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The diets of the White-headed Duck *Oxyura leucocephala*, Ruddy Duck *O. jamaicensis* and their hybrids from Spain

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We studied the gut contents of 17 White-headed Ducks, 25 North American Ruddy Ducks and 26 hybrids between the two species collected from 14 Spanish wetlands. This is the most detailed study to date of Oxyura *diet in the Palearctic region. Food items from at least 27 families of invertebrates and at least ten families of aquatic plants were identified. The method of collection of ducks and rapid digestion of soft-bodied invertebrates may have overestimated the importance of plant matter. However, animal foods were more important, constituting 73% of aggregate volume of gullet contents. In both duck species and their hybrids, benthic chironomid larvae and pupae were the most important food item, present in 69% of gullets and 75% of gizzards, and constituting 35% of aggregate volume and 26% of aggregate percentage in gullets. Angiosperm seeds were the next most important dietary component, and crustaceans (mainly Amphipoda, Cladocera and Isopoda) and green plant material were of secondary importance. No significant differences in diet were detected between duck species, sex or age classes. Birds sampled in the breeding season had more nematodes, but these may have been parasitic. Chironomids were less abundant in Ruddy Ducks collected from northern Spain outside of the range of the White-headed Duck.*

The White-headed Duck *Oxyura leucocephala* is the only stifftail (Oxyurini) native to the Palearctic. It is a globally threatened species with a fragmented distribution and a declining world population.[1,2] In Spain, numbers increased from 22 birds in 1977 to 1453 in 1999 in response to conservation measures.[3,4] The most important threat to the Spanish population is the spread of the North American Ruddy Duck *O. jamaicensis jamaicensis* introduced to northern Europe and now expanding into the range of its congener.[1,5] In Spain, Ruddy Ducks produce fertile hybrids with the White-headed Ducks and both Ruddy Ducks and hybrids are shot by governmental conservation organizations to counter genetic integration.[5–7]

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Here, we analyse the stomach contents of White-headed Duck, Ruddy Duck and their hybrids shot or found dead in Spain. We present the most detailed study to date of *Oxyura* diet in the Palearctic region, and look for variation in diet with sex, age, season or geographical region.

MATERIAL AND METHODS

We studied 25 Ruddy Ducks and 26 hybrids shot during a control programme organized by the Spanish regional and national government administrations[7] at 14 wetlands across Spain at different times of the year, from 14 March 1992 to 17 February 1998 (Figs 1 & 2). Similarly, 17 White-headed Ducks were collected between 19 November 1985 and 28 July 1998 (Figs 1 & 2), 16 of them after 12 March 1992. Six birds were shot incidentally during a Ruddy

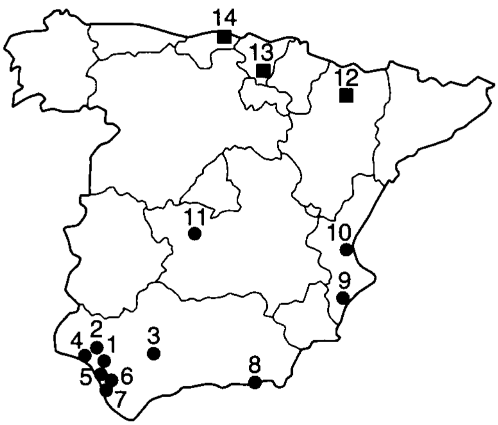

Figure 1. Location of autonomous communities and wetlands where stifftails were collected in Spain. Wetlands 1–11 marked with circles are within the range of the White-headed Duck. Numbers of birds (L, White-headed Duck; J, Ruddy Duck; H, hybrid) collected at each wetland are as follows. Andalucía: 1, Veta la Palma, Isla Mayor, Sevilla, H (6), J (1); 2, Lucio del Cangrejo Grande, Parque Natural de Doñana, Sevilla, J (1); 3, Lagunas de La Lantejuela, Sevilla, L (2); 4, Marismas de El Rocío, Huelva, L (1); 5, Laguna de Tarelo, Sanlúcar de Barrameda, Cádiz, H (3), J (2); 6, Laguna de Medina, Jerez de la Frontera, Cádiz, J (1); 7, Lagunas de Puerto Real, Cádiz, J (1); 8, Parque Natural Punta Entinas-Sabinar and nearby, Almería, J (1). Valencia: 9, El Hondo, Elche, Alicante, J (8), H (12), L (12); 10, Cullera, Valencia, L (1). Castillala Mancha: 11, Dehesa de Monreal, Huerta de Valdecarábanos, Toledo, H (1). Aragón: 12, Laguna de Sariñera, Sariñera, Huesca, J (1). País Vasco: 13, Ullibarri-Gamboa, Álava, J (7). Cantabria: 14, Marisma de Santoña, J (1).

