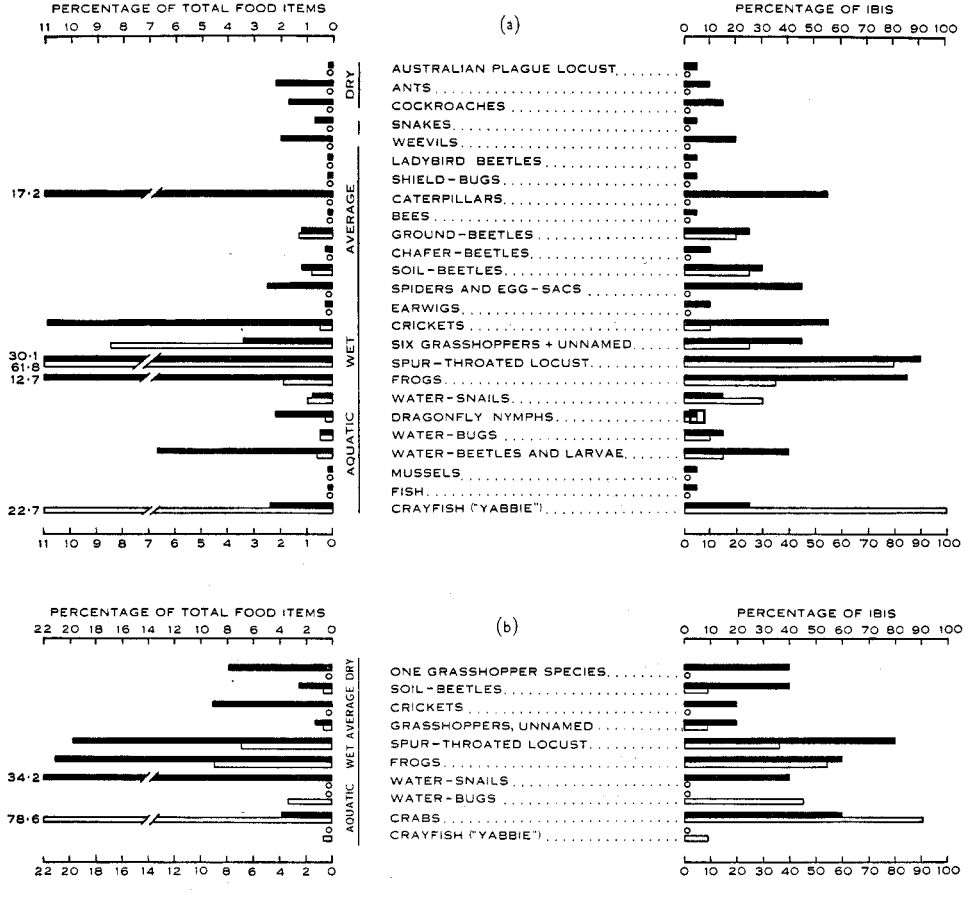

Fig. 2.—Comparison of food organisms in stomachs of two samples of straw-necked ibis and white ibis collected at the same time and place. For explanation of symbols see Figure 1.

(*a*) 20 straw-necked ibis and 20 white ibis breeding at the Macquarie Marshes, New South Wales, during May 5–7, 1955.

(*b*) 5 straw-necked ibis and 11 white ibis at Lake Bullawarra, Queensland, on June 11, 1955.

per stomach were 110 and 38 for straw-necked ibis and white ibis respectively; the difference reflects a difference in size of food species utilized by the two ibises, for it is mainly due to the much greater numbers of smaller insects and spiders in stomachs of the straw-necked ibis. This applies even to aquatic insects, for the larvae of water-beetles in the latter ibis included many about $\frac{1}{2}$ in. in length, while those in the white ibis were consistently about 2 in. long. The smallest items found

in the two ibises were weevils and ants 4 mm long in the straw-necked ibis and weevils 10 mm long in the white ibis. Each species of bird contained centipedes 120 mm long, and the largest freshwater crayfish in the white ibis were 1½ times as heavy as those in the straw-necked ibis.

