

SOCIAL STRUCTURE, DISPERSION AND BREEDING OF THE AUCKLAND ISLAND TEAL

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ABSTRACT

On Ewing Island, Auckland Islands, during the austral summer of 1991-92, Auckland Island Teal *Anas aucklandica aucklandica* were dispersed principally as pairs occupying and vigorously defending small all-purpose territories. Most territories were around the margins of the island, either within a narrow fringe of grassland, or at the very edge of *Olearia lyallii* forest with access to boulder beaches or low wave platforms. Few territorial pairs lived entirely within the forest. A small number of juveniles and unpaired adults assembled as a flock at one protected coastal location where food was super-abundant, but other unpaired birds appeared to live furtively around the margins of occupied territories. Some non-territorial pairs persistently tried to occupy sections of shoreline in the face of defence by territorial pairs. Only territorial pairs were observed breeding. Females sited their nests on the ground well hidden from view above and laid eggs each of which weighed, on average, 14.8% of body mass. Mean clutch size in 45 nests was 3.4 eggs and hatching success of 86 eggs was 93%. Ducklings were first seen on 11 December and most broods had been reduced to a singleton within eight days of hatching. The probability of a duckling surviving from hatching to 30 days was 0.272. The estimated mean size of extant broods at fledging was 1.6. By estimation, only 14% of ducklings may survive to fledging, and up to two-thirds of all breeding pairs may fail to raise any young. Re-laying by unsuccessful pairs may extend the breeding season into April. Males contributed fully to care of the brood but were not always seen in close attendance. By comparison with other related Australasian teals, Auckland Island Teal have a more terrestrial lifestyle and show more enduring territoriality.

KEYWORDS: Auckland Island Teal, *Anas aucklandica*, breeding, population, behaviour, ecology

INTRODUCTION

The geographic isolation and the harsh sub-antarctic climate of the Auckland Islands have proved both a stimulus and an impediment to study of the islands' wildlife: a stimulus in that there was (and remains) considerable novelty and interest in biota from isolated locations; an impediment in that the islands are difficult to visit and any prolonged stay is invariably unpleasantly wet, cold and restrictive. Yet despite this, humans briefly settled on Auckland Island in the mid 1800s (Fraser 1986) and the islands were a favoured destination of naturalists and collectors in the late 19th and early 20th Century. Indeed it is stark testimony to the collectors' zeal that Livezey's (1990) study of Australasian teal morphology was based on more museum

specimens derived from Auckland Islands than from continental Australia or New Zealand, and that the Auckland Island Merganser *Mergus australis* was exterminated by the collectors' guns (Kear & Scarlett 1970).

The Auckland Islands archipelago is the sole home of the small, brown and flightless Auckland Island Teal *Anas aucklandica aucklandica* (taxonomy follows Turbott 1990). It is closely related to (Livezey 1990, Williams *et al.* 1991) and superficially resembles Brown Teal *Anas aucklandica chlorotis* of the New Zealand mainland and (formerly) Chatham Islands, another flightless teal *A. aucklandica nesiotis* from sub-antarctic Campbell Island, and Chestnut Teal *A. castanea* of southern Australia. This small (male 500-620 g, female 365-520 g) duck formerly resided on all substantial islands of the archipelago (Oliver 1956, Kinsky 1970) but is now absent from Auckland Island, the only island still containing introduced mammals (Williams 1985, Turbott 1990). The sexes are not easily distinguished by plumage except during the breeding season when the male's head has a distinctive greenish gloss and its flank feathers are conspicuously striated (Fig.1). Generally, the birds have been reported as pairs fossicking for amphipods and dipteran larvae amongst windrowed kelp on protected island shorelines (Guthrie-Smith 1936, Scott 1971, Weller 1975). However, they are also common in coastal and inland grasslands and about freshwater pools and streams (Falla 1975, Williams 1986, Marchant & Higgins 1990).

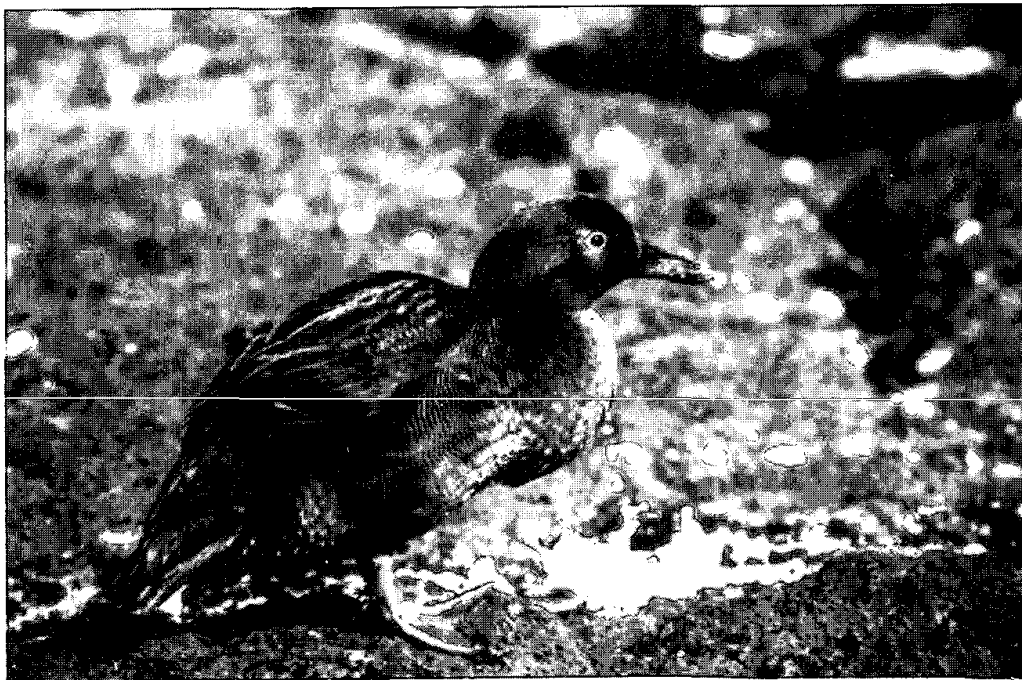


FIGURE 1 – Male Auckland Island Teal showing the prominent and diagnostic striations on the flank feathers, and the characteristically short wings.

Photo: Rod Morris.

Although teal were commonly seen and reported by many early and recent visitors to the islands (Chapman 1891, Waite 1909, Guthrie-Smith 1936, Scott 1971), the first prolonged observations were in December and January 1972-73 (Weller 1975). Weller's study, and his later synthesis on island waterfowl (Weller 1980) remains, 20 years later, the only first-hand account of Auckland Island Teal ecology and behaviour, although the status studies of Williams (1986) and Moore & Walker (1991) have contributed further information.

Whereas the taxonomic relationships of Auckland Island Teal and other 'teals' from the Australasian region have a long history of interest and inconclusive debate (summarised by Dumbell (1986), but see also Livezey (1990) and Marchant & Higgins (1990)), detailed comparisons of their ecology and behaviour are few and recent: Livezey (1990) compared their musculature and morphology and related these to ecological characters; Williams *et al.* (1991) assessed the ecological and behavioural adaptations of these species to life on islands. These comparative studies relied heavily on Weller's (1975) observations for their ecological interpretations, but assessments of mating system, breeding chronology and reproductive output were precluded because that information was not available. In this study I sought to examine the social structure and mating system of a small island population of Auckland Island Teal, to describe the chronology of breeding activities, and to quantify reproductive output.

STUDY AREA

Most data reported in this paper are derived from fieldwork conducted from 7 December 1991 to 17 January 1992 on Ewing Island, one of the islands which define Port Ross at the northern end of Auckland Island (Fig.2). Data on nests and clutches were collected also from nearby Ocean, Rose, and Enderby Islands. The description of post-breeding activity is based on observations made during visits to all of these islands in March 1982 and April 1983 (Williams 1986).

The Auckland Islands, lying at latitude 50°S and about 500 km due south of New Zealand, are within the geographic zone dominated by circumpolar westerly winds. Periods of fine weather occur as brief interludes between fast-moving low pressure systems which can bring strong to gale-force winds, driving rain and stormy seas at any time of year.

Ewing Island is crudely cross-shaped (Figs.2,4), the longer axis extending east-west over 1.25 km, the shorter north-south axis being 1.05 km and the narrowest point through the centre of the island being 500 m. Despite its small area (57 ha), Ewing Island is recorded as supporting more teal (100-180 birds; Williams 1986, Moore & Walker 1991) than other islands in the Port Ross area.

A narrow wave platform, which fringes parts of the northern coast and is more extensive on the east, comprises 13.4% of the island's area. Cliffs up to 15 m high occur on parts of the north and south coasts. Three boulder-strewn beaches occur - two on the south coast, and another which occupies the entire western bay (Boat Bay). Projecting from the western headland is a short spit (Nellie Spit), the tip of which is inundated at high tide.

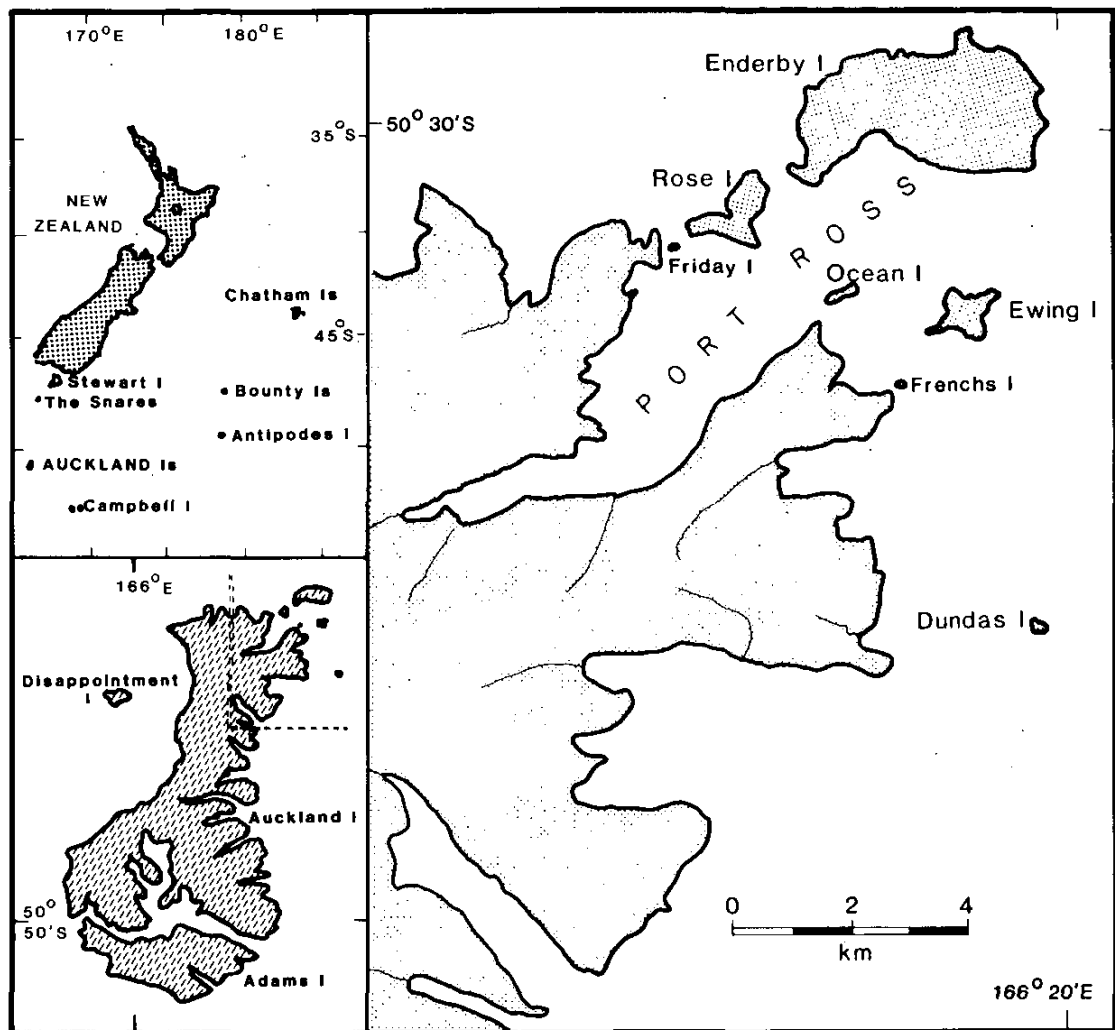


FIGURE 2 – Location of the Auckland Islands, and detail of the Port Ross area.

Apart from a central core of southern rata *Metrosideros umbellata* the island is dominated by the large and sprawling asterad tree *Olearia lyallii*. This vigorous tree grows to the very sea edge in many parts of the island, sprawling over and down cliffs and coastal terraces and out over some of the wave platforms. It has overtopped or colonised much of the island's grassland (Lee *et al.* 1991); 81% of the island is now covered by trees.

Small areas of *Poa foliosa* and *P. litorosa* occur, principally on the southern headland and on Nellie Spit. Elsewhere these grasses, together with two species of *Carex*, the megaherb *Stilbocarpa polaris*, and the shrub *Hebe elliptica*, form a narrow band between forest and wave platform; this plant association covers 5.6% of the island, most extensively on the eastern coast (Fig.3).

