Ecological studies of Falkland Islands' waterfowl

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As part of a study of the waterfowl of isolated southern hemisphere islands, October 1970 to mid-January 1971 was spent on the Falkland Islands. Additional field work was done during week-long visits in early November and late December 1971. Full time was devoted to the study of the more common waterfowl on two study areas on East Falkland Island with subsequent observations at several other islands for comparison. The chief objectives of the study were (1) to relate feeding habits, territory selection and brood behaviour to available freshwater and marine habitats, and (2) to appraise diversity in relation to ecological niches. (See also Plates I, II and V.)

The Falkland Islands are located about 550 kilometres east of the tip of South America between latitude 51° and 52°S. and longitude 58° to 61°W. They are a British colony of about 2,500 people whose activity is sheep farming for wool. Ranches are large, and under 30 landholders manage the total of about 1,200,000 hectares (Cawkell *et al.* 1960). The islands tend to be gently sloping with mountains reaching a maximum of 700 metres, but the southern portion of East Falkland (Lafonia) is low and level, rarely exceeding 90 metres.

Climate is cold-temperate (Murphy 1936) with recorded extremes during 1951-1970 being −8°C. to 25°C., with an annual mean of 5.6°C. Freezing temperatures are uncommon during summer days although nocturnal lows are near freezing. Long-term mean wind velocity was 26.4 km.p.h. Annual rainfall varies from about 635 mm. on the eastern islands to less than 405 mm. on the West Falklands (Moore 1968). Data on temperature and rainfall shown in Table I indicate the general mildness of the period of this study.

As a result of the low temperatures, decomposition is very slow and soil is mostly peat. Deep peat beds are most common on the wetter East Falkland. The islands are treeless and introduced trees succeed only where protected and watered. The dominant vegetation is white-grass *Cortaderia pilosa*, with the low bush, diddle-dee *Empetrum rubrum* dominating drier sites. The tall and dense tussock grass *Poa flabellata* covers small islands and shorelines which sheep cannot reach (names from Moore (1968)).

Study areas

Two major study areas were selected primarily because of their known waterfowl use and habitat diversity, but accessibility and distance are important considerations in an area with no all-weather roads. Most observations were made at the basal portion of Cow Point, where the settlement of Fitzroy is located. The Stanley Commons and Stanley Harbour formed a check area that had the same habitat diversity and exposures, but waterfowl there were more disturbed by human activities.

Additional observations were made at Seal Point, south-west of Stanley; at Kidney Island, north-east of Stanley; at Port San Carlos on the northern extreme of East Falkland; at Fox Bay East on the south-east corner of West Falkland; and at West Point Island.

Methods

Five species were selected for study whose abundance reflected successful adaptation to the area and permitted collection without harming populations,

Table I. Standard climatic measurements at Stanley, East Falkland.
(Data from Daniel Borland of the Falkland Island Meteorological Station.)

	Mean temp.°C.	*Range temp.°C.*	*Rainfall in mm.*	*Nights of frost*	*Mean humidity*	*Mean wind*
1970-1971						
Oct.	5.9	1-16	32.9	7	83.4	15.8
Nov.	7.9	2-18	13.2	6	77.9	12.8
Dec.	8.5	2-22	74.6	4	80.8	15.4
Jan.	8.3	1-19	133.5	8	82.9	14.7
1970 Mean	5.8	−5-22	651.8	—	86.4	15.3

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which represented all major habitats, and provided meaningful amounts of data (Table II). Observations were made regularly on the study areas to record the positions of pairs, flocks and broods in relation to habitat. Broods were classified by standard plumage categories to assess growth in the absence of more precise age estimates. Observations were recorded on field maps and correlated with habitat descriptions of lake type, vegetation and coastal topography. Territorial behaviour and interspecific interactions were noted. Little time was devoted to searching for nests.

Major effort was devoted to recording feeding behaviour, foods and feeding sites. When collected, most waterfowl had been observed feeding intensively for at least 15 minutes. Birds were dissected immediately after collection to avoid post-mortem digestion. Contents of the oesophagus and proventriculus were more easily identified and food estimates were less influenced by the hard, residual objects that remain in the gizzard (Bartonek and Hickey 1969).

At aquatic feeding sites, bottom samples were taken with an aquatic sweep net, 12 in. wide × 3 in. high (30.5 cm. × 7.6 cm.), having 20 meshes to the inch. This allowed both surface and bottom sweeps of 12 in. × 12 in. on most substrates except large boulders. Hydrogen-ion readings were taken with a pHydrion paper; a Secchi disc was used to record turbidity; and water depths were measured at each sampling site. Vertical photographs were taken of each feeding site when water clarity permitted. Terrestrial grazing areas were sampled by collecting representative plants and taking random close-up photographs in those areas where birds were collected. Because of the frequent grazing of short growing plants, mature seedheads were obtained by excluding sheep from field sites or by taking the sod samples indoors.

Waterfowl diversity and abundance

The eleven species observed are listed in Table II. Regular breeding birds include one swan, three southern sheldgeese of the genus *Chloëphaga* and the monotypic Crested Duck *Lophonetta specularioides*, two unique diving ducks of the genus *Tachyeres* and four species of the widespread genus *Anas*. All these species occur in Patagonia and Tierra del Fuego (Olrog 1968) except the Falkland Flightless Steamer Duck *Tachyeres brachypterus*, considered endemic, although a Continental form differs mainly in colour and size (Murphy 1936). Numerous accidentals have been reported (Bennett 1926; Cawkell and Hamilton 1961).

In an effort to estimate relative abundance of species, censuses from three areas were summarized (Table II). Counting only adults, their combined numbers indicate that two herbivores, Upland (or Greater Magellan) Goose *Chloëphaga picta leucoptera* and Kelp Goose *Chloëphaga hybrida malvinarum* were commonest, followed closely by a carnivore, the Falkland Flightless Steamer Duck.

There were several conspicuous differences in populations on the three areas. Only nine species were observed at

Table II. Waterfowl observed at two census areas on East Falkland and one (Fox Bay East) on West Falkland. Number of counts in parenthesis. Br = pairs with broods; Pr = pair only; Ind = individuals and flocks. Rank is based on adults only.

	Fitzroy (8-11)			*Stanley (4-5)*			*Fox Bay (2-3)*			*Total*	*% of*	*Combined*
Species	*Br*	*Pr*	*Ind*	*Br*	*Pr*	*Ind*	*Br*	*Pr*	*Ind*	*adults*	*total*	*rank*
Black-necked Swan *Cygnus melanocoryphus*	0	0	71	0	0	0	0	0	0	71	4.8	7
Ruddy-headed Goose *Chloëphaga rubidiceps*	4	3	0	0	1	0	8	10	39	91	6.1	6
*Upland Goose *Chloëphaga picta leucoptera*	24	3	250	0	0	0	16	5	122	468	31.5	1
*Kelp Goose *Chloëphaga hybrida malvinarum*	11	2	7	0	4	12	1	51	137	294	19.8	2
*Crested Duck *Lophonetta s. specularioides*	9	4	36	0	2	0	3	6	21	105	7.1	4
*Falkland Flightless Steamer Duck *Tachyeres brachypterus*	24	6	31	1	2	27	9	9	112	272	18.3	3
Flying Steamer Duck *Tachyeres patachonicus*	3	0	0	0	1	0	1	2	0	14	0.9	11
*Chilean Teal *Anas f. flavirostris*	11	0	50	2	1	0	2	4	4	94	6.3	5
Chiloe Wigeon *Anas sibilatrix*	2	2	9	0	1	3	0	3	1	29	1.9	8
Brown Pintail *Anas georgica spinicauda*	1	0	13	0	2	4	0	0	1	24	1.6	9
Versicolor Teal *Anas versicolor fretensis*	2	2	7	1	2	1	0	0	0	22	1.5	10

* Study species

Stanley and Fox Bay, but eleven species occurred at the more diversified and less disturbed Fitzroy area. At Stanley there were no Upland Geese on the census area although three were seen nearby.

The frequency of Black-necked Swans *Cygnus melanocoryphus* at Fitzroy was biased because of a concentration on one area, whereas no concentrations of this magnitude were seen elsewhere in the Islands. The second largest group, about 40, was at Swan Inlet, East Falkland.

There was an abundance of non-breeding Kelp Geese at Fox Bay East, but observations at the tip of Cow Point, at Seal Point and elsewhere indicate that this species may very well be the most abundant anatid.

Diversity of waterfowl habitats

Upland vegetation

Natural and cultivated upland grass communities important to sheldgeese were roughly mapped. The most dominant and widespread plant species is the coarse white-grass, which varies from 15 to 30 cm. in height and forms tussocks, especially when grazed. Dry growth of previous years remains and gives a general tan colour to grasslands, even in mid-summer. Finer grasses, such as meadow-grass *Poa annua* and *P. pratensis*, pigvine *Gunnera magellanica*, sedges *Carex* spp. and native rush *Juncus scheuzeroides* often grow between the tussocks of white-grass. These smaller plants are dominants on the well-sloped drainages where light green patches, 'green valleys', are conspicuous in the general tan colour of the white-grass or the dark green heath (Davies 1939). Such swards were often on steep slopes, boggy from subsoil water, but showing little surface drainage. Drier sites, such as fence corners or gate areas intensively trampled by livestock, and abandoned rookeries of Gentoo Penguins *Pygoscelis papua* also tend to be dominated by meadow-grasses and low herbs.

Cereal grains are rarely planted, but pasture grasses such as Yorkshire fog *Holcus lanatus* are cultivated near settlements on drier soils. Roto-tilling is used to level the soil and to eliminate native species and often results in wind erosion, particularly on the drier western islands.