Data concerning the two ibises collected at the same time and place are shown in Table 3 and Figure 2. The birds from the Macquarie Marshes were shot as they flew in to feed large young in a mixed colony, and they had equal opportunity to forage in the same habitats. The difference in feeding habits of the two species is evident. It is most marked with regard to freshwater crayfish; white ibis feeding on those crustaceans contained an average of 2½ times as many of them as did straw-necked ibis. Both species fed heavily on adult spur-throated locusts, which were present in great numbers in wet grass around the swamp. The straw-necked ibis took most of the food organisms referable to dry and average habitats, such as caterpillars and crickets, but also most of the frogs, water-beetles, and dragonfly nymphs. The other sample was taken at Lake Bullawarra, Queensland, when breeding was not in progress and the surrounding country was very dry. Freshwater crabs were the main food of white ibis, supplemented by frogs and spur-throated locusts, while frogs, water-snails, and locusts were most common in the straw-necked ibis sample.

The diversity of feeding performance by individuals of the same species, even when collected at the same time and place, is shown in Tables 4 and 5. Straw-necked ibises 1 and 2, taken together, contained spiders in the ratio 152 : 5 and adult moths in the ratio 4 : 362; No. 1 was a versatile predator indeed, as the 314 items covered by its range of 14 food organisms included all of the 38 tree-crickets (Gryllacrididae) and all of the 35 adult cicadas (Cicadidae) taken by the entire sample of 162 birds of its species. The first two straw-necked ibises had evidently chosen dry to average habitats, but No. 3, with 12 freshwater crayfish and 27 water-snails, had remained in the marsh. The interest of No. 4 is that, despite a surfeit of swarming nymphs of the Australian plague locust, of which it had taken 737, it also contained 79 cockroaches and four spiders. The next three groups (Nos. 5, 6, 7; 8, 9; 10, 11, 12) further illustrate the individual variation that can be found among birds collected together. It is clear that this sometimes stems from choice of habitat, for Nos. 5 and 6 had apparently been frequenting wetter places than No. 7. Nos. 8 and 9, however, were members of one flock feeding in the same type of habitat, and the latter had specialized in caterpillars while the former took crickets, spiders, shield-bugs (Pentatomidae) and other items. Nos. 10, 11, and 12 had concentrated respectively on water-beetle larvae and crickets, on frogs and spur-throated locusts, and on freshwater crayfish within a similar habitat range. The white ibis samples (Table 5) show similar variation among individual birds. No. 1 had confined its activities to the marsh, as many white ibises do, but No. 2 had no aquatic items. Nos. 3 and 4 provide the same contrast, and the former, evidently an average-habitat specialist among white ibises, contained a larger number of caterpillars, ground-beetles, and weevils than any individual of its species. The preponderance of freshwater crayfish in No. 5 is typical of the white ibis, and although the range of non-aquatic food organisms in No. 6 is in contrast, crickets and grasshoppers are important in the white ibis sample as a whole; these two individuals, breeding in the same swamp, were utilizing entirely different sources of food.

TABLE 3

COMPARISON OF STOMACH CONTENTS OF TWO SAMPLES OF STRAW-NECKED IBIS AND WHITE IBIS COLLECTED AT THE SAME TIME AND PLACE

Numerals in ordinary type refer to straw-necked ibis, in *italics* to white ibis

Food Organisms*				Ibis	
Name	Total Number in Each Species of Ibis	Percentage of Total Number of Food Items	Maximum Number in One Bird	Number that Fed on Each Organism	Percentage of Total Sample
(*a*) 20 Straw-necked Ibis and 20 White Ibis Breeding at the Macquarie Marshes, New South Wales, May 5–7, 1955					
Freshwater crayfish ("yabbie")	14	2·4 *aq*†	10	5	25
Cherax albidus	*142*	*22·7 aq*	*22*	*20*	*100*
Spiders (adults and egg-sacs)	15	2·5 *av*	3	9	45
	0	*0 av*	*0*	*0*	*0*
Dragonflies (nymphs)	13	2·2 *aq*	13	1	5
	2	*0·3 aq*	*2*	*1*	*5*
Crickets (adults and nymphs)	65	10·9 *av*	26	11	55
	3	*0·5 av*	*2*	*2*	*10*
Australian Plague Locust	1	0·2 *d*	1	1	5
Chortoicetes terminifera	*0*	*0 d*	*0*	*0*	*0*
Spur-throated Locust	179	30·1 *w*	39	18	90
Austracris guttulosa	*386*	*61·8 w*	*62*	*16*	*80*
Other grasshoppers—six species	15	2·5 *w*	4	7	35
	0	*0 w*	*0*	*0*	*0*
Undeterminable grasshoppers	5	0·8 *w*	4	2	10
	53	*8·5 w*	*21*	*5*	*25*
Earwigs	2	0·3 *av*	1	2	10
	0	*0 av*	*0*	*0*	*0*
Cockroaches	10	1·7 *av*	8	3	15
	0	*0 av*	*0*	*0*	*0*
Water-bugs	3	0·5 *aq*	1	3	15
	3	*0·5 aq*	*2*	*2*	*10*
Shield-bugs	1	0·2 *av*	1	1	5
	0	*0 av*	*0*	*0*	*0*

*Adult form unless otherwise stated.

