Bias in Food Habits of Australian Waterfowl

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Abstract

Most food studies of Australian waterfowl have relied on gizzard analyses. This introduces bias because of differential digestion rates. Oesophageal and gizzard contents collected from feeding grey teal *Anas gibberifrons*, and pink-eared duck *Malacorhynchus membranaceus*, at two sites in south-western New South Wales were determined. Pink-eared duck ate 99·6% animal food (mainly chironomid larvae and ostracods); grey teal ate 74·2% animal food (mainly corixids and dipteran larvae) at one site but 63·9% plant food (mainly grass seeds) at the other. Both species contained higher proportions of animal material in their oesophagi than in their gizzards. Rank correlation analyses showed no significant relationships between oesophageal and gizzard contents in the two species in this study, or in other Australian and overseas waterfowl reported in the literature. It is suggested that gizzard analysis has led to overestimation of the importance of seeds in the diet of Australian waterfowl and underestimation of the importance of invertebrates. It is recommended that future food habits studies of waterfowl use oesophageal contents from feeding birds, and results from previous gizzard studies be treated with caution.

Introduction

Food habits of Australian waterfowl have been determined usually from gizzard contents. Although some workers (Frith *et al.* 1969; Goodrick 1979; Norman and Mumford 1982) were aware of biases in this method, only a few studies have considered both oesophageal and gizzard contents (Delroy 1974; Briggs 1982; Norman 1983). Consequently, most statements in general syntheses (e.g. Lack 1974; Williams 1983) about diets of Australian waterfowl rely on the older published gizzard analyses (Frith 1959; Frith *et al.* 1969; Lavery 1971). Accurate food information for waterfowl is necessary to determine habitat relationships and dietary changes accompanying different stages of their life cycles.

Gizzard analysis introduces bias because of different rates of digestion between hard and soft foods (Swanson and Bartonek 1970). Animals, particularly those lacking a hard exoskeleton, break down very rapidly, whereas hard-coated seeds are retained for much longer. Bartonek (1968; reported in Swanson and Bartonek 1970) found that all animal material fed to mallard *Anas platyrhynchos* ducklings broke down in less than 1 h, but sedge seeds remained undigested after 24 h. Similarly, Swanson and Bartonek (1970) determined that 24% of midge larvae *Chironomus* spp. ingested by juvenile blue-winged teal *Anas discors* had been digested beyond distinction after 10 min. The equivalent digestion rate was higher (100%) for microcrustaceans, and lower (0% and 2%) for sedge seeds. As a result of these and other studies (Perret 1962; Bartonek and Hickey 1969; Dirschl 1969), Swanson and Bartonek (1970) suggested that reliable dietary data for waterfowl should be obtained by using oesophageal contents taken from feeding birds and preserved rapidly.

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Table 1. Food items in oesophagi and gizzards of pink-eared duck and grey teal at two sites in western New South Wales

Tr., trace (<0·1%). All plant items are seeds unless otherwise stated. Oes., oesophagus. Gizz., gizzard. Sample size: Willandra, 12; Kinchega, 16

Food item	Pink-eared duck at Willandra				Grey teal at Willandra				Grey teal at Kinchega			
	Aggregate percentage		Percentage occurrence		Aggregate percentage		Percentage occurrence		Aggregate percentage		Percentage occurrence	
	Oes.	Gizz.	Oes.	Gizz.	Oes.	Gizz.	Oes.	Gizz.	Oes.	Gizz.	Oes.	Gizz.
Animal												
Mollusca												
Gastropoda	9·49		33·3		1·66		10·0			1·27		5·9
Crustacea												
Cladocera					Tr.		20·0					
Ostracoda	15·30	4·13	78·8	58·3		Tr.		29·4	0·44	5·19	21·4	29·4
Conchostraca	0·76		11·1									
Unidentified										Tr.		5·9
Insecta												
Ephemeroptera	Tr.		11·1									
Anisoptera									0·18		14·3	
Hemiptera												
Corixidae	8·39	1·07	44·4	41·7		Tr.		8·3	17·40	19·00	42·9	35·3
Notonectidae	1·62	0·36	22·2	8·3		4·78		8·3	8·04	0·71	28·6	17·6
Neuroptera	Tr.		11·1									
Diptera												
Tipulidae larvae									Tr.	Tr.	7·1	5·9
Simuliidae larvae									6·41	5·13	7·1	5·9
Simuliidae pupae									0·43	0·17	7·1	5·9
Culicidae larvae					6·07	0·87	50·0	33·3	7·67	5·79	7·1	17·6
Culicidae pupae					19·57	6·98	30·0	25·0				
Chironomidae larvae	48·50	29·08	78·8	91·7	1·31	0·93	30·0	16·7	9·22	8·88	42·9	41·2
Chironomidae pupae	0·51	0·31	22·2	8·3	4·98	0·14	10·0	8·3				
Chironomidae adults									0·68		14·3	
Unidentified larvae						0·12		8·3	0·34	Tr.	7·1	5·9
Unidentified adults	11·66	0·25	22·2	8·3	0·83	Tr.	10·0	8·3	6·55	1·19	14·3	11·8
Trichoptera									0·16		14·3	