Duck control programme. Two individuals were shot illegally and confiscated, whilst another nine were found dead (from lead poisoning, *Salmonella* or botulism).

Treatment of birds varied considerably in this heterogeneous sample, involving many organizations and people. Most were frozen shortly after collection, then sent to the Doñana National Park or Doñana Biological Station for necropsy. Birds were sexed and aged (adults or juveniles) based on plumage characteristics, gonad inspection and presence or absence of the bursa of Fabricius. We analysed separately the gullet (oesophagus plus proventiculus) and gizzard, which were stored in 50% alcohol after thawing. Unfortunately, for many individuals, the contents of the oesophagus and proventiculus were either discarded or mixed together before we could analyse them. Foods were sorted and identified to the lowest possible taxonomic level using keys.[8–18]

Volumetric measurement of individual food items in the gullet was expressed as the mean of volumetric percentages (aggregate percent) and percentage of total volume (aggregate volume).[19] The percent occurrence (i.e. the percentage of individual ducks in which each food item was recorded) was calculated separately for gullet and gizzard samples. We also calculated an Index of Relative Importance (IRI).[a]

The percent occurrence of different food items in the gizzard was compared between categories of stifftail using χ^2 and Fisher's exact tests (the latter when expected values fell below five in 2×2 contingency tests). Birds collected

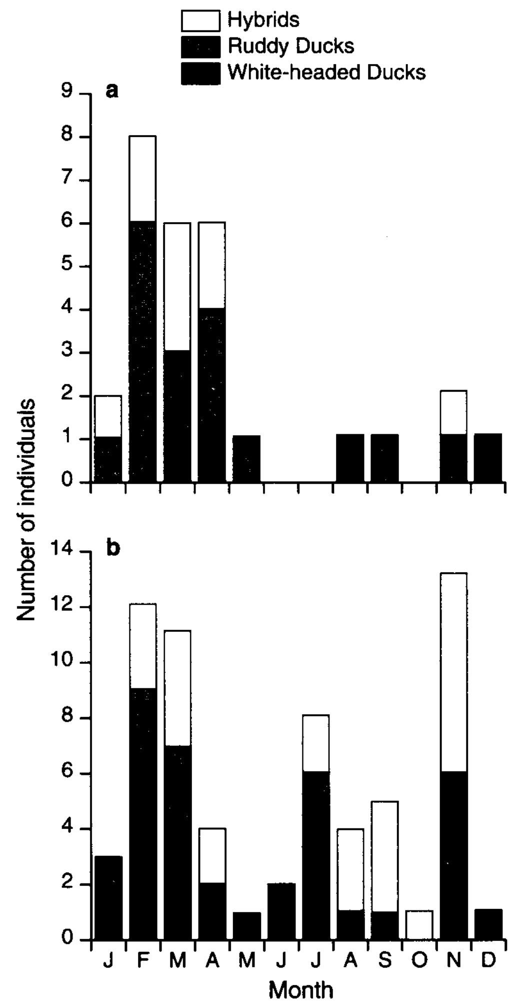

Figure 2. Number of (a) gullet and (b) gizzard samples for each stifftail taxon collected in different months.

in the breeding season (considered as April to September inclusive) were compared with those from the non-breeding season (October to March). Ruddy Ducks collected in northern parts of Spain outside the range of the White-headed Duck (Fig. 1)[3,20] were compared with Ruddy Ducks and hybrids collected further south.

RESULTS

The animal food items identified in the stifftail gullets and gizzards represented a broad range of aquatic invertebrates from at least 27 families (Appendix 1). Seeds were identified from ten families of aquatic plants (Appendix 1). Large numbers of seeds could not be identified, and most of these were from terrestrial plants.

Although food items in the gullet were more intact and easier to identify, a broader range of invertebrates were identified in the gizzards, due to larger sample size (Table 1). There were no significant differences between stifftail taxa

Table 1. Percentage occurrence of different food items in the gullet (A) and gizzard (B) of stifftails in Spain.