Freshwater habitats

Streams are common and vary from small brooks a metre or two wide to so-called rivers, small by northern hemisphere standards. Pools commonly contain native waterweed *Myriophyllum elatinoides*, rich in aquatic crustaceans attractive to certain ducks. Even small brooks may have complex meanders resulting in wide valleys. The streams are highly acid (pH 4.0-4.5) and run through and even under the deep peat where overgrown holes are dangerous to man and livestock.

Shallow bodies of fresh water are abundant in some areas. Even the large ones did not exceed one metre in depth, unless formed as barrier ponds in a steep walled drainage. Deeper ponds, however, have been reported by Vallentin (1924). Such waters are termed ponds on the Falklands even though they may exceed 400 hectares in size; the term 'lake' tends to be used for very large saline areas currently or recently connected to the sea by a narrow channel. An excellent series of government maps (Directorate of Overseas Surveys 1962) prepared from aerial photos shows the distribution of ponds of even a few hectares. The map also reflects limnological characters, the ponds being shown in light and dark blue according to the water colour that appeared on the aerial photographs. Ponds coloured dark blue on the map were peat-bottomed and had brown water, whereas light blue ponds were sand basins with clear water or clay basins with light grey water.

Ponds with peat or clay bottoms are turbid, with Secchi disc readings of 5 to 12 cm. during windy periods. Both tend to have abrupt peat banks because of wave action against the tightly bound soil. Sand-bottomed ponds with sloping shores generally are at low elevations, often near the coast, and tend to be clear. However, water turbidity varies with the nature of the soil of the banks. All ponds are acid, and 19 had pH readings between 4.0 and 5.3. Only one, sand-bottomed, pond reached pH 6.0.

The clay- and sand-bottomed ponds are richest in submergents such as native waterweed and, more rarely, the large, branched algae *Nitella* sp. Sand ponds have marginal stands of the emergent spikerush *Eleocharis melanostachys*, and Vallentin (1924) reported ponds on West Falkland with rushes *'Scirpus lacustris'*.

On both main islands there is some snow on the highlands during winter and sufficient moisture for sizeable ponds to occur in mountain valleys. Extensive peat beds form at elevations about 150 metres, where ridge peat ponds form from cracks produced by soil slippage, and enlarged by wave action and possibly wind erosion during the arid summer months. Sometimes their drainage and erosion on rock bases exposes small 'stone runs' of the type unique to the mountains of the islands, the origin of which geologists still debate (Cawkell *et al.* 1960). With their vertical shorelines, inadequate shallow feeding sites and scarcity of invertebrates, the ponds are generally unattractive to ducks.

Small oxbow ponds formed in stream valleys are excellent sites for the growth of the succulent emergent plants such as *Lilaeopsis macloviana* and *Caltha sagittata* or submergents such as native waterweed.

The Fitzroy study area had a group of over 200 small ponds in peat on the ridge north-west of the settlement. The character of the larger and richer Cow Point ponds were from west to east: Fitzroy Pond—vertical peat shore, but clay- or, rarely, sand-bottomed; North and South Twin Ponds—peat shores and bottoms; Swan Pond—sand- to clay-bottomed with mostly sloping shores and with a relatively shallow peat layer surrounding. Although Fiztroy Pond had some native waterweed, Swan Pond had extensive beds of waterweed, emergent spikerush, submerged algae *Nitella* and mud plantain *Heteranthera* sp.

The ponds on the Stanley Commons were in heavy peat beds, except for two of three barrier ponds near the sea. One of these was deep, rocky and unattractive to waterfowl. The second was shallow, sand-bottomed and rich in native waterweed and very attractive to ducks.

Marine shoreline habitats

Abrupt shores are created by the erosion of the highly angled sedimentary strata on windward shores, but more gradual slopes are characteristic of protected areas. Both the Fitzroy and Stanley study areas had cliff-like or rocky southern shores relatively unprotected from southern storms. Northern exposures of the study areas were better protected and had gentle, gravel-covered slopes. Usually on the exposed shores, but occasionally on the sloping shore, waterworn strata formed shelves exposed at low tide, ideal for marine algae attractive to certain waterfowl. In areas of low topography and soft rock strata, windward shores may be of extensive white sand of key importance to Gentoo Penguins, but are not attractive to waterfowl because of the severe surf action.

Bays resulting from erosion by small drainages or springs were usually covered with sand, fine gravel or small stones. Extensive beds of sand characterise major creeks that sometimes are wholly or partially closed by barrier ridges to form sand-bottomed ponds. Such creeks were suitable for wigeon grass *Ruppia* sp. Older barrier ponds tended to become more turbid and densely populated by native waterweed.

All marine shores, save those dropping abruptly into extremely deep water, are ringed by beds of Leafy Kelp *Macrocystis pyrifera*. In some places these beds are only a metre or two wide, but shallow bays and inter-island areas may be completely covered with the floating leaves. Kelp beds reduce wave action and are rich in snails, limpets and other potential waterfowl foods.

Waterfowl habitat utilization

Census data were classified according to major habitat types to demonstrate general species-habitat associations. On the Fitzroy study area waterfowl distribution was correlated still more specifically with habitat types. Emphasis was placed on pairs or pairs with broods because their food was the likely limiting factor in reproductive success. However, flock use of an area obviously reflected an abundance of food, and such groupings were recorded regularly.

Terrestrial habitats

Upland Geese are completely terrestrial except when flightless or with broods. During the nesting period their foods are taken from well-drained green valleys and other green grass areas created by grazing or farming. Waiting males, or pairs with broods, were isolated one per valley along the shores of lake or sea in relation to distribution of green swards. Green patches along streams and a small green island in Swan Pond were territorial and brood-rearing sites. Larger green areas, especially those some distance from water, were used by flocks of non-breeding birds (probably yearlings) during the breeding season. Pre-moulting birds moved to green areas near the sea which they could subsequently use for escape when flightless (Figure 1).

At Fox Bay East and Port San Carlos green *Poa* slopes, produced as a successional stage following an intensive, but usually single season, use of a vegetated area by Gentoo Penguins, were favoured feeding areas of Upland Geese. Areas in which Magellanic Penguins *Spheniscus magellanicus* burrowed also tended to be rich in meadow-grasses and were grazed by livestock and Upland Geese. Occasionally, Kelp Geese grazed in these areas.

Freshwater habitats

Chilean (or Speckled) Teal *Anas f. flavirostris* and Crested Duck are the major waterfowl frequenting freshwater areas. The former is the major anatid of small upland streams, favouring small pools in streams or shallow ponds rich in waterweed, and most broods were reared in such areas (Figure 2). Teal were the only species that occasionally used steep-sided bog ponds in both uplands and lowlands.

Crested Duck used large sand- or clay-bottomed lakes with gradually sloping shores rich in food. At Fitzroy, Seal Point and Stanley, these ponds were near the sea, but a large inland pond at Fox Bay East also had a pair.

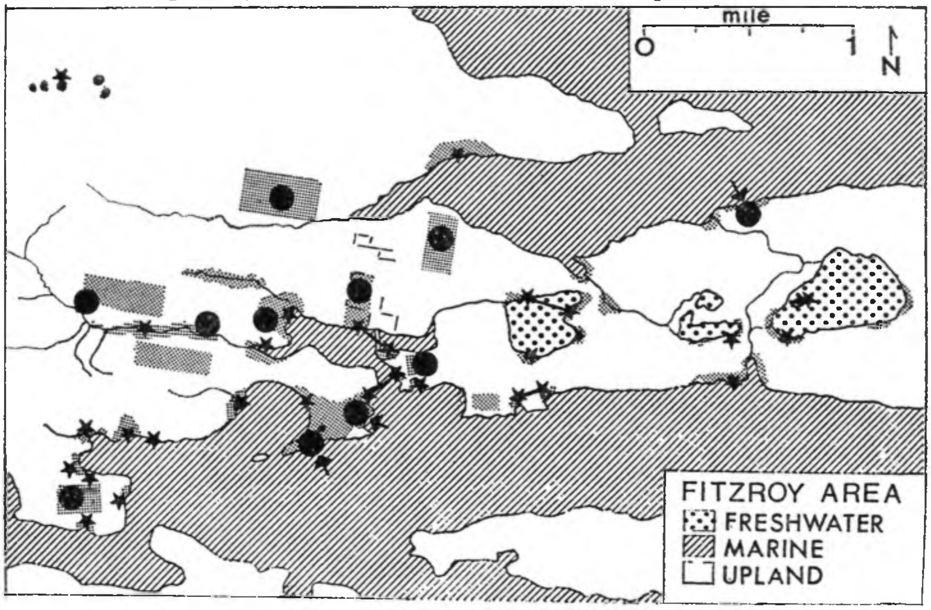

Figure 1. Distribution of broods (stars) and flocks (dots) of Upland Geese in relation to green valleys and cultivated pastures (stippled areas) at Fitzroy.