†Habitats: *d*, dry; *av*, average; *w*, wet; *aq*, aquatic. The habitat given for each item is the one most characteristic of the item concerned.

TABLE 3 (*Continued*)

Food Organisms				Ibis	
Name	Total Number in Each Species of Ibis	Percentage of Total Number of FoodItems	Maximum Number in One Bird	Number that Fed on Each Organism	Percentage of Total Sample
(*a*) Ibis Breeding at Macquarie Marshes (*continued*)					
Moths (caterpillars)	102 *0*	17·2 *av* *0* *av*	75 *0*	11 *0*	55 *0*
Ants	13 *0*	2·2 *d* *0* *d*	12 *0*	2 *0*	10 *0*
Bees	1 *0*	0·2 *av* *0* *av*	1 *0*	1 *0*	5 *0*
Ground-beetles	7 *8*	1·2 *av* *1·3 av*	2 *4*	5 *4*	25 *20*
Water-beetles (adults and larvae)	40 *4*	6·7 *aq* *0·6 aq*	28 *2*	8 *3*	40 *15*
Chafer-beetles	2 *0*	0·3 *av* *0* *av*	1 *0*	2 *0*	10 *0*
Click- and tenebrio-beetles (adults and larvae)	7 *5*	1·2 *av* *0·8 av*	2 *1*	6 *5*	30 *25*
Ladybird-beetles	1 *0*	*0·2 av* *0* *av*	1 *0*	1 *0*	5 *0*
Weevils	12 *0*	2·0 *av* *0* *av*	5 *0*	4 *0*	20 *0*
Freshwater mussels	1 *0*	0·2 *aq* *0* *aq*	1 *0*	1 *0*	5 *0*
Water-snails	5 *6*	0·8 *aq* *1·0 aq*	2 *1*	3 *6*	15 *30*
Fish	1 *0*	0·2 *aq* *0* *aq*	1 *0*	1 *0*	5 *0*
Frogs	75 *12*	12·7 *aq* *1·9 aq*	38 *5*	17 *7*	85 *35*
Snakes	4 *0*	0·7 *av* *0* *av*	4 *0*	1 *0*	5 *0*
Totals: 26{26 *11*	594 *624*			20 *20*	

TABLE 3 (*Continued*)

Food Organisms				Ibis	
Name	Total Number in Each Species of Ibis	Percentage of Total Number of Food Items	Maximum Number in One Bird	Number that Fed on Each Organism	Percentage of Total Sample
(*b*) 5 Straw-necked Ibis and 11 White Ibis at Lake Bullawarra, Queensland, June 11, 1955					
Freshwater crayfish ("yabbie")	0	0 *aq*	0	0	0
Cherax albidus	*1*	*0·7 aq*	*1*	*1*	*9·1*
Freshwater crab	3	3·9 *aq*	1	3	60·0
Paratelphusa leichardti	*114*	*78·6 aq*	*27*	*10*	*90·9*
Crickets (adults and nymphs)	7	9·2 *av*	7	1	20·0
	0	*0 av*	*0*	*0*	*0*
Spur-throated locust	15	19·8 *w*	6	4	80·0
Austracris guttulosa	*10*	*6·9 w*	*6*	*4*	*36·4*
Other grasshopper	6	7·9 *d*	5	2	40·0
Zabrala sp.	*0*	*0 d*	*0*	*0*	*0*
Undeterminable grasshoppers	1	1·3 *w*	1	1	20·0
	1	*0·7 w*	*1*	*1*	*9·1*
Water-bugs	0	0 *aq*	0	0	0
	5	*3·4 aq*	*1*	*5*	*45·5*
Click- and tenebrio-beetles (adults and larvae)	2	2·6 *av*	1	2	40·0
	1	*0·7 av*	*1*	*1*	*9·1*
Water-snails	26	34·2 *aq*	23	2	40·0
	0	*0 aq*	*0*	*0*	*0*
Frogs	16	21·1 *aq*	7	3	60·0
	13	*9·0 aq*	*5*	*6*	*54·5*
Totals 10{8	76			5	
10{7	*145*			*11*	