	All combined		White-headed Duck		Ruddy Duck		Hybrids	
	A (29)	B (68)	A (6)	B (17)	A (15)	B (25)	A (8)	B (26)
Plant	82.76	98.53	100	94.12	73.33	100	87.5	100
Angiosperm seeds	75.86	97.06	83.33	94.12	66.67	96	87.5	100
Charophyta (oospores)	10.34	16.18	–	–	13.33	16	12.5	26.92
Green plant material	48.28	79.41	66.67	76.47	40	80	50	80.77
Animal[1]	96.55	94.12	100	76.47	100	100	87.5	100
Bryozoa	10.34	7.35	–	–	13.33	16	12.5	3.85
Nematoda	–	11.76	–	35.29	–	4	–	3.85
Polychaeta	3.45	10.29	–	–	–	8	12.5	19.23
Oligochaeta	3.45	1.47	–	–	–	4	12.5	–
Achaeta	–	2.94	–	–	–	4	–	3.85
Mollusca								
Gastropoda	10.34	22.06	–	11.76	6.67	20	25	30.77
Bivalvia	–	14.71	–	–	–	20	–	19.23
Crustacea								
Ostracoda	27.59	11.76	16.67	5.88	26.67	16	37.5	11.54
Cladocera	17.24	30.88	–	17.65	20	32	25	38.46
Copepoda	–	1.47	–	–	–	–	–	3.85
Decapoda	13.79	2.94	–	–	26.67	–	–	7.69
Isopoda	6.9	1.47	–	–	6.67	4	12.5	–
Amphipoda	6.9	10.29	–	5.88	–	12	25	11.54
Unidentified	–	8.82	–	5.88	–	12	–	7.69
Arachnida								
Acarina	–	1.47	–	–	–	–	–	3.85
Insecta								
Odonata	3.45	13.24	–	5.88	6.67	20	–	11.54
Corixidae	10.34	17.65	–	11.76	13.33	32	12.5	7.69
Aphididae	3.45	–	–	–	6.67	–	–	–
Ceratopogonidae	–	10.29	–	5.88	–	16	–	7.69
Chironomidae, larvae	65.52	72.06	66.67	58.82	73.33	68	50	84.62
Chironomidae, pupae	37.93	47.06	16.67	35.29	40	48	50	53.85
Other Diptera	3.45	7.35	–	–	6.67	8	–	11.54
Formicidae	3.45	4.41	–	5.88	6.67	4	–	3.85
Coleoptera	17.24	42.65	–	41.18	26.67	48	12.5	38.46
Unidentified insects	51.72	57.35	50	52.94	60	72	37.5	46.15
Unident. invertebrates	3.45	17.65	–	23.53	6.67	16	–	15.38

Values in parentheses = *n*
[1] Excludes nematodes since they may not be food items, see text.

in the percent occurrences of food categories in the gizzards (Table 1). However, a lower diversity of invertebrates was recorded in White-headed Ducks (Table 1). There were no significant differences in percent occurrence between males (n = 44) and females (n = 15) or adults (n = 33) and immatures (n = 22). The only significant difference between samples from the breeding (n = 24) and non-breeding (n = 42) seasons was that nematodes were absent in the non-breeding season but present in 29% of gizzards in the breeding season (Fisher's exact test: $P < 0.001$). Chironomids were recorded from 33% of gizzards in Ruddy Ducks from northern areas (n = 9), compared with 88% of Ruddy Ducks or hybrids from the south (n = 42, Fisher's exact test: $P = 0.0016$). The complete absence of charophyte oospores, Odonata, amphipods and polychaetes from northern samples was noteworthy, although not statistically significant.

In general, the aggregate percents and aggregate volumes of different foods recorded in gullets were similar between stifftail taxa, with Chironomidae and angiosperm seeds the most important components, together with amphipods amongst hybrids (Table 2). This greater importance of amphipods in hybrid gullets was probably due to sampling bias since, in the larger number of gizzards, the percent occurrence of amphipods was similar between stifftail species (Table 1).

The different biases inherent in each volumetric measure (see Discussion) were reflected in marked differences between them (Table 2). For example, angiosperm seeds were 12.5 times more important than amphipods for all stifftails combined by aggregate percent, whereas

Table 2. Volumetric measurements of different food items in the gullets of Spanish stifftails.