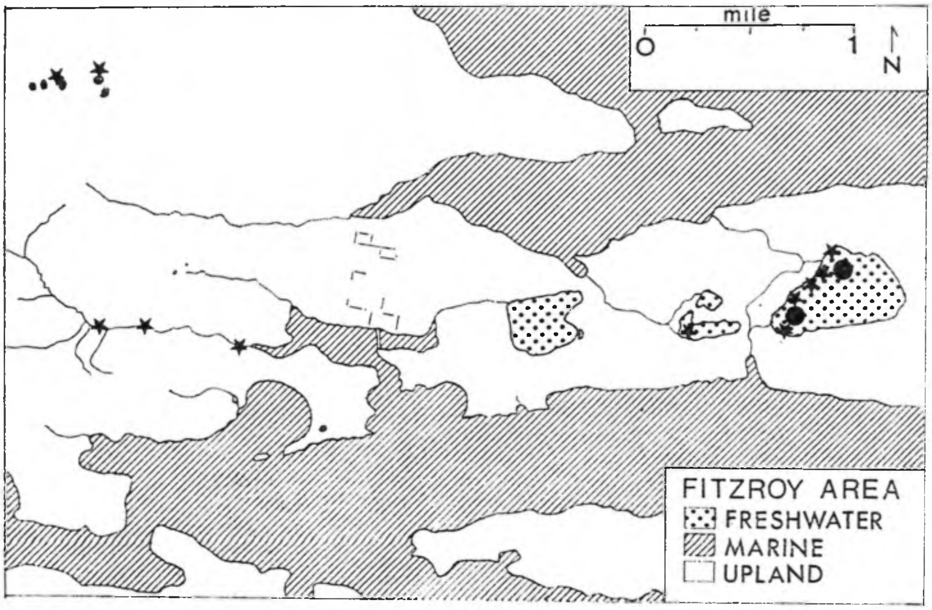

Figure 2. Distribution of broods (stars) and flocks (dots) of Chilean Teal in relation to freshwater ponds and streams at Fitzroy.

Marine habitats

Crested Ducks were the only species studied that regularly established territories and reared broods in both fresh and marine areas, but they were more abundant on the seashore. Pairs were isolated in coves and were strongly associated with gravel shores, but they often fed on algae-covered rocks at low tide. Flocks of non-breeding birds also favoured extensive gravel or silt shores not normally used by breeding pairs (Figure 3). One flock of some 45 birds used a boulder-covered shore where rotting leafy kelp had accumulated.

Falkland Flightless Steamer Ducks are strictly marine and use all types of shorelines where loafing sites occur. However, breeding pairs usually selected territories with well-sloped gravel shores (in which their very young broods fed), probably because they must walk to their nest sites. Flocks of non-breeding immatures frequented more abrupt rocky shores and cliffs. Brackish creeks dominated by silt were also used. Rarely, in storms, adults moved to freshwater barrier ponds along the southern coast.

The Kelp Goose is perhaps the most specialised marine herbivore among anatids and is rarely seen feeding on gravel areas. It frequents rocky shelves or boulders exposed at low tide where certain species of marine algae grow (Figure 4). Flocks of non-breeders feed in extensive rocky areas, but they sometimes loafed on sand or gravel areas sheltered from the wind. Pairs on territory or with broods were regularly associated with coves where there were freshwater seeps, which both adults and young used. Kelp Geese also drank from sewers in settlements as do Falkland Flightless Steamer Ducks (Pettingill 1965; Cawkell and Hamilton 1961) (Plate IIa, p. 17).

At Seal Point, across the bay to the south-east of Stanley, Kelp Geese nested in coarse grasses by freshwater lakes less than a kilometre from the sea. These nests were adjacent to meadows where Magellanic Penguins nested and where meadow-grasses and diddle-dee bushes occurred. A brood was observed on 30th December 1971 feeding on *Poa* sp. near one of these freshwater ponds, and they used the pond as escape cover.

Feeding behaviour and foods

Upland Geese

Leaf tips and seed heads were usually taken, rather than large, mature leaves and stems. There was little variation between the food of young and adults. Five of the nine young and two of the four adults contained *Poa* spp. (Table III). One young contained a small *Juncus* (probably *J. scheuzeriodes*), two contained native carrot *Oreomyrrhis andicola*, and one adult and three nearly full-grown young collected at a sedge meadow

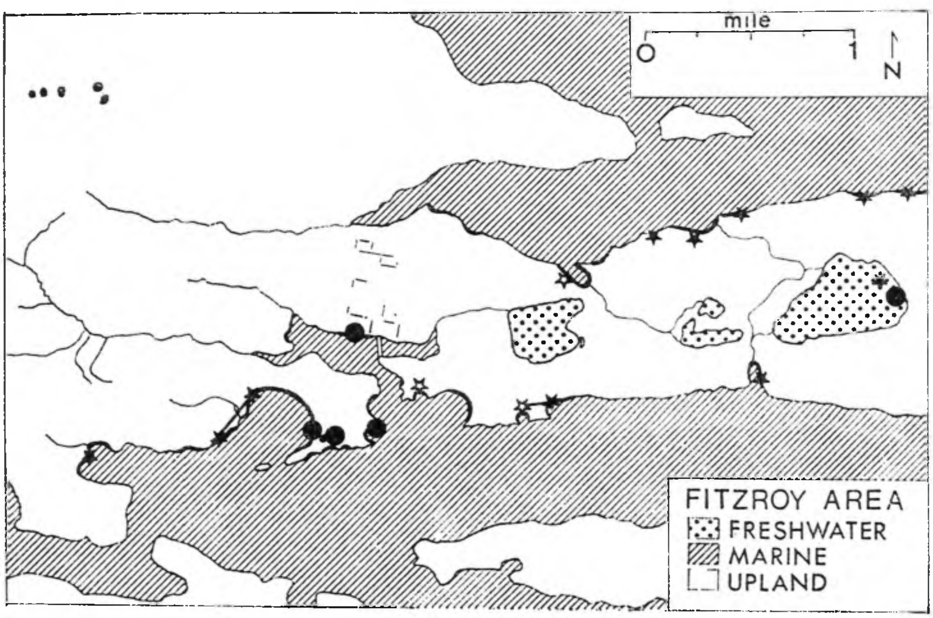

Figure 3. Distribution of broods (solid stars), pairs (white stars) and flocks (dots) of Crested Ducks in relation to gravel shorelines (heavy lines) at Fitzroy.

at Port San Carlos contained mostly tips and berries of brown swamp grass *Roskovia magellanica* and tips of *Carex* sp. Two young collected at Fitzroy contained berries of diddle-dee, and the droppings of all adults in that area showed a dominance of diddle-dee in the diet from mid-December, when the berries started to ripen, until at least mid-January. Information from residents indicates considerable use of this plant by the geese throughout the winter. No animal foods

Table III. Some summer foods of Upland Geese on the Falkland Islands.

	Young (9)		*Adults (4)*	
Food	*% Mean Volume*	*% Frequency*	*% Mean Volume*	*% Frequency*
OESOPHAGUS AND PROVENTRICULUS CONTENTS				
Meadow-grass leaves	28.0	55	46.2	50
Meadow-grass seeds and heads	1.6	44	1.8	50
White-grass leaves	.3	11		
White-grass seedheads	1.0	33		
Yorkshire Fog leaves			24.5	25
Carex sp. stems	.2	22	1.0	25
Carex sp. seedheads	5.4	33	20.0	25
Roskovia magellanica stems	30.7	44	1.5	50
Roskovia magellanica seeds and seedheads	12.1	55	4.0	25
Native Rush stems	1.1	11		
Native Rush seedheads	.3	11		
Native Carrot	7.2	22	1.5	25
Daisy leaves *Bellis perennis*	.5	22	.2	25
Unidentified plant	.1	11		
GIZZARD CONTENTS	*Young (6)*		*Adults (3)*	
Meadow-grass leaves	68.0	100	64.7	66.7
Meadow-grass seedheads	2.7	50	1.0	33.3
White-grass leaves	2.3	16.7		
Yorkshire Fog leaves			33.3	33.3
Roskovia stems	4.8	16.7	.3	33.3
Roskovia seeds and heads	4.5	16.7		
Juncus sp. stems	2.5	33.3		
Native Carrot	1.8		.3	16.7
Daisy leaves			.3	33.3
Diddle-dee seeds	1.3	16.7		

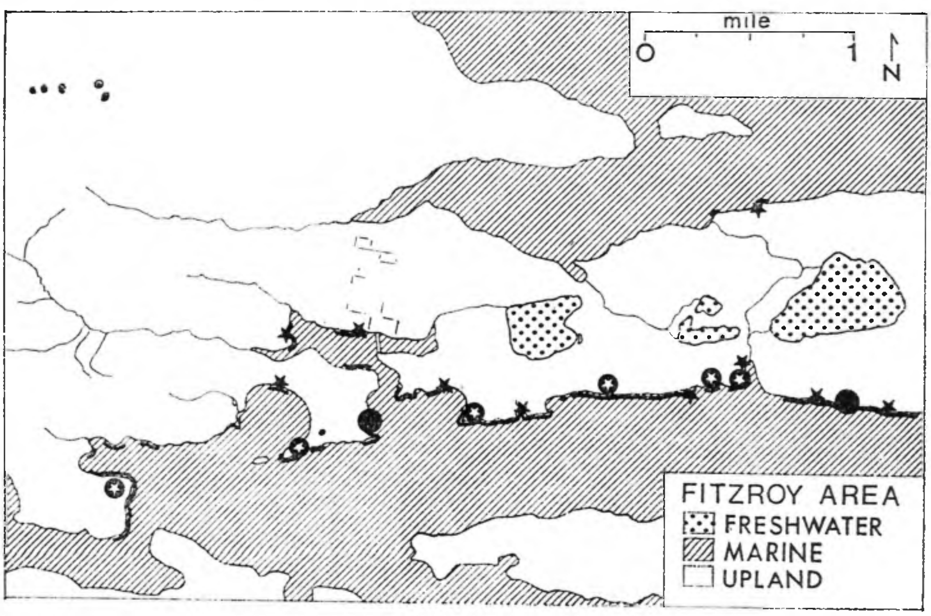

Figure 4. Distribution of broods (stars), nests (circle-stars) and flocks (dots) of Kelp Geese in relation to rock strata (heavy lines) exposed at low tide.

were found even in very young Upland Geese, nor did observations suggest any feeding on insects.