Along three sections of the coast, vast quantities of kelp are washed ashore, especially in north-westerly storms. Almost the entire 250-300 m. shoreline of Boat Bay remains covered by windrows of rotting kelp, as does the northern side of Nellie Spit, while smaller coralline algae collect and rot on South Beach.



FIGURE 3 – The extensive *Poa/Carex* grasslands between forest and wave platform in East Bay are interspersed by numerous small pools in which teal were seen feeding at night.

METHODS

Auckland Island Teal were predominantly crepuscular to nocturnal in habit. To induce them to be active during daylight and to emerge from dense vegetation, taped female “inciting” and “decrescendo” calls (Johnsgard 1965) were broadcast using a standard cassette tape recorder. Territorial males responded very quickly and positively to these calls, but single females generally ran away and solitary males did not respond. Territorial males also responded positively to broadcast male “alarm” and “trill” calls (Weller 1975). This technique was used to map the dispersion of pairs around the island’s coasts and to locate pairs in its hinterland.

As a further aid to locating birds, nests and broods, a dog (German short-haired pointer) was used. All but three of 49 nests were found by ‘Bob’ as were all birds living solitarily beyond the flock site.

Thirty-one birds were caught by hand or in hand nets and banded with metal and/or plastic colour leg bands. They were sexed and aged by plumage and cloacal examination. Banding was restricted to three localities - Boat

Bay, Nellie Spit and South Beach (Fig. 4). One banded bird in Boat Bay was fitted with a radio transmitter and followed intermittently over a period of 12 days.

Most observations and field activities were conducted during daylight (05:00-23:00 NZDT). Details of techniques and observation regimes specific to particular parts of the study are given where relevant elsewhere in this paper.

RESULTS

I. POPULATION DISPERSION

The presence of teal was indicated by finding an active nest, sighting of a pair, or attracting a male by broadcasting a female call.

Interpretation of these field observations is based on several assumptions:

- (i) Each nest was indicative of a pair. I obtained no evidence that any female without a partner established a nest. As a result of repeated visits to nests I was able, in all but five cases, to observe the associated male resting close to the nest and/or observe the pair feeding together and, in the case of coastal pairs, identify the extent of the male's shoreline territory.
- (ii) A pair sighted at one location was different from another seen more than 50 m. distant. With so many indistinguishable pairs, the possibility of assuming two pairs occurred when, in fact, only one mobile pair was present, is real. However, range size of well-known and identifiable pairs was small (see "territory size") and, for many pairs, there were repeat sightings at or very close to a specific location. Broadcasting of female calls was used on the eastern and southern coasts to distinguish between adjacent pairs; these were usually encountered one after another during searches along sections of coast or along tracks in the hinterland. If I had doubt about whether one or two pairs were present in an area, I have recorded only one on Figure 4.
- (iii) Males which gave prompt and vigorous responses to a broadcast call represented a pair. I assumed these were territorial males whose mates were either on nests or were attending a brood because:
 - (a) males of known nesting females responded in this way;
 - (b) several of the males were later found in the company of a female and brood;
 - (c) non-nesting females, in the company of their mates, responded positively to the calls; and
 - (d) two solitary males, initially found by the dog, skulked away on hearing the broadcast calls.

On Ewing Island, the nests of 27 pairs were found, a further 37 pairs were identified, and another 16 males were detected by broadcast calls - a minimum total of 80 territorial pairs.

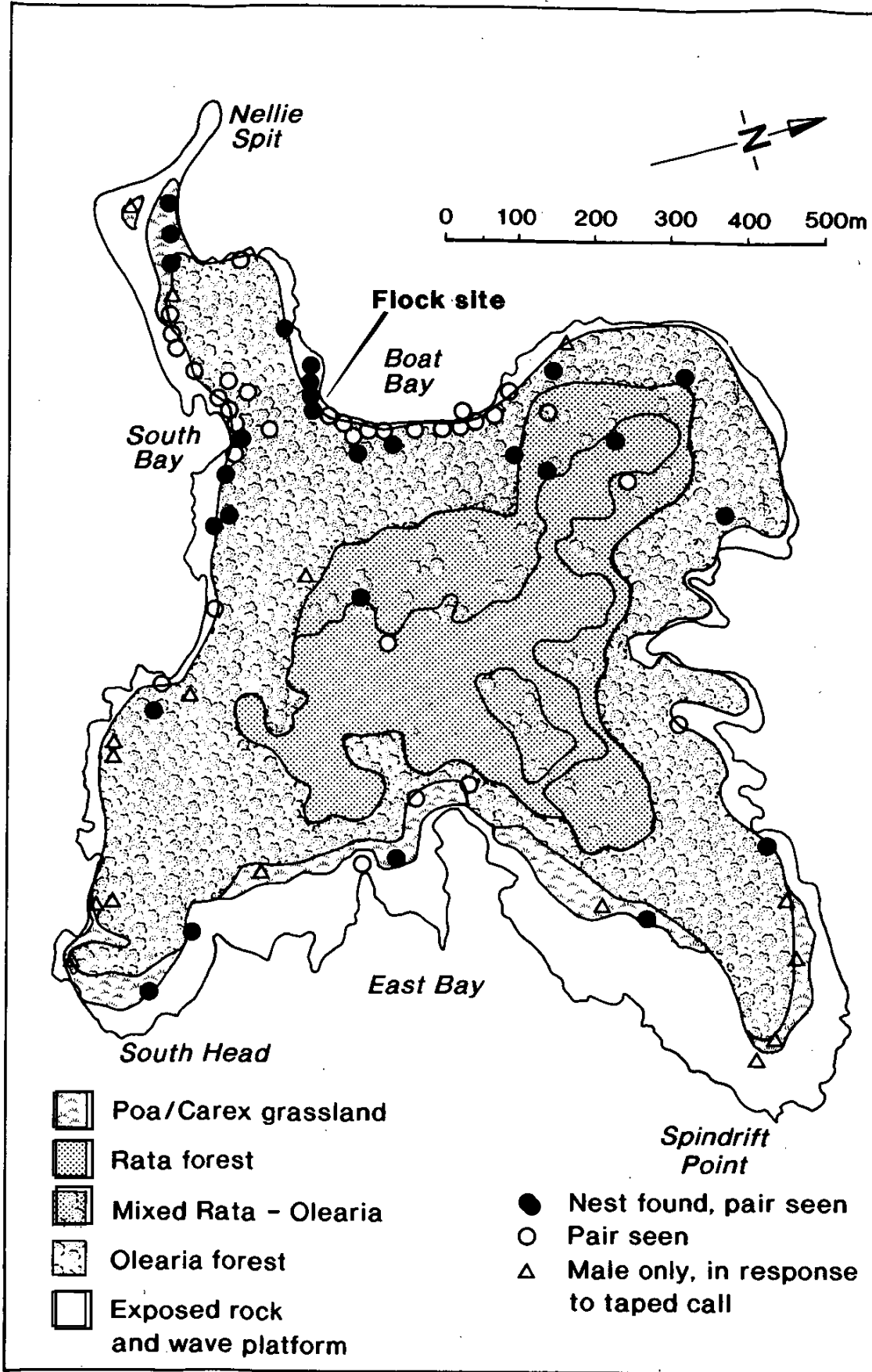


FIGURE 4 – Distribution of territorial pairs on Ewing Island, December 1991 - January 1992. A further five pairs occupied the cavern behind the flock site in Boat Bay (see text for details).

Teal were encountered around the entire coast of Ewing Island and in its hinterland (Fig. 4). The greatest concentration was in Boat Bay and about the western headland; distribution throughout the hinterland and along the exposed and cliff-edged northern coast was sparse.

Figure 4 shows that hinterland sightings were either on the northern headland, an area frequently traversed, or adjacent to access tracks. Because of the tangle of *Olearia*, there were parts of the hinterland that were virtually impenetrable, e.g. the southern headland, and it is likely that additional pairs occurred there and elsewhere in the forest.

Many coastal-dwelling teal occupied damp sites dominated by *Carex* and/or *Poa*. These were mostly within the narrow strips of coastal grassland and associated with patches of *Stilbocarpa polaris* and scattered *Hebe elliptica* bushes. Seepages frequently ponded, had a fringe of *Carex* and the water then spilled out over the rock platform to form small exposed pools.

The grassland fringe was not continuous, having been eliminated in places by *Olearia*. Teal were not recorded amongst the *Olearia* but only where grassland was present. However, part of the grassland on the eastern coast was a pure stand of *Poa litoralis* - I did not detect teal here but they were present in an adjacent mixed *Carex/Poa* stand (Fig. 3).

At Nellie Spit, the extensive grassland comprised mostly *Poa foliosa* and *Stilbocarpa polaris* with several emergent *Hebe* bushes. Unlike teal occupying other grassland sites, the four pairs on the spit had access to food amongst the kelp which collected and rotted on the adjacent boulder beach.

Teal density was highest at Boat Bay and South Beach. On these narrow beaches, where *Olearia* branches overtopped part of a boulder-strewn shoreline (see Fig.7), extensive piles of kelp accumulated and provided abundant food. The adjacent forest floor was carpeted by *Olearia* leaves, fallen wood and clumps of low ferns which, together with the numerous petrel burrows, provided ample daytime refuge or resting sites.

The forest floor at hinterland sites occupied by teal was considerably more occluded than at the coastal edge; taller *Blechnum* sp. and *Polystichum* sp. ferns formed large and dense stands, especially in the damp depressions, and *Stilbocarpa* patches occurred where the canopy was broken. The depressions, some of which were long channels, held water for several days after periods of prolonged heavy rain. Beneath pure rata forest, where the ground was generally drier and sparsely vegetated, teal were not encountered.

II. SOCIAL STRUCTURE

Most teal were encountered as pairs, or as single males subsequently identified as members of a pair. A few birds appeared to live solitarily and somewhat furtively amongst the dispersed pairs and others formed a small flock at the southern end of Boat Bay.

Individuals

Repeated observations confirmed the presence of unpaired birds dispersed amongst territorial pairs in grassland. For example:

- (i) A female was encountered on seven occasions at almost the same location in grassland on the eastern coast. She was, each time, seen skulking amongst scattered *Poa foliosa* clumps on the edge of the wave platform, adjacent to a series of large rock pools and immediately alongside a nesting pair. She was light (330 g), with a deep Bursa of Fabricius, and a tight anal sphincter, all of which I interpreted as characteristics of a young bird.
- (ii) In the east coast grassland (Fig.3), a light (425 g) male was located by the dog. It was seen once thereafter, also at the same location. When examined, its penis was small and not fully sheathed, a distinct contrast to that of a territorial male caught only a few metres away. Although female calls were broadcast in this area the bird never responded to them.
- (iii) A lone female was seen four times along 40 m of forest edge on the northern headland. The bird was unbanded, never caught and each observation was presumed to be of the same bird.
- (iv) Two adult males (580 g, 555 g; one was banded two year's previously as part of Moore and Walker's (1991) study) were caught while feeding at night on Nellie Spit. In contrast to territorial males, and like an unpaired flock bird, these males were seen at two and three different locations, respectively, and never in the company of a female.

In effect, few genuinely solitary individuals were identified. Given that they failed to respond to broadcast calls; and were furtive and isolated, my field techniques and duration of study were insufficient to properly appraise whether solitary-living teal were a significant component of the island's population.

Flock

This was a small grouping of birds consistently present on, or close to, rocks in front of a shallow cavern at the southern end of Boat Bay. In this area, flotsam and kelp accumulated, and after northwesterly storms, the kelp often extended as a raft up to 20 m. offshore. Although the shoreline of the cavern, like that of the rest of Boat Bay, was defended in small parcels by territorial males, territorial defence seldom extended beyond the water's edge. The rocks in front of the cavern were surrounded by sea at all tides thus providing an uncontested roosting site (Fig. 5) from which the teal could disperse to feed amongst the kelp rafts and gain access to the windrows of kelp on the shore.

The greatest number of birds encountered simultaneously at the flock site was nine (eight males, one female). However, 11 identifiable individuals were recorded at the flock site and, on three occasions, three unbanded males were present simultaneously, indicating that at least 14 birds visited the flock site, all but one of which were males.

Generally, more birds were present around the peak of the tide and shortly thereafter than at other times (Fig. 6). However, during strong onshore winds, the flock site was usually deserted as the birds took refuge



FIGURE 5 – The only site at which non-territorial teal gathered on Ewing Island was on a cluster of boulders at the southern end of Boat Bay.

in petrel burrows on shore nearby. Numbers of birds attending also declined as the breeding season progressed. Two full-day watches conducted 10 days apart in early January (Fig. 6, upper) recorded consistently fewer birds during the later period, and single counts in December also recorded more teal than those made at a comparable tide or time in January.

Composition

The variable number of birds encountered at the flock site and the pattern of attendance of individuals (Fig. 6, middle) suggested that few birds restricted their activities to the flock site and the adjacent shoreline. For example:

- i) Four banded males were seen on one in every two or three occasions that the flock site was viewed in December and early January; they were also seen during the all-day observations. None were present for longer than six consecutive hours of each day, and their times of arrival and departure were generally similar. Two of these males were subsequently seen accompanying females in the nearby forest and the nest of one was located on the cliff edge immediately above the cavern. The brood of this latter male roamed throughout the forest and the male did not subsequently visit the flock site. The two other males were not seen at the flock site after 11 January, suggesting that they too had females or broods in the forest nearby.