Coleoptera												
Dytiscidae adults	Tr.	0·11	22·2	8·3								
Hydrophilidae larvae	1·59	23·49	33·3	66·7	Tr.		10·0		0·10	Tr.	21·4	5·9
Hydrophilidae adults		Tr.		8·3					Tr.		7·1	
Elateridae adults										1·98		5·9
Unidentified		0·16		8·3	0·19	1·06	10·0	10·0		Tr.		11·8
Unidentified eggs		0·60		8·3					0·19	0·63	35·7	23·5
Unidentified parts	0·69	1·26	33·3	16·7	0·90	Tr.	10·0	8·3	8·13	7·15	28·6	58·8
Pisces												
Carassius												
Unidentified	0·89		11·1						8·23	0·57	7·1	5·9
Plant												
Algae									0·42	2·66	7·1	11·8
Poaceae	Tr.	2·38	10·0	8·3	37·02	22·29	90·0	75·0	Tr.	0·59	7·1	23·5
Poaceae husks										Tr.		5·9
Cyperaceae		6·46		66·7	2·45	6·62	40·0	41·7	0·42		7·1	
Polygonaceae		8·14		41·7	2·36	16·03	30·0	75·0		1·29		23·5
Chenopodiaceae		2·51		8·3					5·0	4·73	7·1	23·5
Portulacaceae	0·30	0·61	10·0	33·3	4·07	19·29	20·0	23·5		Tr.		5·9
Ranunculaceae					0·97	2·52	40·0	58·3		Tr.		5·9
Fabaceae		5·66		41·7	9·72	9·70	50·0	75·0	8·54	11·88	21·4	29·4
Euphorbiaceae										Tr.		17·6
Malvaceae		1·42		8·3						0·69		11·8
Lemnaceae									0·16		11·8	
Boraginaceae		11·13		58·3	7·04	9·91	10·0	16·7		9·02		17·6
Asteraceae										Tr.		11·8
Cucurbitaceae										5·99		5·9
Unidentified												
Seed fragments										0·49		11·8
Vegetative fragments	Tr.	0·72	10·0	8·3	0·27	Tr.	10·0	16·7	12·53	5·72	71·4	58·8
Total animal	99·61	60·88	100·0	100·0	35·64	15·09	70·0	75·0	74·23	57·87	78·6	88·2
Total plant	0·34	39·03	22·2	100·0	63·90	86·42	83·3	100·0	26·91	43·43	78·6	94·1

The aims of the work reported here were: firstly, to determine food of grey teal *Anas gibberifrons* and pink-eared duck *Malacorhynchus membranaceus* by oesophageal analysis; secondly, to compare oesophageal with gizzard contents of waterfowl reported here and in previous published studies.

Study Sites and Methods

Sites

Ducks were collected from two areas in western New South Wales. Willandra National Park (33°10'S., 145°E.) is described by Hone (1983). It consists of grassland with a few scattered claypans, and is dissected by Willandra Billabong. Kinchega National Park (34°S.,142°34'E.) is described by Johnson and Bayliss (1981). It contains a mosaic of vegetation types, mainly shrublands; it is adjacent to the Darling River, and includes Menindee and Cawndilla Lakes.

Within Willandra National Park, ducks were sampled from two sites: an oxbow lagoon dominated by lignum *Muehlenbeckia cunninghamii* and black box *Eucalyptus largiflorens* with submerged *Vallisneria spiralis* and *Potamogeton* spp.; and an overflow area of flooded grassland *Avena* spp., *Medicago* spp., *Rumex* spp. and other grasses and herbs. Both sites were recently inundated at the time of the study.