	All combined (29)		White-headed Duck (6)		Ruddy Duck (15)		Hybrids (8)	
	A	B	A	B	A	B	A	B
Plant	52.48	27.45	70.29	46.66	44.07	35.25	54.89	14.18
Angiosperm seeds	40.88	9.39	37.12	41.62	36.43	7.25	52.05	9.09
Charophyta (oospores)	2.69	15.42	–	–	5.13	27.22	0.12	0.01
Green plant material	8.91	2.64	33.17	5.04	2.51	0.78	2.72	5.08
Animal	47.52	72.56	29.71	53.34	55.93	64.75	45.11	85.82
Bryozoa	0.33	0.04	–	–	0.15	0.06	0.89	0.01
Polychaeta	0.02	0.05	–	–	–	–	0.08	0.12
Oligochaeta	0.01	0.05	–	–	–	–	0.02	0.12
Mollusca								
Gastropoda	0.04	0.33	–	–	0.01	0.05	0.14	0.77
Crustacea								
Ostracoda	0.51	0.2	0.52	0.12	0.1	0.15	1.28	0.27
Cladocera	3.84	0.93	–	–	2.97	1.55	8.36	0.15
Decapoda	0.43	0.63	–	–	0.83	1.11	–	–
Isopoda	3.28	7.55	–	–	6.28	12.82	0.12	0.74
Amphipoda	3.26	24.57	–	–	–	–	11.82	62.6
Insecta								
Odonata	0.22	1.28	–	–	0.42	2.25	–	–
Corixidae	0.73	0.25	–	–	0.88	0.37	0.99	0.1
Aphididae	0.03	0.04	–	–	0.06	0.07	–	–
Chironomidae, larvae	22.91	32.15	18.39	49.47	33.01	42.26	7.36	15.74
Chironomidae, pupae	2.91	3.27	4.69	2.34	1.71	2.13	3.82	5.01
Other Diptera	0.01	0.05	–	–	0.02	0.09	–	–
Formicidae	0.01	0.04	–	–	0.01	0.07	–	–
Coleoptera	4.01	0.63	–	–	7.4	1.1	0.66	0.01
Unidentified insects	4.95	0.36	6.1	1.41	2.03	0.42	9.57	0.17
Unident. invertebrates	0.02	0.14	–	–	0.05	0.26	–	–

Values in parentheses = n. A, Mean of volumetric percentages (aggregate percent); B, percentage of total volume (aggregate volume). The importance of soft-bodied invertebrates is underestimated in these data (see text).

Table 3. Index of Relative Importance (IRI) values for major foods for stifftails in Spain, calculated for gullet samples.[a]

Food	IRI
Chironomidae	4223
Angiosperm seeds	3813
Green plant material	558
Unidentified invertebrates	275
Amphipoda	192
Charophyte oospores	187
Cladocera	82
Coleoptera	80
Isopoda	75

amphipods were 2.6 times more important than seeds by aggregate volume. Animal matter constituted 73% of aggregate volume, but only 48% of aggregate percent (Table 2). The IRI values show that the Chironomidae were the most important component of stifftail diet in Spain, followed by seeds (Table 3). Both components were more than six times as important as other food items, although plant material and crustaceans were of secondary importance (Table 3).

DISCUSSION

In its native North America, benthic chironomid larvae are the most important food of the Ruddy Duck in both sexes and at all times of the year.[21-24] One study in California found Corixidae to be the most important food in early and mid-winter.[25] Plant food usually constituted less than 20% of aggregate percent in these studies. Benthic chironomids are also the major component of Ruddy Duck diet within the naturalized population in the UK (B. Hughes *et al.* unpubl. data).

This paper provides the most detailed study to date of the diet of White-headed Ducks. In Spain, only three individuals have been studied previously,[26,27] in which chironomid larvae and *Potamogeton* seeds were the most abundant items. There are no quantitative data from other parts of the range,[28,29] although White-headed Ducks were largely dependent on benthic chironomids at their main wintering site in Turkey[30] and on polychaete worms at one wintering site in Greece (authors' unpubl. data).