- ii) One male, when not at the flock site, was usually seen at South Beach, a walk of about 140 m through the forest. This bird, initially caught at night at South Beach, weighed 570 g and was one of the most regular attendees at the flock site. By contrast, another male caught at South Beach (mass 515 g) was seen only once at the flock site; some unbanded birds may also have visited the flock site briefly and irregularly.
- iii) Three attending males were banded two years previously during Moore & Walker's (1991) study. Two were seen irregularly and not after 12 January. The third, however, was a consistent attendee; he was caught (mass 590 g) and fitted with a radio transmitter. His movements were confined to within 80 m of the flock site where he fed along the shoreline of the cavern, roosted with other birds on the rocks and, when not visible, was found hiding in a petrel burrow on a nearby cliff face. During the six weeks of observation, he was never seen with a female.
- iv) One pair of teal (birds 3,4; Fig. 6, middle) was consistently present, the female of which was the only female encountered at the flock site. They roosted together on the rocks along with other birds but the male defended a small area, about 1 m diameter, around his female. They fed only on the shoreline and floating kelp across the mouth of the cavern, and here too, the male kept other flock males at least 2-3 m distant. Neither of these banded birds was seen elsewhere during daylight, although the female was absent for the entire afternoon on 10 January and that night the pair was encountered wandering in the forest approximately 80 m from the flock site.

Activity

A higher proportion of flock birds observed before 08:00 h (85%, $N = 68$), and after 20:00 h (91%, $N = 81$) were feeding than at other times of the day (28%, $N = 108$). Feeding was also more common in the three hour interval spanning high tide (86%, $N = 96$) than at other stages of the tide (47%, $N = 161$). However, birds arriving at the flock site tended to feed immediately, irrespective of time or tide.

The five males who held territories within or adjacent to the cavern attempted to exclude flock birds from feeding on the shore. In their presence, flock birds fed at the very water's edge or on the floating kelp. However, defence of the shoreline did not persist throughout the day and most flock birds fed amongst the cavern's windrowed kelp.

Flock birds seldom attempted to feed elsewhere within Boat Bay. No rafts of floating kelp lingered elsewhere along the shoreline and to feed flock birds had to make landfall, an activity generally met with aggression from resident territorial males.

There was little social interaction amongst birds while roosting or feeding. During eight hours of observation over four days, I recorded 18 agonistic interactions, all of which involved either supplanting or threatening another bird, and 21 occasions on which the paired male, in the presence of his mate, either lunged at, or gave the "trill" call to another male who moved too close. I saw only three displacements of one male by another while

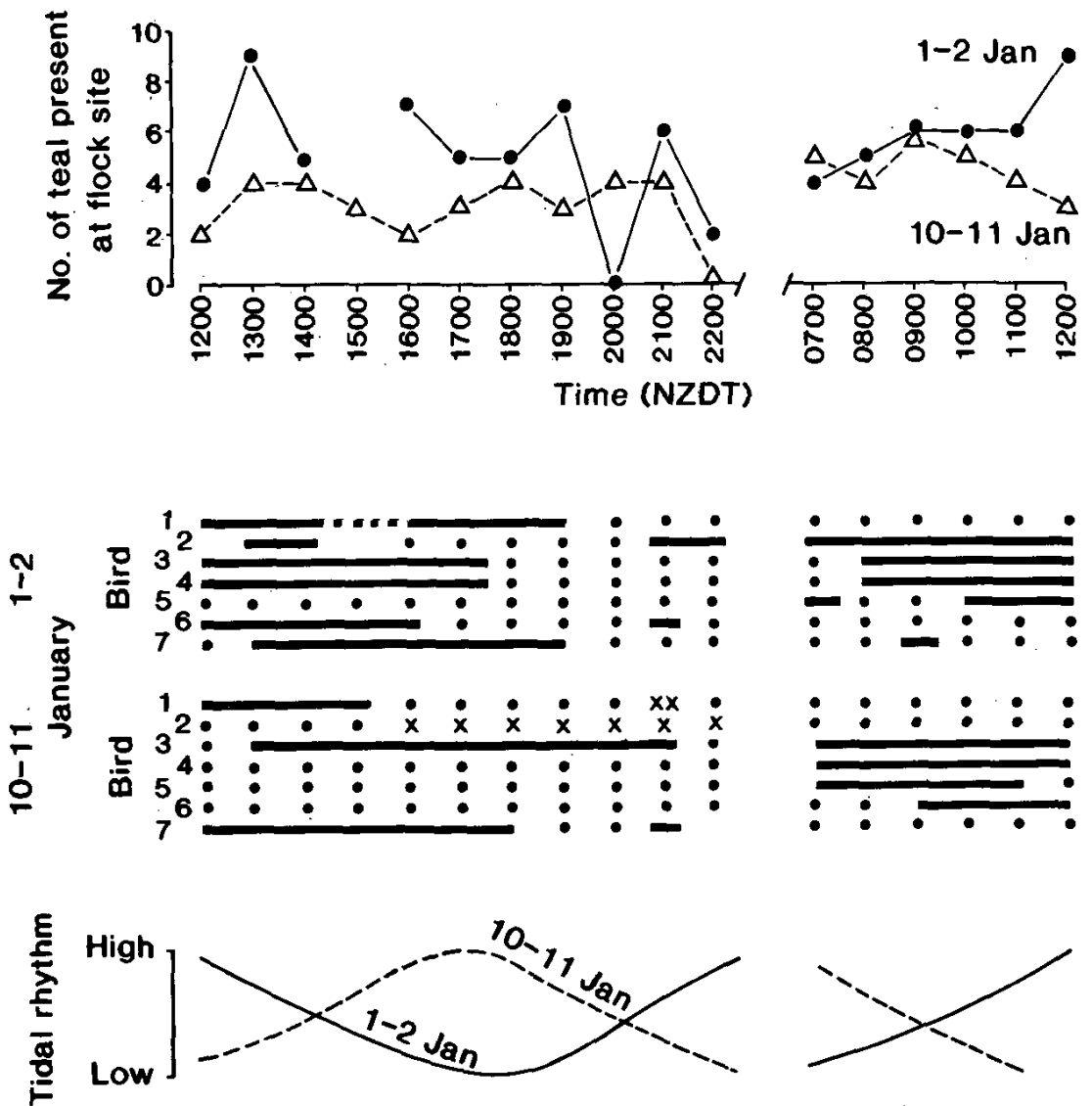


FIGURE 6 - Upper - Number of birds present at the flock site in Boat Bay at hourly intervals during two all-day watches (1-2 and 10-11 January 1992); Middle - sample pattern of individual attendance throughout observation periods (solid bar - bird present; dot - bird absent; x - bird present at South Beach; xx - bird seen feeding in nearby forest with female); Lower - The tidal rhythm during both observation periods.

birds were feeding, but the paired male regularly lunged toward, or gave the “trill” call towards others feeding nearby.

With the exception of the pair, flock birds rested close to each other, often no more than 30 cm apart, and I could identify no dominance relationships amongst these birds.

Pairs

Pairs were widely scattered and encountered all around the island. However, amongst those inhabiting the shoreline of Boat Bay it was possible to distinguish two categories of pairs - those present at a fixed location and

which belligerently drove others away (territorial pairs) and those which, despite moving over a small range, were consistently attacked by territorial pairs, and always forced to flee (subordinate pairs).

Subordinate pairs

In Boat Bay, four pairs persistently fed and roosted over short (50 - 80 m) sections of shoreline and, with the exception of one pair which occasionally moved to the nearby northern headland, were seen only at these localities.

The shoreline over which they ranged was defended by territorial males and in their presence, the pairs rarely made landfall, remaining in the water or on nearby floating kelp. Emergent rocks and long floating tendrils of kelp characterised the sea margins of their ranges. In the absence of territorial males, they came ashore, fed and roosted, and sometimes ventured up to the edge of the forest.

They were subjected to fierce harassment, being chased and physically beaten almost daily. Yet they persisted at their chosen locations and were more consistently visible on the shores of Boat Bay than any of the territorial pairs there.

None of these pairs was seen with ducklings, none of the females appeared gravid, and none of the males was seen alone, suggesting that none of these pairs attempted to breed during the period of study. That conclusion is tempered, however, by the female of the more widely ranging pair having a distended anal sphincter and a re-feathering brood patch, indicative of laying and incubation respectively. Her mate had a large re-feathering patch on his lower neck and mantle, indicative of his involvement in territorial disputes. I concluded that this pair had nested and failed before the study commenced and that they were making forays from a base on the northern headland some 200 m away to exploit the more concentrated food resources of Boat Bay.

Body masses of two of the females were lower (410 g, 460 g) than those of five females nesting nearby (mean 490 g) whereas male body masses (mean 550 g, $N = 4$) were similar to those of flock males (mean 532 g, $N = 7$) and nearby territorial males (mean 580 g, $N = 5$).

At the base of Nellie Spit was another pair whose behaviour was similar to those described above (pair E, Table 1). Their presence was mostly confined to a narrow wave platform backed by a rock face approximately 10 m high. This location offered roosting and escape sites but provided no feeding opportunities. To feed, this pair swam approximately 20 m to the kelp-strewn beach of the spit and fossicked along the water's edge. This section of beach was defended by a pair (pair A, Table 1), the male of which persistently fought or chased them. In his absence, they came ashore and fed unmolested. Just as subordinate pairs did in Boat Bay, this pair would come ashore and feed mostly during daylight and at low tide, when they could see and respond to any approach of the territorial male. During the study, this pair made no detectable breeding attempt and the female never appeared gravid.

Territorial pairs

Territorial pairs occupied a variety of habitat types wherein they defended fixed geographic areas. Where these were contiguous, e.g. along most shorelines and in some grassland, vigorous interaction between the males appeared to establish sharply defined boundaries.

Territorial pairs attempted breeding although it was not possible to determine whether all did so. The breeding effort of only 39 of 80 identified pairs was confirmed either by finding a nest ($N = 27$) or seeing an adult with a brood ($N = 12$). All four adjacent pairs on Nellie Spit nested; five adjacent territorial pairs between Nellie Spit and South Beach were seen with ducklings; and in Boat Bay the breeding attempt of 15 of 17 territorial pairs was detected. These data suggest that most territorial pairs made a breeding attempt.

Body masses of territorial males were 515-620 g (mean 560 g, S.D. = 31 g, $N = 11$) and were not significantly heavier than flock males (range 460-590 g, mean 532 g, S.D. = 43 g, $N = 7$). Territorial females weighed 420-520 g (mean 478 g, S.D. = 34 g, $N = 9$) of which three incubating females weighed 420g, 500g and 520g and one gravid female weighed 520g.

III. TERRITORIALITY

Territories are defined as "defended areas". For Auckland Island Teal these were fixed geographic areas rather than extended individual distances about moving birds, and appeared to be sharply delineated and exclusive.

Although each identifiable pair was seen only within a limited area, active territorial defence by all was not witnessed. Conspicuous pairs, particularly those occupying the shorelines of Boat Bay, South Beach and Nellie Spit, were regularly seen in conflict with their neighbours and it is upon them that the following appraisal of teal territoriality has been based. Birds which lived in less densely occupied habitat, such as in the island's hinterland and in the grassland along the eastern coast may differ in their territorial behaviour, especially in rates of interaction with neighbours and in the exclusiveness of the area over which they roamed.

Territory characteristics

Size.

The limits of a sample of territories were determined by:

- (a) plotting all locations (minimum 10) at which target pairs were seen, and drawing a line around the extreme points ; and/or
- (b) plotting points to which the male could be attracted by broadcasting female calls and delineating the plots, as in (a).

Territories of five pairs occupying grassland habitat on the eastern and northern coasts measured 1000, 1100, 1500, 2100 and 3700 m². These pairs occupied isolated pieces of grassland, and only one appeared to have another pair immediately adjacent. Their territories were flanked by bare wave platform and *Olearia* forest over and through neither of which were they

seen, nor could they be lured during daylight. However, teal were occasionally seen on nearby wave platforms at night.

On Nellie Spit, the 1400 m² area of *Poa/Carex/Stilbocarpa* grassland was occupied by four pairs wherein the smallest territory was 200 m² and the largest 550 m². However, these pairs defended more than just the grassland; the adjacent boulder beach was, on average, 12 m wide and each pair defended a section, roughly demarcated by a straight line from the extremities of their grassland frontage to the water's edge. Effectively this doubled the size of the territory, but the exposed shore was used only for feeding and, occasionally, the male rested there.

The smallest territories were on the foreshore of Boat Bay and South Beach. Along much of Boat Bay, the defended sections of shoreline were only 10-40 m long. How far birds retreated into the adjacent forest, was, in most cases, unknown. One pair was never seen more than 20 m back from the shoreline, hiding amongst fern clumps or in petrel burrows while another pair had its nest 60 m back from the forest edge.

Three of five territorial pairs which defended the cavern shoreline in Boat Bay had disjunct ranges. One pair defended an area of only 8 x 5 m, this being 5 m of shoreline and 8 m from the water to cliff-face behind, in the base of which were small holes used as resting sites. They raised their brood solely within this 40 m² area. However, their nest was on the cliff top immediately above, and to reach it, the duck had to swim about 40 m along the shore and walk 50-70 m inland up a steep bank and through areas defended by two other pairs. The nests of two other cavern pairs were also on the cliff top. One of these pairs raised its brood solely in the forest near the nest site, the male defending the shoreline during the day but accompanying the female and brood after dark.