Incidence of Feeding in Relation to Habitat

	Dry (%)	Average (%)	Wet (%)	Aquatic (%)
(*a*) Macquarie Marshes sample				
Straw-necked ibis	2·4	38·6	33·4	25·7
White ibis	0	2·6	70·3	27·0
(*b*) Lake Bullawarra sample				
Straw-necked ibis	7·9	11·8	21·1	59·2
White ibis	0	0·7	7·6	91·7

TABLE 4

COMPARISON OF STOMACH CONTENTS OF 12 SELECTED STRAW-NECKED IBIS

Food Organisms	Bird No.											
	1	2	3	4	5	6	7	8	9	10	11	12
Freshwater crayfish			12		39	6					1	10
Centipedes	12							1				
Millipedes								2	1			
Scorpions	12	3				1						
Spiders (adults and egg-sacs)	152	5		4			16	19	7		2	
Tree-crickets	38											
Crickets				1	60	1	443	59	5	26	2	
Australian plague locust				737							1	
Spur-throated locust										1	22	6
Other species	8	6		2			9				3	
Cockroaches	1	1		79							1	
Cicadas	35											
Water-bugs					2					1		1
Shield-bugs								12				
Ant-lion (larva)									1			
Moths (adults)	4	362										
Moths (caterpillars)	14	13						3	442		9	6
Fly				1								
Ants											12	
Ground-beetles	13	1		1	3	4	2		4		2	
Water-beetles (adults)					3						1	
Water-beetles (larvae)					2		1			28	4	
Click- and tenebrio-beetles: adults	2							6	1	2		
Click- and tenebrio-beetles: larvae	2											
Weevils	15			1	1		41		1		5	
Water-snails			27								2	
Frogs		1			14	1	1			1	38	1
Lizards	6											

Nos. 1 and 2. Booligal, south-western New South Wales, 16.x.52. Lachlan River and Booligal swamp not flooded; pastures average to dry.

No. 3. Macquarie Marsh, central western New South Wales, 30.xii.52. Marsh not flooded; pastures average to dry.

No. 4. Griffith, Murrumbidgee Irrigation Area, south-western New South Wales; 5.xi.53. Irrigation channels and average to dry pastures; swarms of Australian plague locust, mostly large nymphs.

Nos. 5, 6, and 7. Kerang, north-western Victoria, 30.i.54. Nesting throughout summer after flooding; pastures wet to average, and plague of crickets.

Nos. 8 and 9. Pallamallawa, near Moree, northern New South Wales, 17.viii.54. Lush clover and grass pastures.

Nos. 10, 11, and 12. Macquarie Marsh, central western New South Wales, 6.v.55. Marsh flooded, breeding in progress; wet margins with frogs and spur-throated locust abundant; dry pastures elsewhere.

In the entire sample, only 16 straw-necked ibises and no white ibises were found to have been feeding on the Australian plague locust, *Chortoicetes terminifera*. The occurrences of that insect in the stomachs are analysed in Table 6. One bird (No. 3) was taken while feeding on a locust swarm, at Griffith, New South Wales, on November 5, 1953. It contained 737 large nymphs of *C. terminifera*, two adults of the small plague grasshopper, *Austroicetes cruciata* (Sauss.), and the 87 other

TABLE 5

COMPARISON OF STOMACH CONTENTS OF SIX SELECTED WHITE IBIS

Food Organisms	Bird No.					
	1	2	3	4	5	6
Earthworms		27				
Freshwater crayfish	7			5	12	
Spiders (adults and egg-sacs)			1			3
Crickets		2				319
Mole-cricket		1				
Grasshoppers						35
Shield-bug						1
Moths (caterpillars)			195			
Bee			1			
Ground-beetles			18			1
Water-beetles (adults)	4		2			
Dung-beetle					1	
Click-beetles etc. (larvae)		6				6
Weevils			18			
Freshwater mussels			2			
Water-snails				2		
Fish				1		
Frogs	3					2
Lizard						1

Nos. 1 and 2. Griffith, Murrumbidgee Irrigation Area, south-western New South Wales, 26.ix.53. Irrigation channels and dry to average pastures.