Chilean Teal

These fed on smaller prey items than any other anatid species (Table IV). One adult and several young contained mostly microscopic cladocerans of the genus *Bosmina* and some minute cyclopoid crustaceans, *Cyclops* sp. Other Teal examined regardless of age contained amphipods, midge larvae (Chironomididae), insects, fish eggs and, rarely, pigvine seeds. Broods were accompanied by the female (sometimes by the male as well) and tended to remain isolated from flocks on ponds or on streams. The attractiveness of rich sand ponds filled with native waterweed such as the largest pond, Swan Pond, at Fitzroy was very marked (Figure 2). Such areas had an abundance of bottom organisms such as midge larvae, and amphipods in the waterweed. Flocks of 40 to 45 Teal gathered at Swan Pond late in the breeding season.

This was one of few species that ever used steep-sided bog ponds. Such ponds usually lacked vegetation but bottom sampling always produced a few amphipods and midge larvae. Teal were seen diving for food in two such ponds and a brood was seen feeding by diving in a peat-rimmed, sand-bottomed pond. Two young collected in bog ponds had food contents similar to those of other areas, namely insect larvae and amphipods.

On one occasion late in the breeding season, two adult Chilean Teal were seen on a south shore of Cow Point where leafy kelp had been washed ashore and was rotting. Possibly the Teal were attracted to fly larvae therein which may be a source of food in winter. At two sites Teal were feeding at the mouths of freshwater streams where rotting kelp had been stranded. Local residents indicated that flocks of Teal gather in barrier ponds and creeks and on the seashore in winter and, because lowland ponds rarely freeze, could feed there all year.

Crested Ducks

Because of the scarcity of Crested Ducks on freshwater areas, only two were collected at Seal Point in a rich pond surrounded by burrows of Magellanic Penguins. It was one of the richest ponds sampled, with an invertebrate fauna of small crustaceans, such as cladocerans and amphipods, and insect larvae. Crested Ducks there used these items (Table V).

In general, broods of Crested Ducks were reared in marine situations and clearly favoured areas with extensive growths of green, filamentous algae. These commonly occurred at freshwater seeps in gravel beds or on rock strata exposed at low tide.

Both adults and young of all ages selected marine isopods and amphipods, invertebrate larvae and minute clams (Table V), dabbling with the bill barely submerged. Both adults and young often came ashore to feed in pools a centimetre

Table IV. Some summer foods of Chilean Teal, Falkland Islands.

	Young (6)		*Adults (3)*	
Food	*% Mean Volume*	*% Frequency*	*% Mean Volume*	*% Frequency*
OESOPHAGUS AND PROVENTRICULUS CONTENTS				
Cladocera (*Bosmina*)			29.3	33.3
Cyclopeida (*Cyclops*)			2.3	66.7
Amphipoda	1.2	16.7	1.0	33.3
Trichoptera	23.2	33.3		
Chironomidae (larvae and pupae)			50.0	66.7
Diptera (Helcomyzidae)			1.0	33.3
Osteichthyes (eggs)	8.3	16.7		
Diddle-dee seeds	.5	16.7	1.0	66.7
Unknown plant	16.7	16.7	16.0	33.3
Pigvine	.2	16.7		
GIZZARD CONTENTS				
Cladocera (*Bosmina*)			25.0	33.3
Cyclopeida (*Cyclops*)			4.0	33.3
Amphipoda	4.2	16.7		
Trichoptera	4.2	16.7		
Chironomidae (larvae and pupae)			30.7	33.3
Osteichthyes (eggs)	13.3	16.7		
Diddle-dee seeds	30.5	83.3	4.0	66.7
Pigvine seeds	12.3	50.0	1.3	33.3
Roskovia seeds	6.3	16.7		
Unknown seeds	22.2	50.0	8.0	100.0
Unknown plant material	6.8	16.7		

deep or less. Occasionally they fed in deeper water with head and neck submerged. Some very tiny, probably newly hatched young fed by picking; some older (Class II) birds fed by diving in a creek and also dabbled in algae on the boards of a structure exposed at low tide.

The most spectacular response of Crested Ducks to a food source was demonstrated by a flock of about 45 birds feeding on larvae and pupae of shore flies (Helcomyzidae) in rotting leafy kelp. A flightless adult male and one young of its brood were collected and found filled with these larvae. Occasionally bits of filamentous algae are found in digestive tracts, but this seems accidental.

Crested Ducks are said to feed on the offal of slaughter houses (Johnson 1965), but whether they seek the decaying meat or the invertebrates associated with the offal has not been established.

Thus, it seems that Crested Ducks are almost entirely carnivorous and seek larger organisms than do Chilean Teal.

Falkland Flightless Steamer Duck

When actively feeding, it dives in deep water or feeds with head under water in gravel or kelp. Its association with kelp has misled people into believing that it feeds directly on the plant.

Foods were exclusively marine invertebrates (Table VI) as would be expected from the adaptations for diving and as found by Murphy (1936), Humphrey *et al.* (1970) and Johnson (1965) for the closely related mainland species, the Magellanic Flightless Steamer Duck *T. pteneres*. Mussels *Mytilus* spp. have been reported as a major food but, despite their great density, there was only a trace of them in these summer specimens. Cobb (1933) reported one female with 450 mussels and a male with three crabs and some other bivalves. Brooks (1917) noted large pieces of crabs taken, as well as limpets, chitons, mussels, gastropods and shrimps. Murphy (1936) reported limpets, crustaceans and 'small bugs'. Vallentin (1924) observed 'loggerheads' eating the echinoderm *Hamiaster philippii*.

Downy young of less than two days old mostly fed by dabbling in gravel in shallow water. Diving started at this age, however, and the percentages of time spent diving increased as did the duration of dives. Adults feeding in the same depths stayed under water only a little longer than ducklings, and submergence

Table V. Some summer foods of Crested Ducks, Falkland Islands.

Food	*Young (8)* % *Mean Volume*	% *Frequency*	*Adults (3)* % *Mean Volume*	% *Frequency*
OESOPHAGUS AND PROVENTRICULUS CONTENTS				
Gastropoda	.1	12.5	6.7	33.3
Pelecypoda	1.2	12.5		
Cladocera (*Daphnia*)	6.2	12.5		
Isopoda	25.0	62.5	23.3	66.7
Amphipoda	23.8	50.0	23.3	66.7
Diptera				
Helcomyzidae (larva)	1.4	12.5		
Helcomyzidae (pupa)	10.8	12.5		
Helcomyzidae (adult)	.2	25.0	33.3	33.3
Empididae (adult)	.1	12.5		
Ephydridae (adult)	.1	12.5		
Coleoptera	6.2	12.5		
Filimentous algae	12.5	12.5		
Unidentified algae			6.3	33.3
Unidentified plant material			6.3	33.3
GIZZARD CONTENTS	*Young (7)*		*Adults (3)*	
Gastropoda	3.3	14.3	3.0	33.3
Pelecypoda	4.7	14.3		
Isopoda	16.0	42.9	34.3	66.7
Amphipoda	10.4	42.9	22.7	66.7
Diptera				
Chironomidae (larva)	7.1	14.3		
Helcomyzidae (larva)	4.1	14.3	33.0	33.3
Helcomyzidae (pupa)	8.1	14.3		
Helcomyzidae (adult)	2.0	14.3	.3	33.3
Filimentous algae	7.1	14.3		
Diddle-dee (seed)	23.7	57.2	.3	33.3
Pigvine (seed)	10.9	28.6		
Unidentified algae			3.0	33.3
Unidentified plant material	3.1	28.6		

seemed generally related to estimated water depth (Table VII). Young also probed in surface kelp and presumably pulled off snails and occasionally limpets. Feeding in gravel was common when parents were loafing near shore, however, and it was obvious that young spent considerably more time feeding than did adults.

Young birds fed mainly on marine amphipods, isopods, bottom-dwelling snails and kelp snails. Birds of three weeks old or more differed little from adults and favoured kelp snails and limpets. One consumed bits of crabs dropped by an adult in the process of breaking up the shell.

Large marine crayfish *Munida gregaria* were swallowed whole by adults and were taken in water deeper than kelp beds—probably over 9 metres. One adult taken in a creek was full of soft-shelled clams and fish eggs; another held several small fish. Of the waterfowl studied, Falkland Flightless Steamer Duck ate the largest prey items and also had the largest gravel in the gizzard (Figure 5).

In summary, the Falkland Flightless Steamer Duck shows versatility in food selection by dabbling, probing or diving. Benthos samples suggest great richness and diversity in shallow marine waters where these birds spend most of their time. The foods of young clearly overlap with those of Crested Ducks for the first two weeks of life but the Steamer Ducks were never observed feeding in algae-covered gravel or rock strata. Steamer

Table VI. Some summer foods of Falkland Flightless Steamer Ducks.