There are no previous reports of the diet of White-headed Duck/Ruddy Duck hybrids. With the exception of those collected from wetlands in northern Spain (Fig. 1), feeding Ruddy Ducks and hybrids intermixed and fed together with much larger numbers of White-headed Ducks. No differences in feeding behaviour have been reported, and our results support the view that there is little difference in foraging strategies between the three taxa. Thus, whilst it is not appropriate to collect the globally threatened White-headed Duck, Ruddy Ducks and hybrids shot as a conservation measure can be a useful indicator of food selection by White-headed Ducks at the same wetland.

Studies of diet in Anatidae are subject to many different biases, e.g. differential digestion of soft-bodied invertebrates compared to seeds and other hard components of the diet.[19,31,32] Ideal methods to reduce these biases involve the selective collection of birds seen feeding for at least 10 minutes, immediate extraction and preservation of gullet contents, and exclusive use of oesophagus contents with a minimum volume (e.g. 0.1 ml) for volumetric analyses.[24,33]

Unfortunately, our sample was not collected specifically for this analysis, feeding birds were not selected and there were delays before gut contents could be preserved. Owing to small sample sizes, a volumetric analysis was done on the combined gullet contents of 29 birds without discarding those with a small volume (59% of the gullet samples had a total volume below 0.1 ml). Consequently, the seeds and other plant material in stifftail diet were over-represented in our results, particularly in the aggregate percentages. In reality, chironomids were more dominant in the diet than suggested by the IRI values (Table 3). Owing to prior digestion, often only the relatively hard headcases of chironomids remained in our gullet samples, and the number and size of headcases suggested that the volume of chironomids ingested was at least 20% higher. Nevertheless, seeds are undoubtedly important in the diet of Spanish stifftails.

The relatively lower invertebrate diversity recorded from White-headed Ducks probably reflects the fact that most birds died from disease or were dead for some time before collection. The nine White-headed Ducks found dead had fewer taxa in their gizzards than the eight birds shot (Mann–Whitney U test: $U = 58.5$, $P < 0.04$). Our failure to detect food selection differences between sexes, ages and seasons probably reflects the limitations of our small sample size and its highly heterogeneous nature (i.e. mixing of many years, sites and processing methods). In North America, Ruddy Ducks show sex and seasonal differences in diet.[23,25]

The nematodes found in gizzards of eight birds during the breeding season may be parasites rather than prey items. Five were White-headed Ducks found dead, in four of which nematodes were the only animals present, suggesting they may have infested sick or dead birds.

Chironomids tend to dominate the benthic fauna in wetlands that undergo regular water level fluctuations and in brackish rather than in freshwater conditions.[34–36] The lower chironomid frequency in Ruddy Duck and hybrid gizzards from northern, temperate wetlands may reflect their more freshwater, permanent nature compared to the southern temporary and brackish wetlands characteristic of the Mediterranean region (Fig. 1). The difference in salinity also explains the absence of polychaetes in northern samples.

In conclusion, White-headed Ducks and exotic stifftails in Spain are highly dependent on benthic chironomids throughout the annual cycle. Benthic chironomids are relatively tolerant of eutrophication.[35] This in turn makes White-headed Ducks more tolerant of wetland eutrophication than many other waterbird species (e.g. those dependent on submerged macrophytes).[37] Despite major wetland loss and degradation in Spain in recent decades,[38] a major reduction in hunting mortality has allowed the White-headed Duck population to increase and expand across many wetlands in the southern half of Spain in recent years.[3,5] We suggest that their ability to exploit abundant chironomid resources has played an important role in enabling this expansion. However, the major dietary overlap observed between White-headed Ducks, Ruddy Ducks and their hybrids suggests that the expansion of Ruddy Ducks across the White-headed Duck range threatens the latter via competition as well as by hybridization. This reinforces the need to control the introduced populations of Ruddy Ducks in Europe.[6]

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ENDNOTE

a. IRI = PC × [AV + AP], where PC = percent occurrence, AV = aggregate volume, AP = aggregate percentage. The IRI attempts to correct for differential digestion rates and distortion of volumes by combining all three measures to identify important components of the diet.[33]

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APPENDIX

Taxonomic classification of food items recorded in stifftail guts, showing the number of individual ducks in which each item was recorded