At Kinchega National Park ducks were collected from several sites around Lake Menindee, usually flooded claypans dominated by river red gum *Eucalyptus camaldulensis* or black box *E. largiflorens*. Submerged vegetation was not present. One grey teal was collected from Lake Merrimajeel (35°51'S.,144°50'E.) which is described briefly by Maher and Carpenter (1984).

Methods

Ducks were observed feeding usually for at least 5 min before being shot. Oesophagus and proventriculus (together) and gizzard contents were separately washed into 70% alcohol immediately following retrieval. Any food in the mouth was included with the oesophagus contents. Only a few, intact food items were ever present in mouths, indicating that regurgitation had not occurred. The ducks were aged and sexed by methods described by Braithwaite and Norman (1974), and checked for gonad enlargement indicative of breeding activity. Most of the birds were collected between 0600 h and 0900 h. Grey teal and pink-eared duck were obtained from Willandra in November 1978, and grey teal from Kinchega in December 1978. A grey teal collected from Lake Merrimajeel in January 1978 was included with the Kinchega samples. The collecting sites were not sampled to determine food availability.

Food items were counted with the aid of a 20× binocular microscope, then dried at 65°C, and weighed with a Cahn 21 Automatic Electrobalance. The food analysis data were expressed as aggregate percentage of dry weight and percentage occurrence, following the recommendations of Sugden (1973), Swanson *et al.* (1974*a*) and Reinecke and Owen (1980). Food habits are reported by site and species, but not by age, sex or breeding condition because samples were small. Oesophageal or gizzard food samples of total weight less than 0·5 g were excluded from the aggregate percentage analysis.

Gizzard and oesophageal contents were compared by Spearman rank correlation analysis (Zar 1974). Food items which constituted less than 1% of both gizzard and oesophagus contents were excluded from the correlation analyses.

Results

Food Habits

Foods of both species from the study sites are shown in Table 1. The pink-eared duck from Willandra (all from the oxbow lagoon) comprised two juvenile males, one juvenile female, two non-breeding adult males, two breeding adult males, four non-breeding adult females, and one breeding adult female. Pink-eared duck ate 99·6% animal food, mainly chironomid larvae (48·5%), with some ostracods (15·3%), gastropods (9·5%) and unidentified adult dipterans (11·7%). The only plant foods in their oesophagi were a few Portulacaceae seeds (0·3%), and minute amounts of grass seed and unidentified vegetative material.

The grey teal from Willandra consisted of six breeding adult males (four from the overflow, two from the oxbow lagoon), five breeding adult females (four overflow, one oxbow lagoon) and one non-breeding adult female (overflow). These ducks ate a majority of plant food (63·9%), consisting mostly of Poaceae (37·0%) with some Fabaceae (9·7%) and Boraginaceae (7·0%) seeds. Their animal foods were mainly mosquito larvae and pupae (25·6%).

The grey teal from Kinchega consisted of non-breeding adults (seven males, seven females), and one duckling. One unsexed adult came from Lake Merrimajeel. Their diet was 74·2% animal matter, largely corixids (17·4%), notonectids (8·0%), and simulid (6·4%), mosquito (7·7%) and chironomid (9·2%) larvae, plus other insects including unidentified adult dipterans (6·6%). Plant food consisted mainly of Chenopodiaceae (5·0%) and Fabaceae (8·5%) seeds, and unidentified vegetative fragments (12·5%).

Table 2. Percentages of animal and plant material in oesophagi and gizzards of waterfowl and rank correlation between oesophageal and gizzard contents