	Young (4)		*Adults (6)*	
Food	*% Mean Volume*	*% Frequency*	*% Mean Volume*	*% Frequency*
OESOPHAGUS AND PROVENTRICULUS CONTENTS				
Gastropoda	28.5	50.0	2.2	33.3
Smooth-shell Limpet			.3	16.7
Rough-shell Limpet			.2	16.7
Pelecypoda (soft-shell)			14.0	16.7
Isopoda	41.0	100.0	3.2	16.7
Amphipoda	27.5	50.0	.2	16.7
Decapoda (*Munida* sp.)			45.3	66.7
Decapoda (Hermit Crab)			5.0	16.7
Osteichthyes			13.2	16.7
Unidentified green algae	2.5	25.0		
Unidentified algae			.2	16.7
GIZZARD CONTENTS				
Gastropoda	48.8	75.0	22.3	66.7
Gastropoda (cores and shells)	8.5	25.0	20.2	83.3
Pelecypoda (soft-shelled)			9.2	16.7
Pelecypoda (small)			.8	50.0
Mytilus shell			1.2	33.3
Isopoda	13.0	75.0	.5	16.7
Amphipoda	16.5	75.0		
Decapoda (*Munida* sp.)	10.0	25.0	32.5	66.7
Decapoda (Hermit Crab)			1.5	16.7
Osteichthyes			.5	16.7
Osteichthyes (eggs)			7.5	16.7
Unidentified algae			.5	16.7
Unidentified plant	2.5	25.0		

Table VII. Duration of dives of Falkland Flightless Steamer Ducks.

YOUNG				
Age in days	*Number of dives*	*Range in minutes*	*Mean in minutes*	*Standard deviation*
1-2	6	.04-.27	.137	±.099
21-22	6	.11-.24	.197	±.046
27-28	28	.17-.27	.218	±.127
34-35	11	.20-.29	.252	±.031
ADULTS				
Depth	*Number of dives*	*Range in minutes*	*Mean in minutes*	*Standard deviation*
60 cm.	15	.16-.34	.231	±.054
60-90 cm.	12	.05-.49	.243	±.133
90 cm.	13	.12-.48	.322	±.123
110 cm.	7	.27-.55	.429	±.103

Ducks dabble in gravel, but they tend to select larger food at an earlier age than do Crested Ducks (Tables V and VI).

These birds spend considerable time loafing on shore, often sunning or drying with semi-spread wings. Waiting males, non-breeding but territorial pairs, and flocks of unpaired, non-breeding immatures had specific loafing sites. One, used by over 100 birds, was white-washed with droppings. Presumably, such loafing sites were used overnight as well because there are few terrestrial predators.

Kelp Geese (Plate II, p. 17).

Intensive feeding was on rocky outcrops, shelves or boulders where algae were abundant on the tidal zone. These included an olive leafy algae *Porphyra* sp. (probably *umbilicalis*) that grows on vertical and horizontal surfaces; a pale green filamentous algae *Enteromorpha* sp. on the gravel areas and rocky substrates; and green sea lettuce *Ulva* sp., barely exposed on horizontal rock or gravel at low tide and often taken as drift. All adults collected had fed on these species (Table VIII), and in numerous cases only one food was taken. Large flocks of non-breeding and moulting Kelp Geese occurred only on extensive rocky areas where lush growths of algae occurred. Flocks of 28 and 42 were seen at the tip of Cow Point, the basal portion of

Table VIII. Some summer foods of Kelp Geese on the Falkland Islands.

	Young (3)		*Adults (5)*	
Food	*% Mean Volume*	*% Frequency*	*% Mean Volume*	*% Frequency*
OESOPHAGUS AND PROVENTRICULUS CONTENTS				
Amphipoda			.2	20.0
Arthropoda (mites)	3.0	33.3		
Filimentous algae	12.0	33.3		
Porphyra sp.	84.6	100.0	19.8	20.0
Sea Lettuce (*Ulva* sp.)			40.0	40.0
Diddle-dee seeds			39.8	40.0
Diddle-dee leaves			.2	20.0
Unidentified plant leaf			.2	20.0
GIZZARD CONTENTS				
Filamentous algae	25.0	50.0		
Sea Lettuce (*Ulva* sp.)			40.0	40.0
Porphyra sp.	75.0	100.0	20.0	20.0
Diddle-dee seeds			40.0	40.0
Unidentified plant			.2	20.0

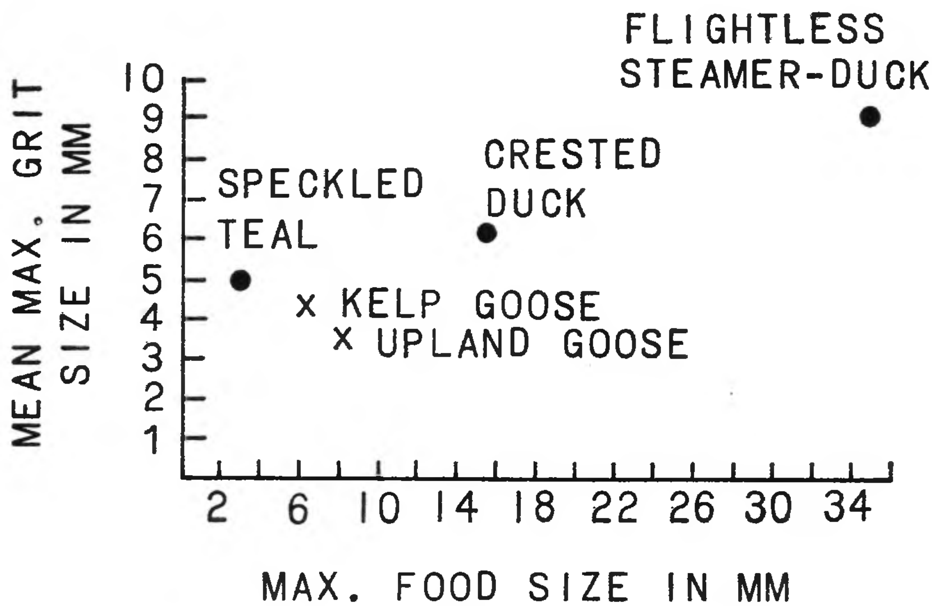

Figure 5. Relationship between maximum food size and of grit in the gizzard.

which formed the Fitzroy study area. At Fox Bay East, 232 adults were scattered continuously over the extensive rock strata exposed at low tide. Birds at Fox Bay seemed to prefer to pick at a very short 'stubble' of *Porphyra* rather than take other species. Indeed, there was evidence of overgrazing of this preferred species. Gladstone and Martell (1968) reported a flock of 316 on New Island.

Males awaiting females on the nest were seen eating green grasses on upland grassy swards near ponds. Pettingill (1965) also noted a family feeding in grassy uplands with Upland Geese. Two adults collected at Fox Bay East were full of diddle-dee berries, and residents indicated that this is a major food in winter.

The diet of young birds was more difficult to establish because those with known feeding histories were difficult to collect. Some observed or collected fed on finer, green filamentous algae, but usually took the same foods as adults. Blaauw (1912) suggested that Kelp Geese eat marine animals, but presented no definite evidence. The occasional amphipods recorded in this study were probably consumed accidentally. They avoided clams even though they fed in algal growths rich in these animals. A few mites were found in the oesophagus of one downy young.

Feeding by Kelp Geese was clearly tide related. During high tides, adults or adults with broods loafed or fed in areas not frequented during low tide. When algal beds were exposed birds walked or flew to choice feeding sites and fed voraciously. On several occasions adults started feeding as the tide dropped by swimming and feeding with their heads under water. Normally, they fed by walking on rocks and did not swim unless forced into water. Young birds fed on some algae found in gravel loafing areas above the high-tide line.

Feeding behaviour and habitat selection of other waterfowl

Because of the uncertainty of their status, observations on the feeding of the other waterfowl were rarely documented by collection. Birds were associated with certain pond types and plant communities, and feeding sites were examined for evidence of use.

Three species of the genus *Anas* used freshwater areas. Two, Brown (or Chilean) Pintail *Anas georgica spinicauda* and Southern Versicolor (or Silver) Teal *Anas versicolor fretensis*, are pond species and feed in the same ponds and in the same general manner as do Chilean Teal. Brown Pintail were seen widely, but never were abundant. The largest number seen on one lake was 15 birds on Swan Pond, Fitzroy. The few broods seen were always on ponds with native waterweed rich in amphipods and insect larvae. Pintails elsewhere in the world are known for their field feeding on grain outside the breeding period, but there are no natural or planted grain crops here to sustain large numbers of these birds over winter. One bird was seen in tidal pools in late summer, and feeding along the seashore is reported commonly in winter.

Versicolor Teal, known locally as Pampa Teal, were not common anywhere, though 13 occurred on Swan Pond during mid-summer. They preferred shallow, food-rich ponds where they fed with the head well under water, or upended. An adult was seen diving with Chilean Teal in a peat pond. One Versicolor Teal collected while feeding had an empty oesophagus and proventriculus, but the gizzard was full of clams and amphipods although it was feeding in an area in which only chironomid larvae were found in the net sample. Presumably it had just moved from a larger pond nearby where clams and amphipods were more common. Versicolor Teal and Brown Pintail were not seen in streams.

The Chiloe Wigeon frequented freshwater streams and ponds and estuaries (=creeks) where aquatic plants were abundant. At sites on small streams from which adults were flushed, uprooted *Lileopsis* sp. was found floating on the water's surface. Several Wigeon were associated with an estuary called Sand Pond at Fox Bay East where dense beds of wigeon grass *Ruppia* sp. occurred in very clear water. In addition, the one Class Ib young collected contained mostly the submergent algae *Nitella* sp. Adults and young were seen dabbling and pulling plants in the areas where *Nitella* grew between patches of native waterweed.

Areas frequented by flocks and broods of Black-necked Swans were often also used by Wigeon, but were always large waters of over 40 hectares. Favoured sites included both freshwater and estuaries, and a few birds spent a little time in marine kelp beds. In Swan Pond at Fitzroy, swans avoided native waterweed and fed in areas where *Nitella* sp. and some mud plantain occurred. In the brackish Swan Inlet west of Fitzroy, where about 40 swans were seen in midsummer, the common plants were water starwort *Callitriche* sp. and native waterweed. On the Murrell River, a favoured wintering area, only a few swans were seen in summer. Plants were sparse but mud plantain did occur.