Nos. 3 and 4. Grafton, north-east coast of New South Wales, 10.viii.54. Average pastures and river banks.

Nos. 5 and 6. Kiewa, near Albury, northern Victoria, 21.i.56. Swamp flooded and breeding ending; pastures wet to average.

items listed in Table 4. The remaining 15 straw-necked ibises contained 88 adult *C. terminifera* as follows: one had 39, one had 29, one had four, four had two each, and eight had one each. The list of other food organisms in their stomachs shows that none of the birds (except No. 3) had concentrated on *C. terminifera*, or indeed on Acrididae, but that they had taken crickets, frogs, crayfish, and other foods when abundant. When the numbers of *C. terminifera* were sparse the numbers taken were uniformly low, except in the case of ibis No. 13, which took 29 in such conditions.

IV. Feeding Behaviour

Much field observation substantiates the deduction that can be drawn from stomach-content analysis, that the straw-necked ibis uses a wider range of habitat than the white ibis, the latter much preferring aquatic or wet situations. This broad distinction applies when the two species have an equal choice of habitats ranging from aquatic to dry and all supplying a good return for hunting effort; it was well shown at the Macquarie Marshes during May 1955, when a transect from the breeding colonies in the marsh out to the dry paddocks showed a decreasing proportion of white ibis. It is also observable that, within the aquatic habitat, the white ibis often penetrates into water 10 in. or more deep when searching for food, whereas the straw-necked ibis prefers shallower water, a difference which is not fully accounted for by their relative bill-lengths.

The distribution and feeding behaviour of ibises were observed in relation to locusts, especially *Chortoicetes terminifera*, of different stages and densities. The summer of 1954–55 was expected to be one of major locust outbreaks, and the numbers and movements of ibises in the important Bogan–Macquarie outbreak area were noted from July 1954 onwards. In early July very few ibises of either species were present in the Trangie–Macquarie Marshes–Nyngan region, but considerable numbers were scattered along the coastal pastures and estuaries of south Queensland and northern New South Wales; large flocks of straw-necked ibis were seen around Moree, New South Wales, in mid August. A build-up in numbers of both species at the Macquarie Marshes had begun during August, and these birds were awaiting suitable breeding conditions; the river level was low and the marsh not flooded. In the first week of September, extensive hatchings of *C. terminifera* began over a wide area adjoining the north-western end of the Marshes, and throughout the entire Bogan–Macquarie outbreak area. As hatching continued and many large swarms of nymphs developed during September and October, straw-necked ibises (singly or in parties numbering from a few up to several hundred), occasionally joined by a few white ibises, fed upon them.

During September 10–16 the daily movements and feeding of ibises around the north-western end of the Marshes were closely observed, and the distribution and abundance of hatchings and swarms of *C. terminifera* in the area were known. The ibis flocks were quite inadequate to have any appreciable effect on locust numbers; although the birds could be seen gorging themselves on the closely packed masses of newly hatched nymphs, and also feeding successfully on older hoppers at densities of the order of 1–10 per square foot, only a small fraction of the swarms was attended by ibises and the rise in locust numbers continued unabated. The advent of this plentiful and easily accessible food supply by no means caused the birds to deviate from their earlier habits, and even straw-necked ibises continued to feed in the swamp and in dry natural pastures, often within a mile or less of paddocks containing swarms. These pastures had sparse populations of several species of grasshoppers, at densities not exceeding one adult per square foot. One of 50 straw-necked ibises feeding on such a pasture contained four *Perelytrana* sp. (a dry-habitat grasshopper), three spiders, and three weevils at 3 p.m. Two others from a flock of 15 which was watched from the time they emerged from the roost