r_s, Spearman rank correlation coefficient

Material	Oesophagus	Gizzard	Species	Source	r_s
Animal	74·2	57·9	*Anas gibberifrons*	This study	0·325
Plant	26·9	43·4			NS, $P>0·2$
Animal	35·6	15·1	*Anas gibberifrons*	This study	0·456
Plant	63·9	86·4			NS, $P>0·2$
Animal	79·6	34·1	*Anas gibberifrons*	Briggs 1982	0·084
Plant	20·3	65·8			NS, $P>0·5$
Animal	98	94	*Anas gibberifrons*	Norman 1983	0·288
Plant	2	6			NS, $P>0·5$
Animal	87	90	*Anas castanea*	Norman 1983	0·212
Plant	13	10			NS, $P>0·5$
Animal	99·6	39·0	*Malacorhynchus*	This study	−0·302
Plant	0·3	60·9	*membranaceus*		NS, $P>0·2$
Animal	88·7	56·9	*Malacorhynchus*	Briggs 1982	−0·027
Plant	10·5	42·9	*membranaceus*		NS, $P>0·5$
Animal	65·8	17·4	*Stictonetta*	Briggs 1982	0·536
Plant	34·4	82·4	*naevosa*		NS, $P>0·2$
Animal	98·3	21·5	*Anas discors*	Swanson and Meyer	0·243
Plant	1·7	78·5		1973	NS, $P>0·5$
Animal	91·2	32·1	*Anas discors*	Swanson and Bartonek	
Plant	8·8	67·9		1970[A]	
Animal	80·9	28·2	*Anas discors*	Swanson and Bartonek	
Plant	19·1	71·8		1970[A]	
Animal	98·5	86·5	*Aythya affinis*	Bartonek and Hickey	0·508
Plant	1·5	13·5		1969[B]	NS, $P>0·1$

[A] t-test for difference between percentage of animal food in gizzard and oesophagus, both $P<0·001$.
[B] Comparison between gizzard contents, and gizzard plus oesophagus combined.

Oesophageal v. *Gizzard Analysis*

Pink-eared duck showed extreme differences between their oesophageal and gizzard contents (Tables 1, 2). The differences in grey teal were less marked but still obvious (Tables 1, 2). Generally the most notable difference was the much greater proportion of seeds in the gizzards than in the oesophagi of both species. A specific exception was the higher percentage of grass seeds in oesophagi of grey teal from Willandra.

Other studies of waterfowl have also shown differences between oesophageal and gizzard contents. Table 2 compares the percentages of plant and animal material in gizzards and oesophagi of waterfowl reported in the literature, by rank correlation. Except for chestnut teal *Anas castanea* (Norman 1983), all the species had higher proportions of animal material and lower proportions of plant material in their oesophagi than in their gizzards. The grey and chestnut teal studied by Norman (1983) were feeding on saline mud flats where seeds were not present.

There were no significant correlations (Spearman rank correlation, $P > 0·1$) between oesophageal and gizzard contents in the comparative studies listed in Table 2. The rank correlation coefficients were calculated according to the taxonomic categories provided by the authors and hence reflect a variety of taxonomic dissimilarities. Food items in oesophagi and gizzards in grey teal and in chestnut teal in Norman's (1983) study thus were not correlated, even though animal items predominated in both organs.

Discussion

The proportions of plant and animal food in the gizzards of pink-eared duck were similar to those reported by Frith *et al.* (1969), but their oesophagi contained almost 100% animal food. Pink-eared duck in this study fed on similar foods as in north-western New South Wales (Briggs 1982), mainly crustaceans and chironomid larvae. Chironomid larvae predominated in their diet at Willandra, suggesting that their value to this anatid has been underestimated previously. The pink-eared duck is clearly an invertebrate feeder, with a diet composed mainly of zooplankton, chironomid larvae and small hemipterans (see also Frith 1959; Briggs 1982).

The percentages of animal and plant food consumed by grey teal varied considerably between the study sites, supporting the earlier findings of Frith (1959) and Frith *et al.* (1969) that the species is an adaptable feeder. Grey teal will apparently feed intensively on abundant foods such as grass seeds. But this duck takes more animal food than gizzard studies have suggested, and dipteran larvae and pupae and hemipterans are major food items. Mosquito larvae and pupae were relatively abundant in the grey teal oesophagi, suggesting that they may be important in waterfowl diets (see also Swanson *et al.* 1974*b*; Reinecke and Owen 1980).

The results reported here and those from other studies summarized in Table 2 suggest that the proportion of seeds in the diets of Australian waterfowl has been overestimated, and the proportion of invertebrates considerably underestimated, by studies of gizzards alone. This bias results from the relative digestibility of different prey items. Most seeds, particularly those from the families Cyperaceae and Polygonaceae, are hard and resist digestion whereas many invertebrates break down rapidly (Swanson and Bartonek 1970). Hard parts of insects, such as chironomid head capsules, can also resist digestion for some time but these are small and may not be obvious in gizzards. The hard parts of insects fed to blue-winged teal *Anas discors* could not be distinguished in their gizzards (Swanson and Bartonek 1970). Regardless of whether hard parts are digested or just not distinguishable in waterfowl gizzards, they are not enumerated and so bias results.