Flying Steamer Ducks *Tachyeres patachonicus* were the least abundant anatid although I suspect that they are sparsely distributed over a wide area and more common than the figures suggest. They were invariably found in large freshwater ponds with either sand or clay bottoms. Of seven ponds checked, five had either small 'fingernail' clams or snails. One brood was seen in an estuary, but this seemed unusual on the Falklands (Bennett 1924), whereas it is common in marine situations in Tierra del Fuego (Humphrey *et al.* 1970). Flying Steamer Ducks fed by diving even in shallow water of half a metre, but dabbling and upending were common, especially by juveniles. One adult hen contained remains of clams in the gizzard, and she and three young had seeds of diddle-dee in the gizzard. Evidently these seeds serve as grit for species that feed chiefly on animals, and they are retained for a long time.

The Ruddy-headed Goose *Chloëphaga rubidiceps* was less common on the East than on the West Falkland Islands, constituting 23% of 31 pairs of geese at Fitzroy but 46% of 39 pairs at Fox Bay East on the West Falklands. Taking all adults into consideration, Ruddy-headed Geese made up only 6% of 318 geese at Fitzroy but 31% of 238 geese at Fox Bay East. It also fed on fine meadow-grasses, but seems more of a grubber than a tip feeder and uses rootstocks and whole small plants as well as seed heads. Only one adult and one juvenile were collected.

Ruddy-headed Geese fed in association with Upland Geese, although broods remained isolated. According to Murphy's (1936) interpretation of Cobb (1933), this bird was known as the Mountain Goose as opposed to the Upland Goose, which was called the Valley Goose.

Invertebrate production in ponds in relation to waterfowl use

Cawkell and Hamilton (1961) observed that the ducks concentrated in the ponds containing waterweed, but that most ponds were rarely used. This response is related to substrate type and pond basin structure.

Ponds of sand and clay base in thin layers of peat tend to have shallow, sloping shorelines and probably more suitable physical and chemical bases for plant growth. Water clarity also may be involved. Those ponds with submergent vegetation provide good substrates for a variety of invertebrates, and it is this food source that obviously attracts all ducks except Chiloe Wigeon.

This pattern was well demonstrated on the ponds of the Fitzroy study area, where the greatest number of taxa of invertebrates and the largest standing crop in ml./m^2 were found in Swan Pond, which had the greatest species diversity of ducks and the greatest concentration of broods (Table IX). The high numbers of waterfowl species found at South Twin is due to its proximity to Swan Pond to which they come when disturbed by humans. The high number of invertebrate taxa in the five small ridge ponds sampled is surprising and biased by one nearly dry pond that was uniquely rich.

In the autumn of 1971 additional samples were taken in the Fitzroy lowland ponds for benthic fauna (Table X), but the ridge ponds were not sampled. These data again demonstrate (1) the richness of Swan Pond that always had the most waterfowl use, and (2) the minimal amount of food on North Twin, never voluntarily used by ducks for feeding. They landed there only rarely when disturbed in the adjacent Swan Pond.

Reproductive behaviour

Territoriality

Territorial behaviour is clear-cut and seemingly effective in all but the several

Table IX. Waterfowl species use of Fitzroy ponds in relation to pond invertebrates. November-December 1970. Figures in parenthesis indicate number of species of waterfowl that actually feed in the ponds.

Pond	*Substrate*	*Waterfowl species*	*Waterfowl broods*	*Invertebrate taxa**	*Invertebrates ml./m.^{2}***
Swan	Sand-Clay	8 (6)	18 (13)	10	82.9
Fitzroy	Clay-Peat	1 (0)	2 (0)	5	8.6
South Twin	Peat	4 (2)	4 (2)	3	6.5
North Twin	Peat	0 (0)	0 (0)	3	1.1
Ridge (5 ponds)	Peat	2 (1)	3 (2)	8	12.9

* Maximum major invertebrate groups recorded in 3 or 4 samples of surface water and bottom substrate

** Maximum invertebrates recorded in 3 or 4 bottom samples

Table X. Invertebrate diversity and mean standing crop of benthic fauna in Fitzroy ponds, 5th November 1971.

Pond	*Substrate*	*Sample size*	*Invertebrates Maximum taxa*	*Mean ml./m.²*
Swan	Sand-Clay	6	10	27.8
Fitzroy	Clay-Peat	6	6	8.6
South Twin	Peat	6	4	7.7
North Twin	Peat	2	3	1.4

species of *Anas* that frequent rich lakes. Pair bonds are distinct and long lasting in all study species except Chilean Teal. However, there are some marked differences in mode of defence.

Kelp Geese are perhaps the most dramatic example of sexual dimorphism in waterfowl, with the male pure white and the female dark brown and white. The male awaits the incubating female in a conspicuous place, defends the site against both other males and females by displays and intense fighting (Pettingill 1965; Gladstone and Martell 1968), and is visible for miles (Vallentin 1924). These and most other Falkland Island waterfowl also show sexual dimorphism in body size, with males larger than females.

What seems to have been an unusual nesting area of Kelp Geese was located south-west of Stanley Commons at Seal Point. In this area, nests were found on peat islands and peninsulas covered by tussock grass and other coarse grasses, in freshwater peat ponds. The nests were all within a kilometre of the sea, but males stood guard and fed in meadow-grass areas. Most of these nests were begun two weeks later than nests at Fitzroy and at least two males in seven nesting pairs had dark tertiaries and primaries suggestive of yearling plumage (Murphy 1936). This may be a case of young birds establishing territories in a suboptimal habitat. Gladstone and Martell (1968) also noted a few breeding males with dark wings, but observed also that such birds were more common in flocks of non-breeders.

Upland Goose males also stand guard near nests or broods. Attacks by males on intruding pairs were seen, but such behaviour seems both less common and less intense than in Kelp Geese, perhaps because the territory is less restricted or better respected, and there is natural dispersion due to habitat (Figure 1).

Crested Ducks are highly aggressive, and waiting males defend the territory actively by flying head-low threat and constant wheezy calls. Such attacks can be intraspecific; one aggressive male on a freshwater pond attacked at least three species of *Anas*. Broods along coasts are normally well dispersed (Figure 3), and one brood per lake is usual.

Falkland Flightless Steamer Ducks are highly aggressive and vocal in their defence. The regular use of distinctive sites and inter-pair actions were so clear-cut as to leave no doubt as to the correctness of statements (Cawkell and Hamilton 1961; Pettingill 1965) that territorial sites are permanent and that females nest in the same sites annually. Battles involve underwater attacks and intensive fighting by both members of two competing pairs.

Flying Steamer Ducks were uncommon, but normally there was one pair per large pond. Two pairs with broods occurred on the very rich Swan Pond at Fitzroy, and occasionally a third male was seen. Some severe battles occurred but generally spacing was maintained at extremes of the pond. A third brood eventually appeared on the adjacent but less rich South Twin Pond.

Although active territorial defence in Chilean Teal was not observed, there is some evidence of spacing of broods (Figure 2). Although the concentration of broods on Swan Pond at Fitzroy may imply lack of territories, the size of territory necessary in a rich lake is probably much less than that in the food-sparse stream habitats. Brood-hens tended to remain separate from flocks of non-breeders, pairs or other broods. Pairs were common among flocks in food-rich lakes and the aggressiveness observed there was associated with competition for feeding sites.

Brown Pintails, Chiloe Wigeon and Versicolor Teal pairs with broods were normally observed as isolated pairs, but this may be a result of the low carrying capacity of the habitat. Once, two Pintail broods occurred in one bay of a large pond. Small flocks of all three species were seen, but Wigeon were usually isolated in pairs. Little aggressive behaviour was noted in any of these species, but their density reduced any opportunity to observe such behaviour.

Black-necked Swans generally were isolated as brood pairs, and residents confirmed these observations. They may be social on large lakes, however, because three nests were within 15 metres of each other at Swan Lake on Dolphin Point (Port San Carlos).

Chronology of nesting

To show the general pattern of nesting by the five study species, the timing of broods of Class I (down feathers only) and of nests at any stage are indicated in Figure 6. It is quite possible that broods occurred outside the mid-October to mid-January observation period. Nevertheless, a pattern emerges that is supported by the general observations of residents. Rather short, seasonally defined nesting periods are suggested, with nests of Falkland Flightless Steamer Ducks and Upland Geese initiated early October and most Kelp Geese starting in early November. Both Crested Ducks and Chilean Teal seem to have longer breeding periods, and broods have been reported in every month of the year by Cawkell and Hamilton (1961) and by residents. Such observations are important in that they demonstrate that when climatic regimes are not so severe, winter breeding is not selected against. However, there is still an obvious concentration of breeding in the summer. Availability of invertebrates in coastal and pond areas may make winter breeding possible, but undoubtedly food resources are more abundant in summer because of increased solar input. Long-term data on temperatures show that means are above freezing in every month of the year, but data are needed on seasonal variations in production rates of plants and freshwater and marine invertebrates.

If birds do not mature precisely at one or two years of age, a spreading of the nesting period could result, where selective pressure for a restricted breeding season is lacking.

Non-breeding populations

Whereas populations of waterfowl in the northern hemisphere are dominated by species of the genus *Anas*, which tend to mature in one year, most species on the Falkland Islands do not seem to mature until two or more years of age. Large flocks of non-breeding birds are common during the summer among Upland Geese, Kelp Geese and Falkland Flightless Steamer Ducks. Non-breeding is suspected also in the Crested Duck and Chilean Teal. However, because the last two species breed at other periods of the year, better data are needed on their annual cycles.