TABLE 6

OCCURRENCE OF AUSTRALIAN PLAGUE LOCUST IN STOMACHS OF STRAW-NECKED IBIS

Bird No.	Date and Place	Stomach Contents			Ibis Sample		Feeding Conditions	
		Australian Plague Locust	Other* Acrididae	Other Main Food Organisms	Number of Ibis	Main Food of Others	Australian Plague Locust	Other Food Organisms
1	7.v.53, Griffith, N.S.W.	2 adults	*w*, 2	*av*, 79 crickets	1		Probably sparse	
2	1.xi.53, Booligal, N.S.W.	39 adults	*d*, 27	*aq*, 21 caterpillars, 8 weevils	1		Abundant	
3	5.xi.53, Griffith, N.S.W.	737 nymphs	*d*, 2	*av*, 79 cockroaches	1		Large swarms	
4	23.xii.53, Albury, N.S.W.	1 adult	*av*, 53	*av*, 68 ground-beetles	2	Grasshoppers and ground-beetles	Probably sparse	Crayfish plentiful
5	30.i.54, Kerang, Vic.	2 adults	*av*, 1	*av*, 193 crickets *aq*, 1 crayfish	11	Few grasshoppers. Many crickets. Some ground-beetles, spiders and crayfish	Present; no swarms reported	Plague of crickets
6		2 adults	*av*, 3	*av*, 275 crickets *aq*, 7 crayfish				
7		1 adult		*av*, 114 crickets *aq*, 1 crayfish				
8	4.vi.54, Griffith, N.S.W.	1 adult		*av*, 10 crickets	3	Many crickets. Few ground-beetles		
9	16.ix.54, Macquarie Marsh, N.S.W.	1 adult	*d*, 31 *av*, 20 *w*, 1	few	3	Mostly grasshoppers	Mass hatching; swarms of nymphs; few adults	Scarce; district and swamp dry

*Habitat classification: *d*, dry; *av*, average; *w*, wet; *aq*, aquatic.

TABLE 6 (*Continued*)

Bird No.	Date and Place	Stomach Contents			Ibis Sample		Feeding Conditions	
		Australian Plague Locust	Other* Acrididae	Other Main Food Organisms	Number of Ibis	Main Food of Others	Australian Plague Locust	Other Food Organisms
10	6.v.55, Macquarie Marsh, N.S.W.	1 adult	*av*, 3 *w*, 22	*d*, 12 ants *av*, few *aq*, 38 frogs	48	Many grasshoppers (mostly spur-throated locust). Many crickets. Many frogs. Some land and aquatic insects	Adults in drier paddocks; but very sparse	After floods, crayfish, frogs, and aquatic insects plentiful in marsh; spur-throated locust very abundant around marsh
11	24.v.55, Macquarie Marsh, N.S.W.	4 adults	*d*, 14 *av*, 62 *w*, 73	*av*, few *aq*, 10 frogs				
12		1 adult	*w*, 22	*av*, few *aq*, 42 frogs				
13		29 adults	*d*, 2 *av*, 34 *w*, 45	*av*, few *aq*, 10 frogs				
14	2.vi.55, Macquarie Marsh, N.S.W.	1 adult	*w*, 29	*av*, 17 spiders 257 crickets 8 cockroaches				
15	21.i.56, Kiewa, Vic.	2 adults	*av*, 77	*av*, 307 crickets 296 soil beetle larvae *aq*, 4 frogs	6	Many crickets. Some grasshoppers. Few centipedes, spiders, insects, frogs	Present; no swarms	Plague of crickets
16		1 adult	*av*, 1	*av*, 208 crickets 98 soil beetle larvae 25 insects *w*, 16 earthworms				

*Habitat classification: *d*, dry; *av*, average; *w*, wet; *aq*, aquatic.

in the swamp at 6·15 a.m. until they were shot at 8 a.m. contained 18 and 53 adult acridids respectively, and only one of these (Table 6, No. 9) was *C. terminifera*. The grasshoppers were noticeably more sluggish in the cool of the morning, and no doubt this enabled the birds to catch adults more easily, even at such low density. Despite the swarms of locusts present, there was a progressive dispersal of both species of ibis from the Macquarie Marshes, and an aerial reconnaissance on October 22 revealed white ibises scattered throughout the marsh but few straw-necked ibises there.

V. Discussion

Ibises are essentially aquatic birds, and both the white ibis and the straw-necked ibis breed, roost, and do much of their feeding in marshes. The former has been shown to be more conservative in habitat selection; consequently its food contains a high proportion of freshwater forms, the staple item being the freshwater crayfish, *Cherax albidus*, which was present in two-thirds of the 202 individuals examined. It was twice as frequent as the next most abundant food organism, crickets (Gryllidae), in the white ibis sample, and more than twice as frequent as *Cherax albidus* in the straw-necked ibis sample (Fig. 1). Half of the 162 straw-necked ibis contained ground-beetles (Carabidae), grasshoppers (Acrididae), and spiders (Araneida), while crickets and frogs were present in about 40 per cent., and caterpillars in one-third, of the sample. The greater range and frequency of food types in the straw-necked ibis, and the high proportion of the white ibis's food that consisted of crayfish (bearing in mind that these are very much larger than crickets, and assuming that the chitinous parts of each would persist in the stomach for a similar period) reflect the relative versatility of the former and specialization of the latter in habitat and food preference. This is most marked in the case of the comparable samples cited in Table 3 and Figure 2.