At South Beach, defended sections of shoreline were 5-20 m long. Territories of two pairs did not extend more than 15 m back from the water's edge, a territory size of about 150 m² within which the female nested, the ducklings hid, and the adults fed.

The sizes of hinterland territories were not determined satisfactorily. Two nests were found approximately 50 m apart and, in another location, two hinterland males were consistently encountered about 30 m apart. By using method (b) above, three territories extended 30-50 m radius from the nest site, but, in one instance of repetitive call playing, the male was encouraged to follow for almost 200 m. This example, and the low number of encounters with teal in the forest, indicates that territory density there, by comparison with that at the coastline, was very low.

Resources

Within their territory, each pair had one or more locations where they could rest unobtrusively. Examples included inside or beneath fallen logs, in petrel burrows, small holes amongst rock piles, or beneath thick fern or tussock. Resident birds also sought a protected location where they could bask in the sun on fine days, and patches of *Stilbocarpa* or fern were particularly favoured for this.

Abundant low vegetation beneath which to escape attacks from Subantarctic Skua *Catharacta skua lonnbergi* and Southern Black-backed Gull *Larus dominicanus* was not universally available. Shoreline territories often had overhead *Olearia* branches to provide initial protection to adults and their broods but in the general bareness of the coastline forest understory teal made use of petrel burrows or any sort of hole as escape cover. Elsewhere, forest-dwelling pairs exploited any available fern clump as escape cover. Grassland pairs used the tussock tillers as an extensive roof as they darted through the numerous small runways that they, penguins and petrels had created.

Teal food is predominantly invertebrates, especially amphipods, isopods and insects (Weller 1975). All territorial pairs seemed to confine their feeding to within their territories. Shoreline pairs fed amongst the rotting, windrowed kelp (in which amphipods and Diptera larvae were very abundant) on their beach front, two banded hinterland pairs regularly fossicked over the same confined area of forest floor, and several grassland pairs were observed to feed only within the grassland. However, under cover of darkness some pairs occupying grassland habitat on the eastern side of the island fed over adjacent wave platforms 50-100 m from their daytime habitat.

There were also some pairs which appeared to move well beyond their "territory" in order to feed amongst the kelp at the Boat Bay flock site and South Beach. For example, three males and one female were caught and banded at night at South Beach while feeding in areas which, during daytime, were very vigorously defended by other males. Two of these birds were seen again only under cover of darkness. The other two were seen regularly at dusk making furtive attempts to feed. When challenged and chased by the defending birds, all scampered back into the forest and later sightings confirmed that they were predominantly residents of the forest edge, separated from the foreshore by a line of other territorial pairs. Nest sites of five pairs occupying grassland on the eastern coast and another four on Nellie Spit were well within the range over which I encountered the identifiable males. I am less sure whether nest sites were within the defended ranges of most Boat Bay and South Beach pairs for I seldom saw territorial defence except along the shoreline. Sixty metres was the furthest inland a nest of five shoreline pairs was located. Separate feeding and nesting areas of some cavern pairs, described earlier, were not detected for other pairs.

Defence

Three methods of territory defence were observed; standing prominently in full view of neighbours or other birds, posture and associated call, and chase and fight.

Shoreline pairs at Boat Bay, South Beach, and to a lesser extent, at Nellie Spit, were often seen standing conspicuously at the water's edge (Fig. 7) or at the top of the beach beneath over-reaching *Olearia* branches. Their conspicuous presence was usually sufficient to dissuade others from transgressing to feed or rest.

Males responded to the approach of neighbours or intruders by first giving a series of piping or whistle-like calls described by Weller (1975) as

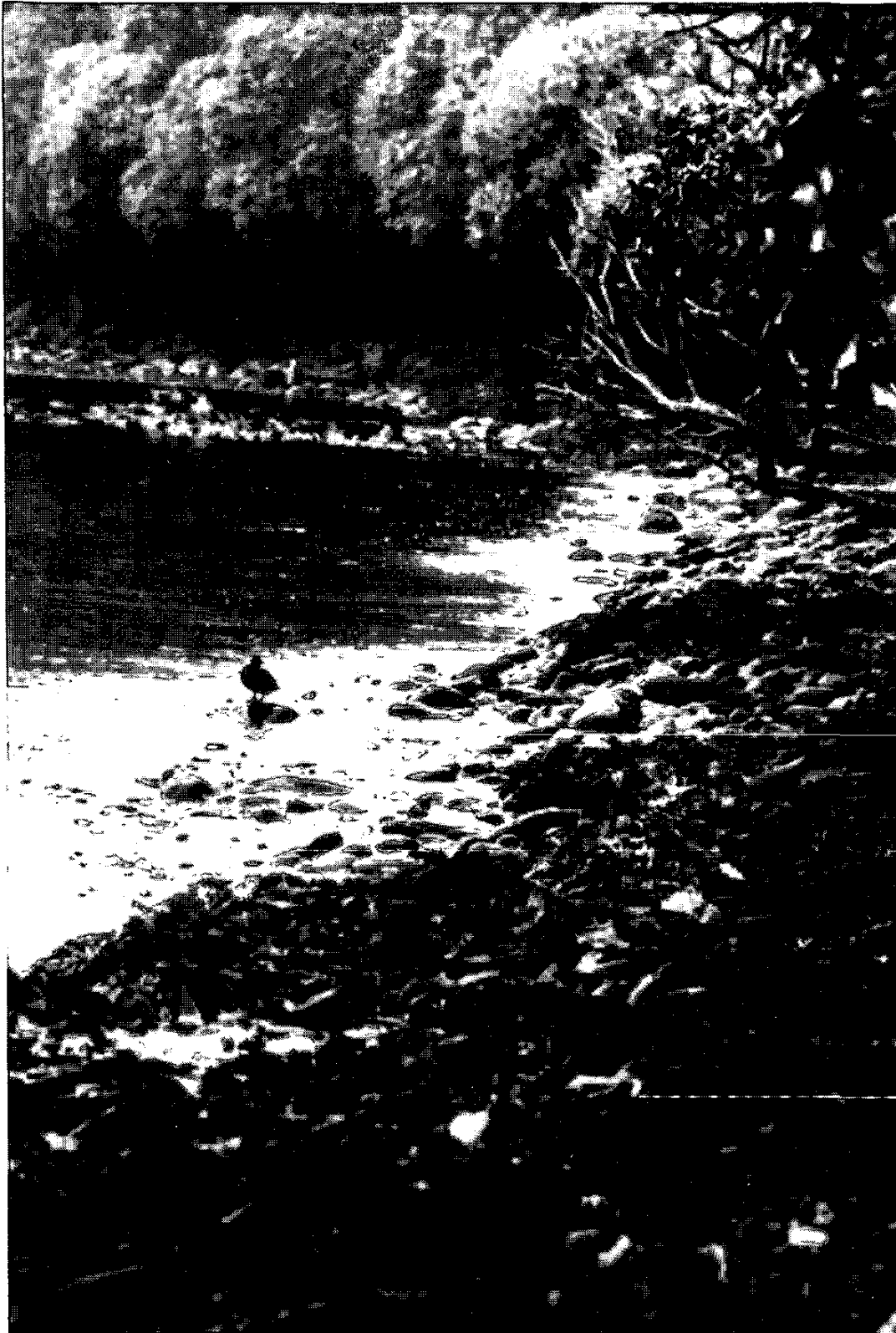


FIGURE 7 – Male Auckland Island Teal standing at the the water's edge on his shoreline territory in Boat Bay. Such conspicuous advertising of territory ownership was shown by all males whose territories extended to the sea.



FIGURE 8 – Interactions between adjacent territorial males generally commenced with trill calls and threat postures as illustrated here. Vigorous fights would ensue if an intruder did not quickly move away.

a “trill”. this call was made when the bird adopted a specific posture - the male stood prominently side-on to the intruder, the head tucked low onto the back and with the bill tilted upward. Generally, this call was sufficient to prevent further encroachment and interaction between the birds. Near territory boundaries, neighbouring males would stand a mere 2-3 m apart and “trill” at each other (Fig. 8). After such an exchange one of the birds would usually move away but if it did not, a chase and fight invariably followed.

Chases and fights were particularly common amongst shoreline pairs at Boat Bay and South Beach. Most territorial males there had large bare patches on their mantle as evidence of the vigour of those fights; the males would be locked chest-to-chest, their bills gripping their opponent’s upper back feathers while each flailed away with their wings, attempting to make full use of the prominent enlarged callous on the leading edge of the carpal flexure. These male to male encounters were often prolonged; eight of 11 timed fights persisted for longer than one minute and one lasted for 2min. 35sec. Disengagement was usually followed by a chase which, if continued into the water, could extend for up to 50 m and end when the chased bird managed to dive and later surface and swim away undetected. Land-based chases were much shorter and I had the impression that once the territory boundary was cleared, the pursuit ceased.

Territorial males also attacked transgressing pairs. At Boat Bay, some of the "subordinate" pairs were attacked whenever they attempted to move onto shore. In most cases there was no preliminary posturing or calling - the male simply raced at the pair and pursued them on to the water. During these chases, the male of the transgressing pair was initially ignored while the territorial male strenuously attempted to catch and mount the female. To escape these mountings, the females would dive and remain submerged for 10-15 secs.; on surfacing, they would swim low in the water with neck outstretched and if possible, attempt to reach the protection of floating kelp amongst which they could hide. However, the pursuing males would also dive and frequently surfaced firmly gripping the female's nape. Only when the female escaped her pursuer was the male of the pair chased, but these chases appeared to be half-hearted and seldom were persistent or vigorous. The territorial male would soon swim back to a prominent rock or disappear under some overhead cover from which he had originally emerged.

Neighbouring territorial pairs were also subjected to similar fights and chases. Several times I saw a known incubating female, while feeding avidly close to a territorial boundary, be vigorously attacked after her partner and the neighbouring male had spent some time trilling at each other. These chases were focussed on the female and so vigorous were the attempted mountings that most territorial females examined had large bare patches on the nape.

The above descriptions of territorial males preferentially pursuing females of intruding pairs corresponds with those of forced extra-pair copulation (FEPC) attempts in other *Anas* species (McKinney *et al.* 1983, McKinney 1985). Weller (1975) reported observing "rape chases" by teal on Rose Island. I did not record whether, during these forced mountings, the male bent his tail below that of the female in order to achieve intromission of the penis and sperm transfer (a diagnostic feature of FEPC attempts: F.McKinney, pers com.). However, two sets of observations may assist interpretation:

- (i) On two occasions I saw a male forcefully mount and copulate his own mate. Both events involved the same pair, one of the "subordinate" pairs present in Boat Bay, and occurred about 10 mins. after the female had been chased and mounted by a territorial male.
- (ii) Chases and mountings of females by territorial males was observed both in March 1982 and April 1983 after breeding had ceased.

These observations suggest that chases and mountings may function both as FEPC attempts and territorial defence.

How grassland territories were defended was unclear. These territorial males responded promptly to broadcast male and female calls by giving the 'trill' call and approaching the source of the sound. However, I doubt that intruders would advertise their presence by calling, leaving resident males the option of making regular patrols around and through their territory via the myriad of small runways amongst the tussock bases. In the grassland on Nellie Spit I regularly heard "trill" calls and chases which suggested that some form of patrolling took place. Interaction there was much more frequent

between two neighbouring pairs with attendant young ducklings (mean 3 interactions h^{-1} , 8 h of observation over 3 days) than between one of those pairs and their other neighbour, a nesting pair (mean 0.4 interactions h^{-1} , 10 h of observation over 4 days).

Pattern of use and activity

The extent of territorial defence and use appeared different at different locations, perhaps reflecting the nature of the terrain and the food resources available.

Nellie Spit pairs.

These four pairs appeared to have divided the grassland habitat between them, using conspicuous features such as prominent *Hebe* bushes, storm-cast logs, and *Stribocarpa* patches as boundary markers. On the beach, the boundaries appeared to be more or less straight lines from grassland to water's edge, modified only slightly by the presence of conspicuous shoreline rockshelves and the contour of the headland.

The relative conspicuousness of these pairs varied (Table 1) and was closely related to their breeding status. Pairs A and C hatched chicks on 12 and 13 December respectively, pair B did so on 14 January while the fourth pair (D) did not commence their nesting attempt until about 10 January. At the base of the spit a "subordinate" pair (E) occupied the headland and attempted to feed on the inner spit.

TABLE 1 – Visible presence on the territory (as percentage of 57 daytime observations between 12 December 1991 and 11 January 1992) of members of five pairs of Auckland Island Teal on Nellie Spit and the percentage distribution of their activities when first seen. "Threat" includes posturing and chasing. Male A was heard but not seen twice, females A and B three times. See text for details of breeding status of each pair.

Individual	Presence (%)	Activity			
		Feed	Rest	Alert	Threat/Flee
Male A	11	17	0	83	0
Male B	11	0	0	100	0
Male C	35	20	70	10	0
Male D	49	25	61	10	4
Male E	25	67	0	27	6
Female A	2	100	0	0	0
Female B	9	100	0	0	0
Female C	7	80	0	20	0
Female D	19	45	55	0	0
Female E	25	100	0	0	0

Conspicuousness was influenced by time of day; all birds were seen more frequently at dusk than at any other time of day. Females A, B, and C were seen on the beach or in the open only during the last two hours of the day. Prior to laying, female D was seen occasionally both during the morning and afternoon. The non-breeding pair (E) was also encountered on the beach

at different times of the day, being present mostly at low tide and when males A and C, over whose territories they fed, were not in view.