Age of sexual maturity is not known even for Kelp Geese, Upland Geese, or Falkland Flightless Steamer Ducks, but two years is minimal (Cobb 1933), and three or more is likely in such territory-

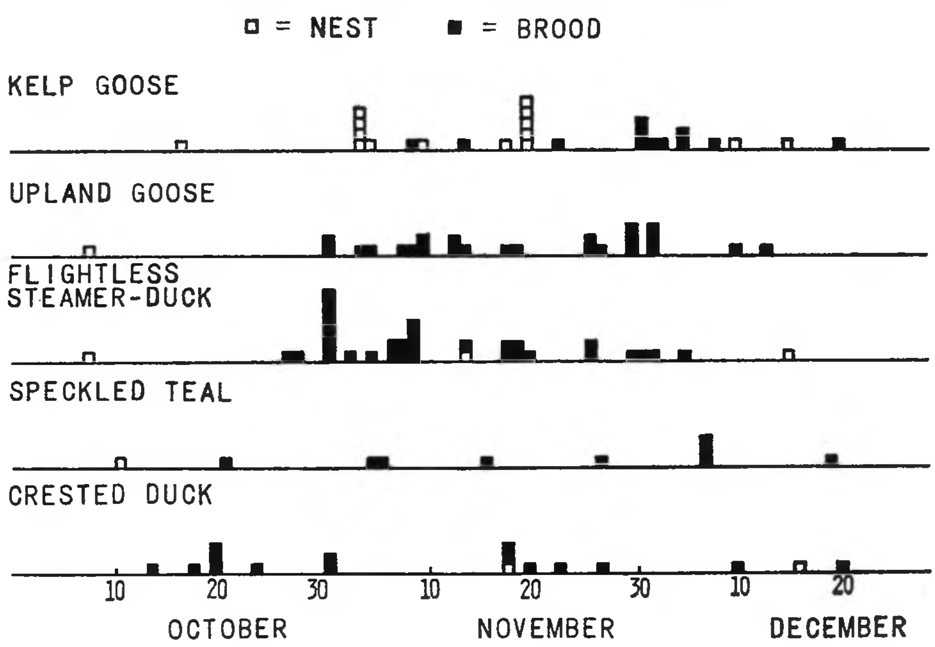

Figure 6. Estimated chronology of nesting based on Class I broods and nests (all stages) in the Fitzroy-Stanley area.

limited species. Residents reported that captive Upland Geese lay at the age of one year, but the large non-breeding population suggests that breeding at this age rarely occurs in the wild. Breeding of Kelp Goose males with dark primaries suggestive of immaturity has been noted earlier.

Some Falkland Flightless Steamer Duck pairs were on territory during the breeding season, but gave no evidence of nesting. Some were clearly young by both plumage and bill colour, but also distinctly more mature than birds in the large flocks of non-breeders, which are probably mostly yearlings. These flocks numbered 20-30 at the Fitzroy and Stanley study areas, but exceeded 200 in one flock at Port San Carlos. Banding studies are essential, because these birds may not breed until they are much older and can find and maintain a territory.

Pair bonds and parental care

Unlike northern hemisphere forms and more like many Argentine anatids (Weller 1968), Falkland Island waterfowl are strongly monogamous, probably permanently paired and remain with their broods until these are fully grown. This pattern was clear-cut in all five study species except Chilean Teal, which are also not clearly territorial.

Chilean Teal were commonly in pairs even in flocks, and sometimes when with broods. Generally, however, only females accompanied broods, and deserted the young when they reached the Class III stage (fully feathered but not flying). Females did attempt to protect their young by injury feigning, a behaviour pattern not seen in the other species, which normally just led the brood to water for safety. Distraction displays were reported in female Upland Geese by Gladstone and Martell (1968).

Males play a key role in defence of the young. Aggressive displays were seen in two male Upland Geese that stood their ground to protect young collected for the food studies. Male Falkland Flightless Steamer Ducks regularly charged gulls in defence of young. Females are more likely to merely lead the brood away from the interaction and are less defensive than are males. Losses of young were mostly at early ages (Table XI), as is typical of most waterfowl.

Males accompanied broods in several species not studied intensively: Black-necked Swan, Flying Steamer Duck, Chiloe Wigeon, some Versicolor Teal, Chilean Pintail and Ruddy-headed Goose.

The age at which young are ejected from the territory has not been determined for most species. One Falkland Flightless Steamer Duck brood observed regularly in Stanley was followed carefully by Mr. John Bound who reported that the parents chased the young when the latter were three months old and had full-grown wings. Pettingill (1965) presented data suggesting that young of both Falkland Flightless Steamer Ducks and Kelp Geese were ousted from the territory at about four months of age. Similar data need to be gathered for all species because of the importance of correlating growth rates with climate.

Growth rates of young

There is some evidence to suggest that Arctic species of waterfowl which are limited in the length of the breeding season by availability of ice-free water, food and good weather tend to have rapid growth rates. Hence Lesser Snow Geese *Anser caerulescens* mature in six weeks, whereas smaller dabbling ducks in temperate areas require six to nine weeks (Weller 1964). Since long day length and availability of food may be influential factors, it seems logical that less selective pressure is exerted on growth rate of birds where temperature is not limiting.

In the absence of marked birds, the assumption was that pairs remain in the territories and observations of broods observed periodically, if not from hatching to maturity, could be pieced together.

Table XI. Brood size in relation to age estimated at first observation by brood classification. Sample size, mean and range are presented.

	Ia			*Ib*			*Ic*			*IIa*			*IIb*			*III*		
Species	*N*	*M*	*R*	*N*	*M*	*R*	*N*	*M*	*R*	*N*	*M*	*R*	*N*	*M*	*R*	*N*	*M*	*R*
Upland Geese	19	5.5	1-9	37	4.4	1-7	26	3.8	1-7	21	4.1	1-7	11	3.9	1-6	3	4.0	4-6
Kelp Geese	17	3.8	1-9	3	2.7	1-5	3	2.7	2-3									
Falkland Flightless Steamer Duck	23	4.3	1-8	26	4.6	1-9	11	3.9	1-7	8	5.2	2-9	4	3.8	2-7			
Crested Duck	16	4.0	1-6	8	4.3	3-6	2	5.5	5-6	3	3.7	3-5	1	—	6			
Chilean Teal	4	3.2	2-5	4	2.7	1-5	3	2.3	1-4	5	2.2	1-4	3	6.0	5-7	4	2.0	1-3
Ruddy-headed Sheldgoose	13	4.4	2-15	4	2.5	2-3	3	3.3	1-5	3	2.3	1-5						
Flying Steamer Duck	5	4.3	1-6	2	3.5	2-5												
Versicolor Teal	3	4.7	4-5															
Brown Pintail	2	2.0	1-3							2	3.0	2-4						
Chiloe Wigeon	3	5.0	4-6	1	—	2												
Black-necked Swan	3	3.7	3-5															

Only a few cases were satisfactory for estimating growth to the flight stage, and these are summarised in Table XII. In general, the birds had much longer pre-flight periods than would be expected for a similar size in the northern hemisphere.

Table XII. Estimated growth periods to each flight stage in five common Falkland Island anatids.

Species	*Time weeks*	*No. obs.*
Chilean Teal	6-7	1
Upland Goose	9-10	1
Crested Duck	10-11	2
Falkland Flightless Steamer Duck	12	2
Kelp Goose	12-13	1

Chilean Teal differed only a little from the five and a half to six weeks maturation period of the northern Green-winged Teal *Anas crecca*, but Falkland Flightless Steamer Ducks and Kelp Geese required at least three months to reach maturity.

Discussion

The waterfowl fauna of the Falkland Islands is essentially that of continental South America or Tierra del Fuego (Olrog 1968). There is no subspecific differentiation among the ducks, but both the Upland Goose and the Kelp Goose are considered recognisable subspecies. Only the Falkland Flightless Steamer Duck is considered an endemic species.

In spite of the latitude, the small land mass and the moderating influence of the ocean reduces winter-summer temperature extremes, and there is little freezing of ponds and no heavy snow. As a result, there is less selective pressure toward time-specific breeding periods or toward rapid growth rate of the young as has occurred in the northern hemisphere. Moreover, pair bonds probably remain intact all year except for some species of *Anas* such as the Chilean Teal. Thus parental care of the young involves both sexes in contrast to the usual pattern in northern hemisphere Anatidae.