Some seeds, for example, those of Poaceae and water lily *Nymphaea* spp. (family Nymphaeaceae) are relatively soft, and like invertebrates have also been underestimated in studies of food habits using gizzards (Goodrick 1979). Delroy (1974) showed that seeds of widgeon grass *Ruppia spiralis* predominated in gizzards of chestnut teal and Australian shelduck *Tadorna tadornoides* on the Coorong in South Australia, whereas tubers of muskgrass *Lamprothammium papulosum* predominated in their oesophagi.

The time of day when birds are sampled is not usually stated in reports of dietary studies. This could affect foods in oesophagi and gizzards if birds showed diurnal feeding changes. But all field and experimental studies of waterfowl feeding on mixed diets have found that hard seeds are overestimated and soft-bodied invertebrates are underestimated in gizzards (Bartonek and Hickey 1969; Swanson and Bartonek 1970; Swanson and Meyer 1973; Danell and Sjöberg 1980; Briggs 1982). It is unlikely that time of sampling is responsible for such widespread bias over this number of studies and range of species.

Composition of the diet may influence the disparity between oesophageal and gizzard contents. Swanson and Bartonek (1970) and Danell and Sjöberg (1980) noted that hard seeds in the gizzard abrade soft foods consumed concurrently; hence the proportion of soft food in the gizzard partly depends on the amount of hard food present. Oesophageal and gizzard contents from grey and chestnut teal sampled by Norman (1983) contained similarly high percentages of animal material and no seeds. These ducks were shot after they had been feeding intensively on what was presumably an abundant invertebrate food resource. Although their oesophageal and gizzard foods were not correlated ($P > 0 \cdot 5$, Spearman rank correlation), both contained similar proportions of the most abundant invertebrate, a species of mollusc.

Several Australian authors have commented on the lack of food in oesophagi from sampled waterfowl (Lavery 1971; Goodrick 1979; Norman and Mumford 1982). This problem can be avoided by sampling feeding birds. Swanson and Meyer (1973) found differences in oesophageal contents between resting and feeding blue-winged teal. Resting ducks had no food in their oesophagi, and seeds and shell fragments in their gizzards, whereas feeding birds had mainly animal food in their oesophagi and plant material in their gizzards. Swanson and Bartonek (1970) noted that the magnitude of the bias associated with gizzard sampling increased with time between feeding and sampling. In addition, oesophageal samples that are not immediately removed and preserved in alcohol are subject to post-mortem digestion (Dillery 1965; Swanson and Bartonek 1970).

There is considerable evidence from this and other studies (Bartonek and Hickey 1969; Krapu 1974; Swanson *et al.* 1974*b*; Serie and Swanson 1976; Woodall 1979; Connelly and Chesemore 1980; Danell and Sjöberg 1980) that chironomids form a high proportion of the diet in many waterfowl. Bengston (1971) showed that clutch sizes in four species of diving duck were significantly lower in a year when chironomid larvae were scarce. Chironomid biomass and productivity were high in recently flooded wetlands to the south of Willandra National Park (Maher and Carpenter 1984). These authors suggest that chironomids, particularly of one species *Chironomus tepperi*, may be important in the nutrition of breeding waterfowl. This has been found elsewhere (Bengston 1971; Swanson *et al.* 1979).

The results of this study illustrate the biases introduced by gizzard analysis and support the previous findings of Swanson and Bartonek (1970) and authors cited therein. All food studies in North America (e.g. Drobney and Frederickson 1979; Reinecke and Owen 1980) and elsewhere (e.g. Geldenhuys 1977; Danell and Sjöberg 1980) now use oesophageal contents from feeding birds. It would be desirable to routinely follow this practice in Australia. There is little point in broad-scale sampling of ducks to determine their diets. Rather, a few birds should be sampled after they have been observed feeding. Behavioural observations can be combined with oesophageal analysis in food habits investigations. Until such studies are undertaken, data from gizzard analyses should be used with care.

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