South Beach pairs.

The 60 m shoreline of South Beach was defended in small sections by six pairs. In contrast to Nellie Spit, the food available on this beach was also exploited by several other pairs and solitary males. The area over which the kelp accumulated was about 40 m in length and extended 6-8 m back from the water's edge. The territories of resident pairs extended from the water's edge, across the beach and beneath the overhanging *Olearia* branches to the foot of a steeply-sloping 10 m high bank 15-20 m from the sea. These and other pairs visiting the beach were visible only when they emerged from beneath the forest canopy i.e. when they were on the exposed half of the resident pairs' territories.

The breeding status of pairs were as follows: Pair A (Table 3) hatched their eggs on 13 January, pair D nest was still being incubated on 15 January, male C was seen escorting a female and 4-7 day-old ducklings on 23 December, and pair F were escorting 10-12 day-old ducklings on 26 December. The status of pairs B and E were less well known - an unmarked female with a single chick was seen in the range of male B on 13 December, and female E had an enlarged abdomen and appeared about to lay on the same day.

Sixty-three spot observations of South Beach were made between 10 December and 15 January to record teal presence and activity (Table 2).

TABLE 2 - Visible presence on the territory and the percentage distribution of their main activities when first seen of territorial Auckland Island Teal on shoreline territories on South Beach (10 Dec. 1991 - 15 Jan. 1992; 6 pairs, 63 observations) and Boat Bay (9 Dec. 1991- 16 Jan. 1992; 17 pairs, 42 observations), Auckland Island. Data are means. South Beach observations include intruders. "Threat" includes posturing and chasing, "other" includes various comfort movements.

Group, location	Presence (Range)	Activity				
		Feed	Rest	Alert	Threat/Flee	Other
Males, South Beach	28 (16-35)	35	26	25	12	2
Females, South Beach	5 (3-10)	100	0	0	0	0
Intruders, South Beach	58	70	6	6	18	0
Males, Boat Bay	26 (7-4)	41	13	31	10	5
Females, Boat Bay	14 (0-48)	75	17	0	3	5

From these observations three main points emerge:

- (i) All females, when present, were busily feeding;
- (ii) Territorial males devoted more time to guarding their space than to feeding;

TABLE 3 – Visible presence on territory of six South Beach territorial Auckland Island Teal males (A-F) and non-resident intruders on the shoreline of South Beach and the percentage distribution of their activities. "Threat" includes posturing and chasing, "other" includes various comfort movements. Based on 848 one-minute interval observations spread over five days between 23 December 1991 and 4 January 1992.

Individual	Presence (%)	Activity				
		Feed	Rest	Alert	Threat/Flee	Other
Male A	37	11	25	47	2	15
Male B	23	56	13	17	2	12
Male C	19	43	10	10	21	16
Male D	31	35	18	25	19	3
Male E	19	41	11	23	15	10
Male F	11	43	13	23	3	18
Males A-F (mean)		33	16	28	10	13
Intruders	35	68	2	6	17	6

- (iii) Intruders spent the greater part of their time feeding or responding to threats and chases from the resident males.

I made more prolonged observations of South Beach in order to determine presence and activity of resident and intruding birds. This totalled 848 minutes over various periods of five days between 23 December and 4 January, during which time I recorded the activities of all birds present at one minute intervals (Table 3).

These data confirmed that a high proportion of each male's time was spent in territorial defence (alert/stand, threat/chase). However, they understate the amount of time devoted to vigilance. Most males were clearly watching for intrusions from locations where I could not view them. Regularly, when an intruder was feeding conspicuously over the top of the kelp rather than inconspicuously along its seaward face, a territorial male would rush out from beneath the trees and chase it into the water. Yet, periods of three-four hours could elapse when intruders were able to feed unmolested over the claimed area without the resident male making an appearance; perhaps, as was the case at Nellie Spit and Boat Bay, territorial males retreated to a resting place to sleep or bask in the sun.

Collectively, intruders were present on approximately one-third of the sampled times (Tables 2,3) and spent most of their time feeding or responding to attacks or threats from the territorial males.

Boat Bay pairs.

Seventeen pairs were dispersed along the shoreline of Boat Bay including along the back edge of the cavern. On eight (19%) of 42 occasions when the entire bay was scanned to determine the conspicuous presence of pairs, no birds were visible; on two occasions, both towards dusk, I saw members of 14 of the pairs but mostly birds representing 5-7 pairs were visible at any one time.

When visible on the shoreline of the bay, males spent similar amounts of time guarding their territory and/or their mate and feeding (Table 2). However, there was considerable variation between males and not all were equally belligerent. The five males who claimed territories within the vicinity of the cavern and flock site had a much higher rate of interaction than those spaced well apart at the northern end of the bay. Similarly, members of three pairs concentrated about a small rock shelf in the centre of the bay had more recorded interactions with each other and their immediate neighbours than did other pairs scattered elsewhere along the bay.

As at Nellie Spit and South Beach, females, when present on the beach, fed avidly before returning to the safety of the forest to resume nesting or parental duties; only those whose breeding attempt had failed were recorded resting on the beach.

At all three beaches, pairs remained inconspicuous for most of the daylight hours. Males were seen, on average, for about one-third of the time, and females considerably less so.

At all three beaches, intruding males or pairs found opportunities to trespass and exploit the food resources of the beach; only in the obvious presence of the male was that part of the territory an "exclusive area".

IV. BREEDING

Nests

Twenty-seven nests were found on Ewing Island, 20 on Rose Island, and one each on Ocean and Enderby Islands. On Rose Island eight of the nests were found after eggs had hatched, another three nests were occupied by a brood, and in one, no eggs had been laid. Incubating females were present on all other nests when first found.

Nest sites on Ewing and Rose Islands reflected the different vegetation on the two islands (Table 4). Rose Island has a small, central rata forest but the majority of the island is covered with *Poa litorosa* tussock (Taylor 1971).

TABLE 4 – Locations of Auckland Island Teal nests found on Ewing Island (N = 27) and on Rose Island (N = 20).

Nest Site	Ewing Island	Rose Island
Base of <i>Carex</i> spp.	7	4
In fern	12	2
Beneath/ inside log	7	0
Amongst <i>Stilbocarpa</i>	1	0
Base/crown of <i>Poa litorosa</i>	0	14

Nests built in *Carex* were small (10-15 cm diameter), deep (approximately 10 cm) cups composed entirely of *Carex* tillers with a deep base of tiller fragments. Down feathers, after initially being around the nest rim, became incorporated into the nest floor. All nests were wedged into

the base of the *Carex* plant and totally hidden from view by overarching tillers. Three nests in *Carex* had a litter base over 10 cm deep containing old eggshell fragments, indicating that the site had been used previously.

Nests in *Poa litorosa* on Rose Island were composed of dry tillers woven into a deep bowl and tucked into the base of the tussock, well hidden from view. Three nests, built in the tussock crown, were constructed similarly but were exposed to view from above.

Short *Hypolepis subantarctica* fern was a common nest site on Ewing Island. Seldom growing more than 25 cm high, but forming extensive swards, it allowed teal to construct their nests deep within and be overtopped by numerous fronds, so providing a dry and windproof site, even in exposed cliff-top locations. Small tunnels through the fern clumps provided pathways of entry and egress. In the forest, three nests were built amongst the taller and sparser *Polystichum vestitum* fern. Although visible at close quarters from above, these nests also had the protection of the forest canopy.

Six nests on Ewing Island were tucked beneath prostrate *Olearia* trunks, and one was 2 m inside a hollow log. These nests were mere depressions in the mass of fallen *Olearia* leaves which littered the site and when the female was off the nest, eggs were covered by down feathers and leaves.

The single nest in *Stilbocarpa polaris* was, like others, a small deep bowl, and formed entirely from the dead leaves and litter present. The one nest found on Ocean Island was in the base of *Poa litorosa*, that on Enderby Island was amongst *Asplenium obtusatum* fern.

Eggs

The uniformly pale fawn eggs were ovoid and tapered to one end. Ninety-nine eggs from 22, 6 and 1 clutches on Ewing, Rose and Enderby Islands, respectively, were measured. Mean size was 64.8 (S.D. = 2.3) x. 44.8 (S.D. = 1.1) mm, the ranges in length being 59.0-71.4 mm and in width 42.4-47.6 mm.

The average difference between the lengths of the longest and shortest eggs within a clutch was 3.0 mm (range 0-9.1 mm), and between widest and narrowest eggs 1.4 mm (range 0-2.8 mm).

Clutch

A clutch is defined as the maximum number of eggs in the nest bowl throughout the observed period of incubation. In no nest did this change. Clutch size in eight nests that had hatched was determined from the number of eggshell membranes present. In nine of 10 nests found when eggs were present and examined again three to eight days after hatching, all eggshell membranes were accounted for; one of four membranes was missing from one nest when examined four days after hatching.

Mean size of 45 clutches was 3.4 (S.D. = 1.0) and clutches of 1,2,3,4,5 and 6 eggs were found in 1,6,17,15,5 and 1 nests respectively. Clutches of three and four eggs comprised 38% and 26% respectively of 26 clutches from Ewing Island, and 39% and 44% respectively of the 18 clutches from Rose Island. Clutch sizes on Ewing Island (mean 3.54, S.D. = 1.07) and Rose

Island (mean 3.40, S.D. = 0.95) were not significantly different ($t = 0.44$, d.f. = 42, $0.7 > p > 0.6$).

Incubation

The female alone incubated the eggs. During incubation the male either waited at a regularly used hiding place (those found were seldom more than 10-15 m from the nest) or, in the case of birds holding shoreline territories, often stood or rested conspicuously at the water's edge.

No nest was found into which the female laid further eggs so the incubation period was not determined unequivocally. The longest period between finding a nest and its eggs hatching was 30 days (three nests) and one nest contained pipping eggs 30 days after being found.

Incubating females rarely left their nest during daytime. Females were absent from their nest on 10 of 103 occasions that 26 Ewing Island nests were checked during the period 08:00-21:00 NZDT. Most observations of nesting females feeding in their characteristically avid manner were at dusk.

Despite possibly feeding only once each day, some incubating females were heavy; two weighed within one week of hatching their eggs were 520 g and 500 g, and an incubating duck weighed 520 g. A fourth female, weighed four days after completing her clutch, was only 420 g.

Hatching chronology

Searches for nests commenced on 7 December 1991. By 15 December, 21 of the 27 nests eventually recorded on Ewing Island had been found and no new nests were found after 26 December. Because the first brood was not encountered until 11 December, it would seem that, fortuitously, searches commenced prior to hatching. However, the distribution of hatching dates (Fig. 9) may not fully describe breeding chronology; the order in which the nests were found and the order in which they hatched were correlated (Spearman $r_s = 0.72$, $p < 0.01$). Thus, this distribution under-represents those nests that hatched early in the season.

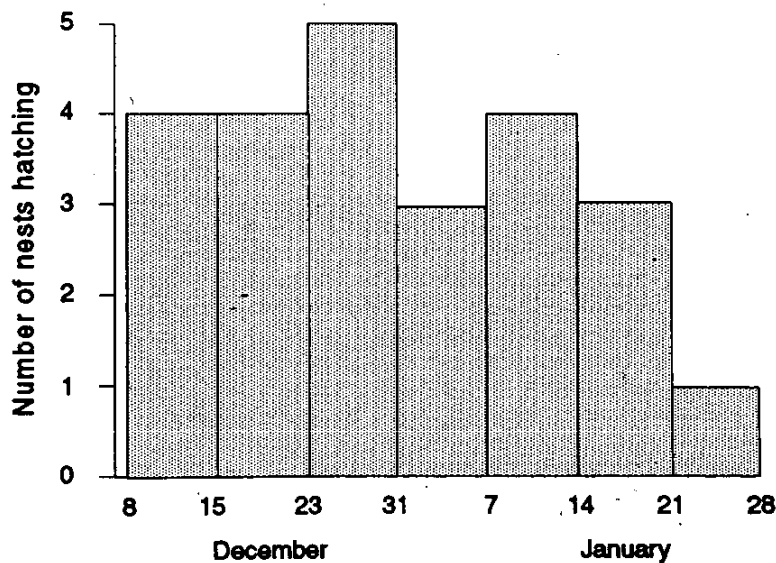


FIGURE 9 – Distribution of hatching dates of 24 Auckland Island Teal nests on Ewing Island, December 1991 – January 1992.

Allowing 30 - 35 days for incubation, and a two-day interval between the laying of successive eggs in the clutch (data from captivity, S. Anderson pers.comm.) these field data suggest that (i) laying commenced at the beginning of November, and (ii) most females initiated their breeding effort within six weeks of each other (but see later for evidence of breeding seasons being more protracted).

Hatching success

Of 27 nests found on Ewing Island, one was not revisited, one deep in a hollow log could not be viewed well enough to confirm clutch and hatch details, and one, sited beneath a log, was deserted, its eggs found scattered but unbroken approximately 50 cm from the nest. Of the 86 eggs which comprised the remaining 24 clutches, all but 6 (7%) hatched (four rotten, one infertile, one near-term embryo). One or more ducklings hatched in each of the 24 nests.

On Rose Island, hatching success in eight nests was determined by counting the number of egg shell membranes and unhatched eggs remaining; 25 of 27 eggs (93%) hatched.