Species abundance

The relative abundance of various species (Table II) seems a product of available food resources. As would be expected, the most abundant species are herbivores on land (Upland Goose), sea (Kelp Goose), or brackish/freshwater (Black-necked Swan and Chiloe Wigeon). These herbivores constitute 65% of the total waterfowl observed (Figure 7). The remaining species are mainly carnivores, at least during the breeding season. Species that take food from the very rich tidal zone, the Falkland Flightless Steamer Duck and Crested Duck, rank first (18.6%) and second (7.1%) in abundance. Nearly as abundant is the Chilean Teal (6.4%), which is dominantly a freshwater species during the breeding season and has adapted to small widespread foods such

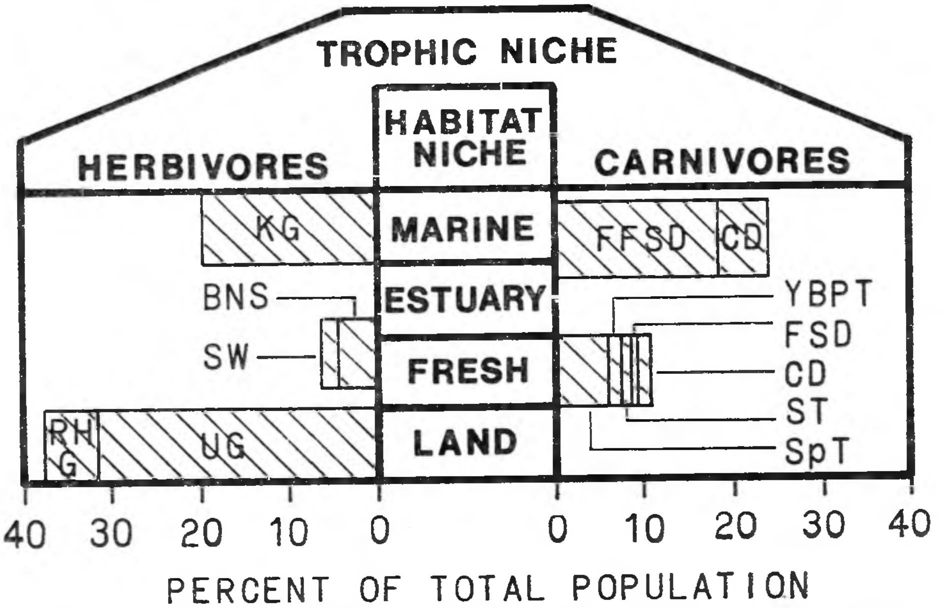

Figure 7. Niche segregation and relative abundance of 11 breeding anatids of the Falkland Islands.

as crustaceans and insect larvae in fresh water. It can also utilise seeds and berries in non-breeding periods. Teal, therefore, can use more diverse habitats, but often at low density.

Although basic primary productivity and complex food relationships primarily limit the numbers of many ducks, social structure and behaviour also may determine the size of the effective breeding populations. Productivity obviously is greatest in the shallow sea, so linearity of territories along the coast is a common pattern, and the number of possible territory sites probably limits the number of breeding pairs. Although the productive sea supports great numbers of non-breeding Falkland Flightless Steamer Ducks and Kelp Geese, further population increase may thus be limited. Upland Geese are less restricted to the seashore and also use rivers, creeks and ponds where drainage produces the green valley plant associations they use as food.

Niche and species diversity

The eleven regular species of breeding waterfowl probably survive with little competition because of the diversity of habitat niches (Odum 1971), which provide different sources of food. Where two species seem to use the same general habitat niche, they tend to differ in trophic (=food) niche. For example, of the three species that regularly use the seashore (Figure 7), Kelp Geese feed on marine algae along the shore, Falkland Flightless Steamer Ducks normally gets most food in offshore diving, and Crested Ducks tend to feed on invertebrates in algae, silt or gravel. The Steamer Ducks also may dabble in gravel, but favour deeper water even when not diving for food and select larger prey items (Figure 5). There is greater overlap in feeding sites and food item sizes of young birds of these two species, but generally the foods of Falkland Flightless Steamer Ducks are larger than those of Crested Ducks.

Although Chiloe Wigeon and Black-necked Swans are often found in areas with the same succulent food plants, the swans are limited to large, open areas, whereas Wigeon may use confined creeks and small pools. Moreover, their competition for food may be minor because of the abundance of their source. Further, more detailed studies may reveal that they utilise different food items or different parts of the same plant.

Among freshwater species, Flying Steamer Ducks obviously are the deep-water birds, which efficiently use a niche less easily and less regularly used by dabbling ducks. The situation in members of the genus *Anas* using shallow portions of freshwater ponds is more complex. They seem to overlap more in food use, but it was not possible to collect all species nor to have samples of sufficient size to be significant. From observations of these species in Argentina (Weller 1968) as well as from limited food data from Falkland Island birds, the species probably do differ slightly in habitat and trophic niche. Chilean Teal tend to feed on small food items and, having a bill with fine serrations, strain minute crustaceans out of the shallow and muddy pools or shorelines where they often feed. Versicolor Teal seem to feed in more permanent ponds, rich in submerged vegetation, and to select larger food items. No Chilean Pintails were collected on the Falkland Islands, but they are known for great adaptability in choices of food items and sizes. Their long neck equips them for bottom feeding on benthic organisms that smaller, short-necked species cannot reach. Hence, they often feed in deeper, more central parts of the ponds. Although there may be overlap in use of foods by dabbling ducks, the great seasonal abundance of such food organisms in rich ponds may not induce serious competition. Moreover, the social intolerance of the ducks may limit the density of flocks feeding there.

Because of the extensive and diversified grassland, the dominance of terrestrial grazers (Upland and Ruddy-headed Geese) is not surprising. What separates these species is uncertain, but the Ruddy-headed Geese would seem less dependent on green valleys and able to use drier sites and coarser grasses. They are most abundant on the drier western islands and in the drier regions of Tierra del Fuego.

Grass, geese and sheep

A conflict has arisen between man's efforts in wool production and the grazing by Upland Geese and Ruddy-headed Geese. This problem probably has been magnified by the creation of cultivated grasslands and expansion of meadow grass areas due to trampling livestock, resulting in increased carrying capacity for geese.

Both geese and sheep favour the green valley formations for grazing. Davies (1939) indicated that preferred foods of sheep include several plants also shown in Table III as being favoured by Upland Geese: meadow-grasses, native rush and native carrot. Overlap in food selection, however, is not complete. Geese do use white-grass, *Roskovia*, *Carex* and diddle-dee berries, which are less favoured by sheep. Moreover, the competition with sheep is probably most severe in the breeding season, when goose pairs are restricted to areas suitable for brood rearing and moulting adults remain near water.

The conflict between geese and ranchers is exaggerated by the current poor price of wool, difficulties in marketing mutton or beef, and the resulting struggle for maximum production and financial reward. Bounties have been paid on geese for many years, but there is little evidence that they have led to a reduction in goose populations. Bounties are also paid in Tierra del Fuego (Ripley 1950), and farmers in Buenos Aires Province of Argentina harass and drive the geese by plane (Weller 1968). Such efforts are of questionable value and add to operational costs. On the Falkland Islands, the use of young geese for food is an effective means of population management where there are sizeable settlements, as at Stanley. Few Upland Geese survive there, although suitable habitat is abundant (Table II). If much discussed plans to limit goose numbers on farms are activated, some regulation over the extent of population control is essential, because the species is an important part of the attractive avifauna of the islands. Moreover, the role of geese in adding much-needed nitrogen fertilizers to poor, acid soils needs to be thoroughly investigated.

The future

The conservation of the Falkland Island fauna is essential for scientific reasons, but it may well become important to the island economy because of developing tourism. Although the waterfowl are not unique faunistically, the birds of the Falkland Islands collectively represent a fascinating group in which waterfowl are quite conspicuous. This, in combination with the rugged setting, will be attractive to lovers of natural history. A concentrated effort must be made to retain as much of the natural area as possible in an undisturbed state. Drainage of wetlands already has been initiated to increase grazing areas, and this procedure reduces bird species diversity, with greatest impact on the less common waterfowl. For example, Cawkell *et al.* (1960) called attention to the abundance of Flying Steamer Ducks on Burnside Pond near Darwin, but now visitors will see no water; only green grass, sheep and Upland Geese. Loss of such areas means loss of rare species and an increase in a few dominant species that sometimes become a nuisance.

Cawkell and Hamilton (1961) have suggested that some ducks have declined due to hunting. However, the decline has not been documented and harvest through sport hunting is not great. Hunting is probably not a controlling factor for even the rare ducks because it tends to be density dependent. Decreases in the diversity and richness of habitat niches are of greater significance.

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Summary

A variety of marine and freshwater habitats occur on the cold-temperate Falkland Islands. Although thirteen species of waterfowl have nested on the islands, only eleven are seen regularly. Intensive study of habitat selection, food utilization and reproductive behaviour of five species and general observations on six others revealed that waterfowl species were well-distributed with little overlap in food use even in the same habitat. Herbivorous species constituted 65% of the total waterfowl observed and different species fed on marine algae (Kelp Geese *Chloëphaga hybrida malvinarum*), upland grasses and forbs (Upland Geese *Chloëphaga picta leucoptera* and Ruddy-headed Geese *Chloëphaga rubidiceps*) or freshwater submergents (Black-necked Swan *Cygnus melanocoryphus* and Chiloe Wigeon *Anas sibilatrix*). Two carnivores utilizing marine inshore and tidal zones were next in abundance; Falkland Flightless Steamer Ducks *Tachyeres brachypterus* fed on bottom organisms by diving and Crested Ducks *Lophonetta s. specularioides* fed in the gravel and silt on smaller invertebrates. Three species of dabbling ducks were more social and omnivorous but mainly utilized the abundant invertebrates of freshwater ponds. Although some inter-specific competition was noted at edges of territories or feeding sites, species generally are segregated in different niches.

Reproductive behaviour patterns are influenced by a climate moderated by the sea and, although seasonal breeding is common in Upland Geese and Kelp Geese, nests of Crested Ducks and Chilean Teal *Anas f. flavirostris* have been recorded in all months of the year. Growth rate of young is slow by northern hemisphere standards, and territorial behaviour is more pronounced.

Upland Geese have become a dominant species because development of grazing lands provides choice habitat. In spite of competition with sheep for grass, protection is essential for all species of sheldgeese because they are important components of a unique avifauna significant to scientists and attractive to tourists. Although generally like the waterfowl fauna of Tierra del Fuego, that of the Falkland Islands is unique in one species (Falkland Flightless Steamer Duck) and two endemic subspecies (Upland Goose and Kelp Goose).

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