Food item	No. of ducks
Seeds	
Polygonum spp	J(7)
Atriplex spp.	J(1), H(3)
Suaeda spp.	L(1), J(3), H(1)
Alisma spp.	J(2)
Potamogeton pectinatus	L(9), J(17), H(12)
Potamogeton pusillus	J(2), H(1)
Ruppia drepanensis	L(1), J(2), H(3)
Ruppia spp.	L(10), J(14), H(21)
Zannichellia spp.	J(1), H(1)
Scirpus spp.	L(10), J(13), H(10)
Eleocharis spp.	H(6)
Phragmites spp.	L(5), J(9), H(5)
Trifolium spp.	L(1), J(6), H(2)
Unidentified seeds	L(10), J(23), H(21)
Algae	
F. Characeae, oospores	J(6), H(7)
Green plant material	L(15), J(20), H(21)
Invertebrates	
Cl. Phylactolaemata (Bryozoa)	
Plumatella repens, floatoblasts	J(4), H(2)
Cristatella mucedo, floatoblasts	J(3)
Cl. Insecta	
O. Diptera	
F. Chironomidae	
SF. Chironominae	
Tr. Chironomini	
larvae	L(6), J(11), H(12)
pupae	L(2), J(7), H(9)
Unidentified chironominae, larvae	L(1), J(8), H(4)
SF. Tanypodinae	
larvae	J(5), H(1)
pupae	J(1)
SF. Orthocladinae, larvae	J(2)
Unidentified chironomidae	
larvae	L(8), J(11), H(14)
pupae	L(4), J(12), H(10)

L, White-headed Duck; J, Ruddy Duck; H, hybrid. Cl, class; O, order; F, family; SF, subfamily; Tr, tribe.

continued

APPENDIX continued

Food item	No. of ducks
F. Ceratopogonidae	
SF. Ceratopogoninae, larvae	J(2), H(1)
Unidentified ceratopogonidae	
larvae	J(2), H(1)
pupal case	L(1), J(1)
F. Stratyomyidae	
Nemotelus spp., larvae	J(1)
F. Muscidae, pupal case	J(1), H(1)
Unidentified diptera, larvae	H(2)
O. Odonata	
F. Libellulidae, larvae	J(1)
Unidentified odonates, larvae	L(1), J(5), H(3)
O. Coleoptera	
F. Dytiscidae, adult	J(1)
F. Hydrophilidae	
Berosus spp., larvae	J(2)
Unidentified coleoptera	
larvae	J(1)
adult	L(7), J(13), H(11)
O. Hymenoptera	
F. Formicidae, adult	L(1), J(2), H(1)
O. Hemiptera	
F. Corixidae, nymph	L(2), J(8), H(2)
F. Aphididae, adult	J(1)
Unidentified insects	
adult	L(10), J(20), H(11)
larvae	J(7), H(3)
Cl. Crustacea	
O. Podocopa	L(2), J(6), H(4)
O. Cladocera	
Daphnia spp.	J(1), H(1)
ephippia	L(3), J(8), H(10)
Eurycercus lamellatus	J(1)
Unidentified cladocera	J(2), H(2)
O. Decapoda	J(4), H(2)
O. Amphipoda	
Echinogammarus spp.	J(2), H(2)
clutch	J(2), H(3)
Unidentified amphipods	L(1), J(1)
O. Isopoda	
Sphaeroma hookeri	J(1), H(1)
O. Cyclopoida	
Cyclops spp	H(1)
Unidentified crustacea	L(1), J(3), H(2)
Cl.Arachnida	
O. Acarina	H(1)
Cl. Annelida	
O. Polychaeta	J(2), H(5)
O. Oligochaeta	
F. Lumbricidae	J(1)
Unidentified oligochaeta	H(1)
O. Achaeta	

L, White-headed Duck; J, Ruddy Duck; H, hybrid. Cl, class; O, order; F, family; SF, subfamily; Tr, tribe.

continued

APPENDIX continued

Food item	No. of ducks
F. Hirudidae	J(1), H(1)
Phylum Nematoda	L(6), J(1), H(1)
Cl. Gastropoda	
F. Hydrobiidae	H(4)
F. Physidae	J(1)
Unidentified gastropods	L(2), J(5), H(6)
Cl. Bivalvia	J(5), H(5)
Unidentified invertebrates	L(3), J(1), H(1)
Unidentified invertebrate eggs	L(1), J(5), H(2)

L, White-headed Duck; J, Ruddy Duck; H, hybrid. Cl, class; O, order; F, family; SF, subfamily; Tr, tribe.