Ducklings

Brood behaviour

Broods were cryptic and furtive and for most of each day the female remained with them at a regularly-used hiding place. Fern clumps and seabird burrows were common daytime hiding places, but so too was the nest site. Three broods on Ewing Island made regular use of the nest bowl, being there throughout most of each day - one brood used theirs for 28 days before a reclining Hooker's Sealion *Phocarctos hookeri* flattened it. Three of 20 nests on Rose Island contained 5-15 day-old ducklings when first located.

Daytime foraging, when undertaken, was always amongst dense cover such as beneath *Stilbocarpa* and *Hebe*, or amongst tussocks and *Carex*. Some broods were seen moving and feeding over the forest floor, especially beneath *Olearia*, but when doing so the ducklings moved rapidly from one piece of cover to another and stayed very close to the guardian adult. Very rarely did pairs with shoreline territories take their ducklings on to the beaches to feed. When they did so, it was usually high tide and the ducklings did not venture beyond the overhead canopy of the sprawling *Olearia*.

At dusk, and during the initial hours of darkness, broods were especially active and their cohesion not nearly as obvious as during daylight. Ducklings frequently lost visual contact with their broodmates and parents as they foraged amongst shoreline rocks and kelp, over wave platforms and the forest floor, and through grassland. High-pitched separation calls from the ducklings and contact calls from the female were very audible during their nocturnal feeding bouts.

Survival

Because few females were banded or individually recognizable, only five families were recorded frequently enough to provide an indication of survival over the first 30 days of life. Two of these occupied adjacent territories in grassland on Nellie Spit, and they hatched on or about the same day.

Interaction between these broods and their parents resulted in four of five ducklings from one brood joining with four in the other. Three days later, the amalgamated brood comprised seven ducklings but over four days thereafter six had been lost; each of the two females involved subsequently attended but one duckling.

Within 10 days of hatching, four of the five study broods had been reduced to a singleton. Three of them remained so at 36, 34 and 32 days after hatching, the fourth had disappeared by day 15. The fifth brood retained its initial four young until day 28 when observations ceased.

Nine other broods were seen during their first eight days of life. One brood of four was exterminated by a Subantarctic Skua as the ducklings left the nest, and the mean size of the other eight was 3.25 ducklings (range 1-5). There were 20 sightings of broods with downy ducklings aged 9-30 days; average brood size was 2.0 ducklings (range 1-4), with eight of these broods comprising but a singleton.

Combining data from all broods seen more than once and applying Mayfield's analysis of survival (Mayfield 1961, 1975; Johnson 1979) yielded the following duckling survival probabilities:

- (i) days 0-8. Daily survival probability: 0.904, s.e. = 0.0228; survival probability to day 8: 0.447, 95% confidence interval 0.296 - 0.662.
- (ii) days 9-30. Daily survival probability: 0.978, s.e. = 0.009; survival probability to day 30: 0.608, 95% confidence interval 0.403 - 0.909.

The probability of a duckling surviving from hatching to 30 days old was 0.272, 95% confidence interval 0.119 - 0.602.

Predation was an observed cause of death. In addition to the skua reported above, one Black-backed Gull twice snatched and swallowed whole ducklings feeding solitarily on the shoreline of Boat Bay. Ducklings also tended to become separated from adults and their broodmates; seven solitary ducklings were seen during daylight wandering about the forest floor or foraging on the shore, where they were vulnerable to predation.

Growth

Field studies ceased before any ducklings had developed conspicuous feathers. The oldest ducklings caught and examined were 33 days old and although tiny scapular feathers were discernible, they were not long enough to protrude beyond the down.

Williams *et al.* (1991) provided a growth curve for three captive-reared ducklings relative to the adult female body mass; those data are reproduced giving actual duckling body masses and culmen lengths (Fig. 10) together with comparable data from four known-aged wild ducklings. Data from the wild ducklings indicates that, at 29-33 days, they were growing at a comparable rate to those raised in captivity.

Parental attendance

The female was usually the adult seen attending the brood, but the male was regularly seen or heard close by. Five readily-identifiable broods were seen in total, 35 times: on 14 occasions only the female was in attendance;

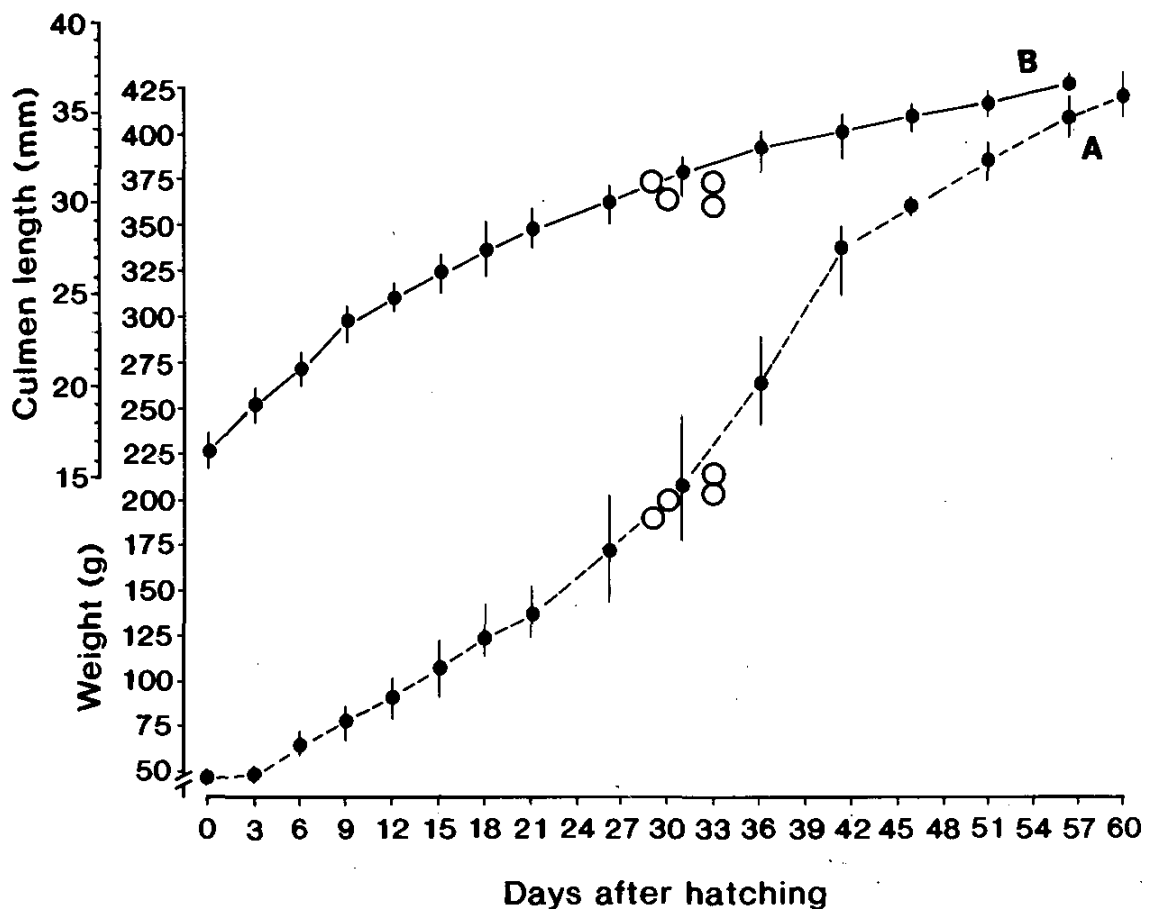


FIGURE 10 – Body mass (A) and culmen length (B) growth curves for three captive raised Auckland Island Teal ducklings (data reworked from Williams *et al.* 1991) and single measurements from four known-age wild ducklings (open circles). Vertical lines indicate range of measurements.

on 21 occasions both adults were present, although on nine of these the male was not immediately visible and was up to 15 m distant. Similarly, from 29 sightings of other broods, 16 had only the female present, 11 had both adults and, twice, only the male was seen. these were not prolonged observations and it is possible that I failed to detect another attending adult. Most of the sightings of males in close attendance to the female and brood were at dusk or early evening.

On 12 occasions adults known to have ducklings were seen feeding without them. Four of the five frequently-observed pairs did this; two fed in exposed locations on the beach of Nellie Spit, the other two pairs did so on a wave platform beneath overhanging *Olearia* at a site to which they had previously brought their brood. Another pair, whose territory was a short section of Boat Bay shoreline backed by a rock wall, regularly left their single duckling in their roosting hole to forage over the kelp, about 6 - 8 m away.

All males which occupied territories along the shoreline of Boat Bay and Nellie Spit and which were known to have ducklings were seen, at times, resting conspicuously on the shoreline or feeding there alone. Females and duckling(s) of three such males were located resting in petrel burrows or in the old nest site while the males were on the shoreline.

Breeding Success

When regular observations ceased on 17 January 1992, some females were still incubating, some still had tiny ducklings, while the breeding attempt of others had already failed. Thus, I cannot record the final breeding success of the studied pairs [but see below for details from 1982 and 1983].

The breeding status of 31 pairs present along Boat Bay, Nellie Spit and South Beach on 17 January was as follows: eight were still incubating, 12 attended broods, eight had failed, and three either had eggs or ducklings because only the male was being observed. All of the failed pairs occupied territories along the shoreline of Boat Bay.

Breeding, moult and social structure in March 1982 and April 1983.

I was present on Ocean, Rose, Ewing and Enderby Islands in the first three weeks of March, 1982 and the first 10 days of April, 1983. Although the purpose of the fieldwork was to determine the numerical status of teal on the various islands (see Williams 1986), I recorded the numbers and size of all broods, whether birds were encountered as singles, pairs or groups, the state of moult of all birds handled, and details of social behaviour. These observations provide an indication of teal biology after the main breeding period.

Breeding activity

Some pairs on all four islands were still attending young. In March 1982, 21 broods and 33 pairs were seen (Table 5). Eight (38%) broods were attended by a single adult. Thus, 39% of adult pairs were still attending young. Some of the 23 males amongst the 32 single birds seen probably represented pairs (as their overt territorial defence would suggest), indicating that, in reality, the percentage of the pairs still with young was perhaps as low as 27%.

TABLE 5 – Status of birds seen on Enderby, Ocean, Rose and Ewing Islands in March 1982.

Location	In flock	Single	Pair	Pair, with chick(s)	Single, with chick(s)
Enderby I.	0	5	13	1	1
Ocean I.	0	2	2	1	0
Rose I.	0	5	3	0	1
Ewing I.	11	20	15	11	6

In April 1983, seven broods were seen: three on Rose Island where 36 birds were viewed (at least 11 pairs) and four on Ewing Island where 58 birds (at least 17 pairs) were seen.

All ducklings were classified according to their stage of plumage development (Williams 1974) and 17 were weighed, measured and their ages retrospectively calibrated from the growth rate curve (Fig.10).

TABLE 6 – Number of ducklings and broods seen on Enderby, Ocean, Rose and Ewing Islands (combined) in March 1982 and on Rose and Ewing Islands (combined) in April 1983.

Duckling age	1982		1983	
	Number of ducklings	Number of broods	Number of ducklings	Number of broods
10-35 days	11	8	0	0
36-45 days	10	5	3	2
>45 days	7	3	6	5
unrecorded	6	5	0	0
Total	34	21	9	7
Mean brood	1.6		1.3	

The ages of ducklings seen in 1982 (excluding one brood on Ocean Island barely 10 days old) ranged upward from 25-28 days old. In 1983, the youngest brood encountered had ducklings with flank and scapular feathers just extending beyond the down and were 36-40 days old. The mean size of broods encountered in 1982 was 1.6 ducklings and, in 1983, 1.3 (Table 6). Sixteen (57%) of the 28 broods comprised but a singleton and apart from one brood each of three and four ducklings, the remainder had two ducklings.

State of wing and tail moult

All adult birds handled were examined to determine the state of their post-breeding moult. Wing and tail feathers, in particular, were inspected to provide an indication of timing of the moult within the population. In 1982, three females guarding chicks were caught, and in 1983 another one - none had commenced wing or tail moult.

In 1982, 26 teal were handled and another 10 pairs were examined at close quarters through binoculars; in 1983, 39 teal were handled and examined. Despite the one month difference in the timing of these two samples, there was little difference in the state of the moult (Table 7). This may indicate that the wing and tail moult is a prolonged event for in 1982, three (12%) of the moulting birds had completed the wing moult but the tail was still growing whereas in 1983, nine (53%) of the moulting teal were at that stage. Of 16 pairs, the state of the moult was synchronous in five, the male was more advanced in five and the female more advanced in six.

TABLE 7 – Numbers of Auckland Island Teal in different states of wing and tail moult on Enderby, Ocean, Rose and Ewing Islands (combined) in March 1982 (N = 46) and April 1983 (N = 39).

Year	Not Moulting	Wing/tail moulting	Moult completed
1982	13 (28 %)	25 (54 %)	8 (18 %)
1983	11 (28 %)	17 (44 %)	11 (28 %)

Social structure

In March 1982, 32 single birds and 33 pairs without young were seen (Table 5). In April 1983, on Ewing and Rose Islands, I saw at least 28 pairs and 38 individuals. Many of the single birds seen were probably members of a pair as six banded males initially seen alone were sighted later accompanying a female. Apart from the small number of birds aggregated as a flock, the population at this time of the year was still dispersed as pairs, many of which showed determined territorial defence.