Proof of the extent to which the two species really compete for food, and are ecologically separated in this respect, would entail very complex and exhaustive studies, and the present data do no more than indicate the possible answer. As Lack (1946) has pointed out in a discussion on competition for food by birds of prey, communal feeding on temporary superabundant foods is not effective competition, but merely overlap; in the case of the ibises, this applies to plagues of crickets and locusts (though it is more marked in the wet-habitat *Austracris guttulosa* than in *Chortoicetes terminifera* owing to the limited use of dry ground by the white ibis) and to crayfish and frogs during the peaks of abundance that follow floods. When these foods become scarce, any differences in the food-finding skills of the two predators will be enhanced, and there are indications that these may exist, similar though the species are. Birds continue to feed when the reward is adequate, and move on when it is not; in the absence of a superabundant supply of food, the white ibis does not commonly feed on pastures where the straw-necked ibis can find enough to eat, but the white ibis's ability to catch crayfish, and perhaps burrowing crabs (Table 3(*b*)), exceeds that of the straw-necked ibis. The latter appears to be the more agile predator and to depend to a greater extent on visual, as compared with tactile, methods than the white ibis does, for in habitats used extensively by both species the straw-necked ibis obtained relatively more water-

bugs, water-beetles, and frogs while the white ibis took proportionately more of the burrowing forms such as crayfish, crabs, and earthworms.

The differences in stomach contents of individuals of the same species collected at the same time and place and sometimes from the same flock, examples of which are given in Tables 4 and 5, raise intriguing questions about the behavioural basis of food-searching, a largely unexplored field of bird research. A flock of ibises, especially in a paddock, usually feeds as a compact group and covers a good deal of ground, so that a food species would have to be very concentrated and patchy to be highly available to a few birds and not available to others. This is unlikely in the case of the spiders and insects taken, and the alternative is that some birds are biased towards particular food organisms as a result of successful experience, which could be very temporary or might even date back to their initial period of learning how to feed. Intensive field observation and collecting could throw more light on this problem, but it requires experimental investigation, and a versatile, visual predator such as the straw-necked ibis would be a suitable subject.

The difficulty of pronouncing upon "economic status" on the basis of food eaten by birds is evident, and has been stressed by Hartley (1948). In the case of the ibises the argument is not complicated by evidence for both "beneficial" and "harmful" activities. The destruction of plague locusts by the straw-necked ibis and of freshwater crayfish in irrigation channels by the white ibis are both potentially useful contributions to agriculture; the question is, how useful? It has been shown that predation pressure by ibises on early swarms of *Chortoicetes terminifera* fell far short of effective control and even of its potential at the time, and that this abundant food supply did not stimulate the breeding of ibises. Similarly, although great numbers of locusts are eaten by ibises during an extensive plague, it does not follow that these birds are important factors in the control of plagues. After the widespread plague of 1955–56, when aerial spraying north of the River Murray was carried out in an attempt to stem the tide of locusts advancing south toward Victoria, Mr. T. W. Hogan, Senior Entomologist of the Department of Agriculture, Victoria, assessed the overall effect of ibis predation as follows (personal communication):

"We saw many square miles of dense hopper swarms from which it was clear that hundreds of square miles were infested. One band was 4 miles across, and reputed to be equally wide, with a density of 50 per square foot as a fairly representative figure.

The numbers of ibis were large on a bird numbers' scale, but there would be hundreds of acres of hoppers to each bird.

In spite of their large numbers, and even assuming that they are feeding exclusively on hoppers, I do not consider that they could have any general effect (as against a localized effect) once an outbreak has taken place."

The indications are no more promising that ibises are likely to destroy sufficient numbers of plague locusts during periods of low density to prevent or even delay swarm production. In such conditions, several of which are illustrated in Table 6, the take of *Chortoicetes terminifera* is poor and is much diluted by non-economic

food organisms, some of which are always likely to be present in numbers that make *C. terminifera* far from being the only candidate for the appetite of the straw-necked ibis.

VI. Acknowledgments

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VII. References

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