I found no aggregation of fledglings other than at the cavern in Boat Bay on Ewing Island. The highest count of the flock there in March 1982 was 11 birds, and 15 in April 1983. In 1983, five flock birds were caught: two were recent fledglings, two were moulting adults and one an adult male caught in the near vicinity the previous year. Three other adults caught elsewhere along the shoreline of Boat Bay were also later seen roosting with birds at the flock site.

In both years, pairs were present in the flock. In a group of eight teal in 1982 were two obvious pairs; amongst 12 present the following year were three pairs, plus another female being subjected to close attention by two males. At all times when the flock site was viewed in both years, at least one obvious pair was present.

The shoreline of the cavern was defended by at least three pairs in both years. The flock birds roosted only on the large rocks at the water's edge and fed in the water along the shoreline, coming ashore to feed on the kelp only when the shoreline territory holders were not actively defending their area. The same behaviour was shown during the breeding season in 1991-92.

I attempted to determine the age composition of the flock by discriminating those which looked "cleaner and darker" (fledglings) from the others (adults) which often looked scruffy and/or were obviously moulting. In 1982 I identified only two juveniles (one confirmed as such when caught) present at any one time whereas moulting adults were always part of the flock. In 1983, the flock was never smaller than eight birds when viewed; four of the regular members of the flock were birds banded in Boat Bay the previous year (two as juveniles) and only one of five unbanded birds caught in the cavern in 1983 was a juvenile. The greatest number of juveniles seen at the flock site at one time (when 15 birds were present) was four.

In both years, active territorial defence was observed along the shorelines of Boat Bay, Nellie Spit and South Beach on Ewing Island, along the protected eastern shoreline of Rose Island, and on the streams and small lakes of Enderby Island. Despite my visits coinciding with the birds' moult, territorial defence was pursued with vigour. On South Beach, for example, breast-to-breast pushing and wing-flailing occurred between neighbouring males, one of which was full-winged and still guarding ducklings, the other having no visible primary feathers at all. In 1982, on Ewing Island, I recorded eight territorial altercations, five of them involving males in full wing moult; three were chases of pairs along the shore and out over the water, one was a fight (above), and four involved conspicuous "trill" calls by the defending male. Two of the three pair chases involved the chasing male mounting the fleeing female.

Thus, during March and April, the adult component of the population was dispersed as territorial pairs similar to that observed during the breeding season by Weller (1975) and myself.

DISCUSSION

As a location for the study of Auckland Island Teal, Ewing Island was, perhaps, an unfortunate choice. The island's almost total forest cover is unlike that of all other islands on which the bird presently occurs. About the margins of Auckland Island and over almost all of the small islands of the group, a coastal tall-tussock grassland community dominates, flanked by patches of megaherb and shrubland (Fig.11). *Olearia lyallii*, now so dominant on Ewing Island, is a recent colonist. Lee *et al.* (1991) consider it to have established very early in the 19th century and its spread on Ewing Island to have been at the expense of the coastal grassland on peat soils with high total soluble salts, Na, P and K concentrations derived from the marine aerosol and in areas subjected to high use by sealions and petrels.



FIGURE 11 – Grassland on Ocean Island is typical of the habitat occupied by Auckland Island Teal throughout most of its range.

The replacement of most of Ewing Island's grassland by a forest with, apart from scattered fern clumps, a bare forest floor, has resulted in teal being more visible than on any other island, and thus more amenable to study by direct and prolonged observation. On the other hand, the extent to which its ecology as reported in this paper is "typical" of the species throughout most of its range will remain open to debate until a complementary study is undertaken within a predominantly grassland environment.

Population size and density

Ewing Island has long been considered to house the densest, and probably largest, single population of Auckland Island Teal (Chapman 1891, Falla 1975, Williams 1986, Moore & Walker 1991), a perception obviously based on the birds' visibility there and inconspicuousness elsewhere. The present study identified a minimum of 80 territorial pairs on the island - at the very top of the range of estimates provided by Williams (1986) and Moore & Walker (1991). Allowing for undetected pairs, solitary individuals and the flock, a population in the order of 200 is likely.

Pair density was highest at those locations on the island where kelp was washed ashore, decomposed and supported dense concentrations of kelp flies and amphipods upon which the teal fed. Territories there were as small as 40 m² and comprised but a single hiding or roost site and a defendable food supply. The highest density of pairs and the smallest territories were at South Beach and at the southern end of Boat Bay where the kelp windrows were the largest and the most persistent; territories here seemed to extend only as far back into the forest as was necessary to find suitable overhead cover. Shoreline territories elsewhere, such as at the northern end of Boat Bay and on the southern coast, were distinctly larger. Pairs there ranged over more than 50 m of beachfront and were encountered feeding or wandering short distances back into the forest. Their ranges often included several clumps of fern or clusters of tree debris and petrel burrows that offered both nesting and roosting sites.

There was a similar contrast in the size and density of territories in grassland. Those established on Nellie Spit were considerably smaller than those measured in grassland on the northern and eastern coasts. The principal difference in the two locations was the availability of storm-cast kelp on the shoreline of Nellie Spit; food there was available in abundance at the tidal edge, whereas the other grassland pairs had to derive all of their food from within the grassland.

The most difficult territories to delimit were those of the few pairs dwelling solely within the *Olearia* forest. Using taped calls, I was able to attract one male almost 200 m from the site of initial encounter near the nest, but I have no evidence that the bird defended such a range. During many hours of wandering through the forest, sightings of teal within the forest interior were rare. Twice I encountered adults and ducklings, and three times a pair feeding, during daylight, over the bare forest floor. These encounters were all within 100 - 150 m of the forest edge. The six truly hinterland pairs occupied areas containing dense stands of fern, and

occasionally, *Stilbocarpa*, amongst the windthrown *Olearia*. I gained the impression that the bare forest floor, lacking cover which ferns could provide, was not a place teal chose to be; the replacement of grassland by *Olearia lyallii* forest must have significantly decreased the carrying capacity of Ewing Island for teal.

How does the present density and abundance of teal on Ewing Island compare with that on other islands? Nearby Rose Island (81 ha) has about 15 ha of rata forest fringed by *Dracophyllum longifolium* and *Myrsine divaricata* scrub, with the rest of its surface covered by grassland, mostly the tall tussock *Poa litorosa*. Falla (1975) estimated that approximately 30 pairs of teal resided there. In 1983, capture-recapture studies indicated 50 ± 31 (minimum 36) teal occupied the island (Williams 1986). However, birds were seen only along the coastal margins in the water, on wave platforms, on beaches and amongst *Poa* tussocks at the beach edge; none were seen in the island's small watercourses, amongst grass in the hinterland or in the rata forest.

It is now clear that the numbers of Auckland Island Teal on Rose Island have been considerably under-estimated. Using taped calls and a dog, my colleagues were able to detect teal all over Rose Island in every extensive area of tall tussock grassland (J. Andrew, D. Barker pers.com.) spaced at about 50 - 100 m intervals. They found 20 nests and three broods of ducklings in only three days of effort. A spacing of 50 - 100 m between pairs implies a territory or home range of 2000 - 8000m²; at least two of the eastern grassland territories on Ewing Island were judged to be of this size. As a conservative estimate, Rose Island may contain 100 pairs of teal.

Moore & Walker (1991) reported sightings of 74 teal (including 24 pairs) along approximately 23 km of the Carnley Harbour shoreline of Adams Island in late November 1989. A small flock of up to 11 birds feeding together on a delta at the head of a sheltered bay was their only sighting of birds other than as singles or pairs. They also reported the presence of teal in streams away from the coast and amongst dense megaherbs on the south side of the island. Subsequently, in February 1993, broadcasting of taped calls elicited responses from teal at numerous locations in the alpine grassland of Adams Island (K. Walker pers.com.) indicating the presence of teal in a variety of habitat types on the island although at undetermined densities.

Disappointment Island (Fig.2), like Rose Island, is covered predominantly by tussock grasses and megaherbs. Teal have been sighted on the island's summit and in the seepages draining into Castaway Cove (pers. obs.). In February 1993, broadcasting of taped calls elicited responses from teal over much of the island, and, on the more open ridge tops, those responding appeared to be 50-100 m apart (K. Walker, C.J.R. Robertson pers.com.).

Thus, it seems that territory or pair density along the kelp-strewn beaches of Ewing Island was greater than that recorded from the coastlines of other islands. However, within the island's remnant grassland on the eastern coast this density was probably similar to grassland habitat on most other islands. Forest areas with uniformly bare floor seems to be unappealing habitat everywhere.

Social organisation

The most conspicuous feature of the social organisation of this population at breeding time was its dispersion as territorial pairs. More than 90% of the birds detected on the island were separated in this way. Territories appeared to be fixed geographic entities in which the nest was located, the brood was reared and most feeding took place; in short, they provided all necessary resources to support the breeding effort.

However, there was some apparent flexibility in the way resources were acquired, used and defended. Pairs endeavouring to claim space in localities where abundant food accumulated (e.g. Boat Bay, South Beach) had to contend with the determined and persistent encroachment of other birds. Despite considerable effort (e.g. Tables 2,3), the resident males were unsuccessful at protecting their terrain for their exclusive use even though their territories were amongst the smallest I measured. I was unable to determine whether such concerted territorial defence inflicted some reproductive cost.

Clearly, some males, such as a few of those recorded at the Boat Bay flock site, did wander beyond the confines of their territory to seek food. At South Beach, birds whose territories were in the forest edge above the beach, made regular sorties, mostly in the dark, through the territories of shoreline pairs to feed in the kelp piles.

The defended feeding range and nest locality of three pairs were separated; all were shoreline occupants of the cavern in Boat Bay. Despite all their feeding being done on the shoreline, their nests were amongst ferns and grass on the cliff top immediately above the cavern. There was no way to clamber to the nest other than by passing through the territories of at least two other pairs, a particularly dangerous venture for the females who appeared to undertake the journey without the company of their mates. All of these males vigorously defended their shoreline ranges but one of them later abandoned the area to raise his brood in the grass and forest close to the nest site.

Elsewhere, and away from the abundant concentrations of rotting kelp, the territories appeared to be exclusive, all-purpose ranges that were vigorously defended and continuously occupied by the pair.

The dispersion of the bulk of the population as pairs on territories may well be a year-round feature of teal biology. Not only during the breeding season but as late as April, when some birds were moulting and others had completed their moult, a significant proportion of the population was recorded as pairs and vigorous territorial defence observed. Although there are no published accounts of teal behaviour during winter, approximately half of the birds seen on shorelines and freshwater pools during a fleeting visit to Ewing and Enderby Islands in June 1984 were in pairs (J. Cheyne pers. com.).

Year-round territoriality of adults implies that life for each year's crop of fledglings involves either gathering together as a flock at some readily available feeding site(s), living a furtive life amongst occupied territories, or immediately attempting to establish themselves as territory holders.

Neither Weller (1975), Moore & Walker (1991), nor I, recorded significant flocks during or after the breeding season. The flock at Boat Bay has not been seen to exceed 15 birds (in April 1983). During the breeding season the highest count has been nine but with 14 individuals attending (this study). Weller (1975) confirmed the presence of immature birds in this flock in December by reporting that three males he collected "had poorly developed sex organs and worn dull plumage, like yearlings". However, the flock I observed contained: one male at least three years old who clearly had no mate or territory; a pair without a territory; males with distant territories but who exploited the food resources surrounding the flock site; and males that wandered between the flock site and the other area of abundant feeding at South Beach. In other words, both breeders and non-breeders attended the flock site. Considering that only one flock persisted on the island, that it was consistently small relative to the total population of teal on the island, and that a few territorial males were sometimes present in that flock, it seems that, for young, unpaired or non-territorial birds, gathering together as a flock is not a major pre-breeding strategy.

Perhaps the significant observations were those of five apparently solitary birds living furtively in the grasslands. Two of these birds (one male, one female) had anatomical features typical of young immature birds, and light body masses relative to those of territorial birds. Two males, one of which was at least three years old, also appeared to "wander" amongst some of the grassland and forest margin territories suggesting they were unpaired. These solitary individuals would not want to advertise their presence too boldly so it is very likely that I failed to detect many other solo-living birds. On the other hand, if they were seeking unoccupied areas or looking to disrupt existing pairbonds, they would need to interact with some of the territory holders and physically engage resident males.

What remains to be determined is how widely solitary individuals wander and whether they show any natal affiliation with areas in which they attempt to reside. All seven sightings of a young female in grassland on the eastern coast were at the same location, four sightings of another lone female were also within a small radius of each other and both sightings of a young male were only 10 m apart. While these observations suggest that solitary individuals may have a small range, the movements of two adult males I also judged to be living solitarily were more extensive and ranged through areas occupied by several pairs. Clearly, more sightings of genuinely solitary individuals are needed to resolve this aspect of teal social organisation. As for natal affiliation, the relatedness of neighbouring territory holders needs to be established.

Another route to entering the breeding component of the population may be that demonstrated by "subordinate pairs". I have interpreted their behaviour as indicating they were without ownership of feeding and breeding resources and on the lookout for opportunities to obtain them. Persistence of attempt may be the tactic by which they eventually force their way between existing pairs and, with that toe-hold, attempt to expand their range and resource ownership. Constant conflict with the same pairs may lead to an opportunity to beat and evict the residents, or effect a change of pairing. The pairs I saw acting in this way were all at the shoreline where the

proximity of the water afforded them escape and feeding opportunities. It may be considerably more difficult and more risky for a pair to adopt this tactic away from the shoreline, in grassland and forest habitat, where they would be surrounded on all sides by territorial pairs intent on evicting them. Perhaps this is why I gained no hint of the presence of "subordinate pairs" elsewhere on the island.

Breeding

Although I concluded that breeding was restricted to territorial pairs, I could not determine whether every territorial pair attempted to breed. Detectable evidence of a breeding attempt was limited to finding a pair's nest, sighting a pair with ducklings, or detecting an active or re-feathering brood patch on a territorial female. For about half of the pairs, I failed to find any of these. Does this imply that some did not attempt breeding?

In Boat Bay, I obtained evidence that 15 of 17 pairs attempted breeding, yet despite using the dog in this area on several occasions, only seven nests were found. Broods of five pairs were seen only once (at one to eight days old). At various times thereafter only the adults were seen, and despite evidence that some pairs would "park" their brood and go off feeding without them, I concluded, from the pattern and frequency of sightings, that they had lost all of their ducklings. Clearly, I may have failed to see some pairs attending ducklings at all before their brood was exterminated. Given this possibility, and that the breeding effort of only two of the 17 pairs was undetected, it seems reasonable to conclude that all territorial pairs here attempted to breed.

Of the four pairs resident in the grassland of Nellie Spit, the nests of two and the broods of three were located. However, the breeding cycle of the fourth was considerably different and only at the very end of the study period did the sudden change in the conspicuousness of the female indicate that nesting was underway. This indicates that there may be significant variability in the timing of breeding attempts (a point emphasised by finding unfledged young in March 1982 and April 1983) and suggests that my study did not commence early enough nor persist long enough to detect all breeding attempts.

Timing and extent of breeding season

The duration of breeding is longer than this study would suggest. On Ewing Island I saw the first brood on 11 December, the first hatched nest was found the following day, and at 17 January, the oldest brood was 36 days old. However, in early March 1982, the younger of the broods encountered were, based on body mass and measurement, 25-28 days old, (the youngest was 10 days on 13 March), while, in early April 1983, the youngest ducklings were 36-40 days old. Combining data from all years and allowing a 40-day laying and incubation interval, suggests that nest initiation occurs throughout the months of November, December and January, hatching can extend from early December to the end of February, and that the last ducklings may fledge at the end of April.

If, in 1981-82, 1982-83 and 1991-92, the general timing of breeding was not significantly different, then the combined data infer two nesting pulses, perhaps indicating replacement layings. The 1991-92 chronology (Fig. 9) was shown to under-represent early nestings; in other words December hatchings were more numerous relative to those in January than Figure 9 records. Table 6 records that half of the broods seen in March 1982 were in the order of one month old and that the smallest number of aged broods were in the oldest age class. One explanation for this is that in late December - early January a second burst of laying took place i.e. about three - four weeks after the initial hatchings. Early loss of the brood could well prompt a repeat laying in an environment where food is available in abundance, and the high proportion of younger broods in 1982 (and somewhat less emphatically in 1983) is evidence of that. I failed to detect this phenomenon in 1991- 92, because the dog was not used on Ewing Island after 26 December.

Productivity

A conspicuous feature of the teals' reproductive efforts was the rapidity with which broods were reduced to a singleton; 57% of 28 broods half-grown or older encountered in 1982 and 1983 had only one duckling while, in 1991-92, 40% of 20 broods 9-30 days old were singletons. Additionally, four (80%) of five study broods were reduced to this size within 10 days of hatching. Clearly, a significant number of broods must perish very quickly.

I hesitate to apply these findings to the population as a whole, however. Most of the pairs and broods comprising these data were the conspicuous ones. That very conspicuousness may have made them more prone to predation and, thus, early brood reduction. There was a hint that, away from the Boat Bay and South Beach shorelines, the same early loss and reduction did not occur. Eight of the 20 broods 9-30 days old recorded in 1991-92 were seen within the forest or grassland; only two of these were singletons and three each comprised four ducklings. In contrast, six of 12 shoreline broods were singletons and only one comprised four ducklings.

Data gathered during this study were not sufficient to estimate annual productivity of the population with confidence but suggested the following:

- (i) about half of the ducklings hatched died within eight days;
- (ii) close to three-quarters of all ducklings hatched had died by day 30;
- (iii) if the daily survival probability of 9-30 day-old ducklings (0.978) applied throughout the second 30 days of duckling life, only about 14% of hatchlings may survive to fledging;
- (iv) the breeding status of 1991-92 pairs (at 17 January) indicated eight (35-40%) of 20-23 pairs that had attended ducklings had lost their entire brood within 30 days;
- (v) renesting by some failed breeders is likely;
- (vi) mean size of observed broods (data from all years combined) were: Age 1- 8 days, N = 19, mean size 3.2; Age 9-30 days, N = 32, mean size 1.8; Age 30-45 days, N = 9, mean size 1.7; Age >46 days, N = 8, mean size 1.6; and

- (vii) based on a mean brood size at hatching of 3.4 (the mean clutch size), 14% duckling survival to fledging, and a mean brood size at fledging of 1.6, up to two-thirds of all pairs may fail to raise young in any year.

In short, Auckland Island Teal have a low breeding rate and low annual productivity at both the individual and population levels.

Parental care

The Auckland Island Teal is one of a growing list of tropical and southern hemisphere dabbling ducks (*Anas* spp.) in which males are reported to accompany the female and brood (McKinney 1985, 1991; McKinney & Brewer 1989). McKinney (1991) has suggested that, in some species which retain pairbonds year-round, male parental care evolved in response to the hazardous nature of brood habitats and the predation pressure to which the ducklings are exposed. He noted that, in species occupying hazardous brood rearing sites, such as white water sections of rivers, open water areas devoid of escape cover, terrestrial habitats, and areas of very dense vegetation, males actively contributed to the care of the young.

Brood habitat on Ewing Island can readily be described as 'hazardous'. Ducklings reared on shoreline territories fed predominantly amongst the exposed windrows of kelp where they were especially vulnerable to predation by Subantarctic Skuas and Black-backed Gulls. All eight pairs which lost their entire brood occupied shoreline territories. Grassland territories may be 'hazardous' for another reason; some ducklings quickly became separated from the female and broodmates (e.g. Nellie Spit broods) and some were seen wandering alone in the forest edge or on the adjacent shoreline.

I observed males contributing parental care by:

- (i) detecting and signalling danger to the female and ducklings;
- (ii) responding to the calls of separated ducklings;
- (iii) waiting for and escorting straggling ducklings; and
- (iv) escorting the brood.

Males were also seen chasing other pairs away from the vicinity of their broods but this behaviour could be equally interpreted as territorial defence.

Males were not always obviously accompanying a brood; approximately half the observations of broods recorded only the female in attendance. Some males rested conspicuously on or actively defended their territory while their brood and female were resting and, frequently, they were seen feeding alone during the day. However, where were the unobserved males when their broods are active? Once a male resting on the shoreline of Nellie Spit responded to the calls of his female when she and her ducklings were attacked by a neighbouring male while moving about in the nearby grassland. On another occasion a male was disturbed from beneath a clump of fern while his female and brood were feeding 20-30m away on a wave platform. On the tiny 40 m² cavern territory in Boat Bay, the male frequently remained at rest within a small cliff hole or amongst some shoreline debris while his female and duckling fed, but the family was always visible to him. Except for these three examples though, the activities of the absent males were undetected.

Males with broods have two simultaneous tasks - providing care for the brood and ensuring territory defence. To a large extent males seemed to temporally separate these tasks. Almost all of the observations of parental males conspicuously resting on their territories or actively defending them were during daylight when most broods were inactive. Most (79%) of 47 sightings of males accompanying broods were during the dark, a time when skuas most actively hunted teal and petrels on the forest floor and shorelines (Weller 1975, pers.obs.). However, it was at dusk that 71% of the sightings of females alone with their broods were made. Dusk was the most active part of the teal day and the time when many territorial intrusions were seen or heard. I suspect males not close to their brood at that time were actively patrolling their territories.

Comparisons with other Australasian teals

Grey Teal *Anas gracilis*, Chestnut, Brown and Campbell Island Teals are considered close relatives of Auckland Island Teal (Delacour 1956, Livezey 1990). These Australasian teals now occupy diverse and contrasting niches ranging from continental Australia to large, small and isolated islands from the tropics to the subantarctic. Their contrasting spacing behaviour, mating systems, social organisation, signal systems, diet and population ecology provides one of the best examples of the adaptive radiation of waterfowl and, in particular, graphically illustrates the importance of ecological factors in shaping social systems, behavioural repertoires and reproductive characteristics (Frith 1967, Lack 1970, Weiler 1980, Marchant & Higgins 1990, Williams *et al.* 1991).

While the results of this study provide more data for Auckland Island Teal upon which to base comparisons, they do not alter conclusions derived by using limited reproductive data, for example, by Williams *et al.* (1991) in their comparison of the ecology and behaviour of the four brown-plumaged Australasian teals. However, the larger sample of eggs and clutches than hitherto available and field mass of breeding females requires some alteration of the widely-quoted statistics on relative egg and clutch mass (e.g. Lack 1968, 1970; Rowher 1988, Livezey 1990) as outlined in Table 8.

No other Australasian teal is presently known to reside year-round as pairs on territories or to have a non-social courtship and pairing system. In this respect, Auckland Island Teal have spatial and mating arrangements that, within the Anatini, seems to be shown only by riverine species (Anderson & Titman 1992). Although several *Anas* ducks are endemic to small islands (Lack 1970, Weller 1980), none has yet been described to have a social system comparable to that of Auckland Island Teal. Perhaps the most similar system known so far is that of Brown Teal in northern New Zealand where some adult pairs have been found throughout the non-breeding season in sections of streams or on ponds that were part of their breeding season's range (unpubl. data). However, in the generally agricultural environment in which the species now struggles to survive, most adults seem to leave their territories after breeding and join with juveniles in large summer flocks possibly forming new pairings there prior to the next breeding effort (Dumbell 1987).

TABLE 8 – Body mass, clutch and egg size and mass of four species of Australasian teals.

	Auckland I. Teal ¹	Brown Teal ²	Chestnut Teal ³	Grey Teal ⁴
Male breeding mass (g)	560	721	683	507
Female breeding mass (g)	480	663	593	474
Clutch size	3.4	6.0	8.9	8.3
Egg length (mm)	64.8	60.4	53.3	50.0
Egg breadth (mm)	44.8	43.2	38.4	36.0
Egg mass (g)	71.2	63.3	44.0	36.0
Egg mass as % female breeding mass	14.8	9.5	7.4	7.6
Mass of clutch as % female breeding mass	50.4	57.3	66.0	63.0

¹This study; Mass: male N = 11, female N = 8; Egg mass - from equation $\text{Mass (g)} = 0.547 \times \text{length (cm)} \times \text{breadth (cm)}^2$ (Williams, unpublished).

²Mass: male N = 38, female N = 22 (Williams, unpublished); Clutch - Dumbell (1987) and Williams (unpublished); Egg size/mass - Reid & Roderick (1973) & Williams (unpublished).

³Mass - Norman & Hurley (1984) sourced from all times of year; Clutch/eggs - Norman (1982), Marchant & Higgins (1990).

⁴Mass - Frith (1967) sourced from all times of year; Clutch - Marchant & Higgins (1990); Egg size - Frith (1967); Egg mass - Rohwer (1988).

Another distinctive feature of Auckland Island Teal relative to other Australasian teals is their highly terrestrial lifestyle. Although, on Ewing Island, the bulk of the population was dispersed around the coastal margins, the majority of teal on nearby Rose Island, and on the larger Disappointment and Adams Islands, live well away from the coast in the damp *Poa/Carex* grasslands. There is an exclusively terrestrial way of life in what appears to be a remarkably stable environment, both seasonally and annually.

Finally, and perhaps most distinctively, is the flightlessness, a characteristic shared only with nearby Campbell Island Teal amongst *Anas* ducks and with two species of Steamer Ducks *Tachyeres* of the Magellanic region of South America and Falkland Islands (Livezey & Humphrey 1986) amongst other extant waterfowl. What is it about the subantarctic or island environment that has promoted such extensive reduction in wing size (largely the result of a shortening of the primary remiges) and a disproportionately small pectoral muscle mass in the teal (Livezey 1990) - and also in the recently extinct Auckland Islands Merganser (Kear & Scarlett 1970, Livezey 1989)? Why, in Australasian teals, has the tendency to flightlessness been accompanied by decreasing body size when, in all other avian groups (and in Steamer Ducks), body size increases (Pennycuik 1975)? McNab (1994a,b) has presented hypotheses linking body size reduction (and thus reduced energy expenditure) to lower resource availability and use on islands but notes that "... the evolution of a flightless condition appears to be more central to [island] survival in rails [Rallidae] than in ducks". Livezey (1990) interprets the range of skeletal reductions as "paedomorphic conditions [= retention of embryonic or juvenile characters in the reproductive adult], adaptive as developmentally economic changes related to year-round residency in a

predator-depauperate insular environment, and are most likely the result of progenesis [= early onset of sexual maturity]". However, attempted explanations which fail to consider and account for concomitant changes in ecology, behaviour and reproduction in this species (Williams *et al.* 1991), and others (e.g. Livezey 1992 a,b) still leaves many questions unanswered and invites further contributions. The comparative biology of the Australasian teals still has much to contribute to the understanding of these, and similar, evolutionary processes.

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