

Breeding of brown teal (*Anas chlorotis*) at Okiwi, Great Barrier Island

DAVID BARKER

Department of Conservation, Private Bag 92055, Port Fitzroy, Great Barrier Island, New Zealand
Present address: 14 Dillons Point Road, Blenheim, New Zealand

MURRAY WILLIAMS

Department of Conservation, P.O. Box 10-420, Wellington, New Zealand
Author for correspondence: mwilliams@doc.govt.nz

Abstract Breeding performance of brown teal (*Anas chlorotis*) nesting in a pastoral environment at Okiwi, Great Barrier Island, New Zealand was studied during 1997-99. Mean (\pm SD) clutch size in 47 nests was 5.4 (0.9), eggs hatched in 74% of nests ($n=50$), and 66% of eggs ($n=236$) hatched. Of 31 females fitted with radio transmitters, the nesting attempt by 7 (23%) was not detected and the remainder fledged a total of 15 young, a mean (\pm SD) annual productivity of 0.5 (1.3) fledglings female⁻¹. Most broods (72%, $n=32$) became extinct within 10 days of hatching. Limited wetland habitat in the pastoral landscape concentrated nesting and brood rearing. Breeding statistics from this environment may not be representative of the wider population.

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INTRODUCTION

Great Barrier Island is the last significant stronghold of brown teal (*Anas chlorotis*) (Williams & Dumbell 1996). From being a ubiquitous species on lakes, streams, and swamps throughout New Zealand and on Chatham Island at the dawn of the 20th century (Buller 1888; Hayes & Williams 1982; Dumbell 1986), brown teal have plunged toward oblivion in the wake of pastoral farming and the introduction of a plethora of carnivorous mammals (King 1984; Bell 1991). Absent from Chatham Island since about 1915 (Fleming 1939), brown teal were last reported on Stewart Island in 1980 (Dumbell 1986). Extirpation on New Zealand's main islands appears imminent. The last South Island population, in Fiordland, has been reduced to a tiny remnant, apparently by stoat (*Mustela erminea*) predation, and is now being hybridised to extinction (Gemmell & Flint 2000). The North Island residuum, in Northland, has

declined by 65% during 1988-99 and teal are restricted presently to an enclave covering a mere 20 km of the province's eastern coastal lowlands (Parrish & Williams 2001). Great Barrier Island presently is refuge for over 80% of the world's brown teal (Williams & Dumbell 1996).

On Great Barrier Island too, teal numbers have declined recently. Counts of birds at flock sites in summer since 1986 record significant reductions, especially in the centre and north of the island (Dumbell 1987; Williams & Dumbell 1996; Barker 1998, 1999). The central Awana population which, in 1986, contained almost 25% of the island's teal population had, by 1999, declined by c. 85%. The northern Whangapoua population contained, in 1986 and 1987, c. 60% of the island's teal; numbers there have declined steadily at about 5% yr⁻¹ to be, in 1999, merely half of its 1986 size. While Awana and Whangapoua are coastal lowlands with the lowest densities of human settlement on the island, they are also areas where intensive pastoral farming is most concentrated. Intensive cattle grazing and stock trampling can destroy brown teal breeding and refuge habitat and have been

implicated in local population declines and expiry (Guthrie Smith 1927; Williams 2001).

The role of predators as agents of the brown teal's decline on Great Barrier Island have yet to be resolved. The island lacks brushtail possum (*Trichosurus vulpecula*) and mustelids (*Mustela* spp.), predators implicated in the decline of brown teal in Northland (Hayes & Williams 1982; Williams 2001). However, there are feral cats (*Felis catus*), 2 species of rat — kiore (*Rattus exulans*) and ship rat (*R. rattus*) — are widespread, and domestic dogs (*Canis familiaris*) are allowed to wander unattended. Cats and dogs have been identified as predators of adult teal on Great Barrier Island and elsewhere (Hayes & Williams 1982; Barker 1999; Williams 2001). Both rats are known predators of birds, especially at nests, and brown teal eggs lie within the size range they can break (Holdaway 1999). Rats have been recorded visiting unattended teal nests (D. Agnew pers. comm.). Known avian predators of teal include Australasian harrier (*Circus approximans*) and pukeko (*Porphyrio porphyrio melanotus*) (McKenzie 1967). The latter often occurs in stunningly high densities (>50 ha⁻¹) in some of the island's wet *Juncus* spp.-dominated pastoral areas (DB pers. obs.). In the face of these widely distributed predators, mortality rates of adults and juveniles may simply be too high to be balanced by current productivity.

Nesting and brood rearing, which extends over 3 months, is a time of special vulnerability for ground-based species like brown teal. As a response to the exclusively avian predator guild of pre-human New Zealand, brown teal evolved a predominantly crepuscular-nocturnal activity cycle and relied on dense vegetation to provide daytime resting sites, nesting sites, and escape cover for their broods. During breeding, brown teal are dispersed, characteristically, as territory-holding pairs with restricted and (mostly) exclusive feeding and brood rearing ranges, often along watercourses, in marshland or about the edges of waterbodies (Marchant & Higgins 1990; Williams 2001). On Great Barrier Island this dispersion, which also extends into damp, grazed pastoral areas (Dumbell 1987; Marchant & Higgins 1990), places brown teal in habitat in which pukeko appear to be most abundant, while the teal's activity cycle overlaps that of most of its known and potential predators. Within the pastoral environment the generally cryptic behaviour of this small dark-plumaged duck may provide little protection for its reproductive efforts, and annual productivity may be significantly affected.

It was against this background of uncertainty about demographic processes within the Great Barrier Island population of brown teal that we

attempted to quantify the outcomes of teal breeding attempts in pastoral environs at Okiwi.

STUDY AREA AND METHODS

The study was confined to 225 ha of Okiwi Station (Fig. 1), a mixed sheep and cattle farm lying on slopes at the head of Whangapoua estuary in northern Great Barrier Island (36° 08'S, 175° 24'E). We chose this area because it appeared to be representative of the pastoral areas within the Whangapoua basin in which brown teal were known to feed and nest. It had the added advantage of being close to a flock site (see below), and its elevated and uneven terrain and mix of pasture and wetland areas allowed field observations to be conducted with minimal disturbance to the teal.

From the upper estuarine edge and the tidal reaches of Whangapoua Creek, the land within the study area slopes towards the head of the basin and its high points of Coopers Castle (450 m a.s.l.) and Hirakimata (Mt Hobson, 621 m a.s.l.). The pastoral area of the slopes extends to about 100 m a.s.l. and thereafter the basin is swathed in regenerating mixed broadleaf-podocarp-kauri (*Agathis australis*) forest, the lower margins of which are dominated by kanuka (*Kunzea ericoides*). The Whangapoua Creek formed the southern margin of the study area; the northern limits were near the Okiwi settlement.

Within the pastoral environment were numerous seeps, some of which trickled continuously throughout the year while others dried up during prolonged dry spells in summer and autumn. Natural hollows, shallow scrapes, old drains, and 3 stock ponds were included within the studied area. Kikuyu grass (*Pennisetum clandestinum*) dominated much of the pastoral area and in regions from which stock were excluded it grew rank and formed thick, impenetrable mats. In damp grazed areas, rushes (*Juncus* spp.) grew in abundance while clumps of *Carex virgata* and *Cyperus ustulatus* were prominent in seeps and around areas of permanent water.

Teal nesting in the study area also frequented the upper tidal reaches of Whangapoua Creek, aggregating there as a flock, especially during December - May. This flock site (Fig. 1), 1 of 5 such sites within the Whangapoua basin at which teal numbers were regularly monitored (Williams & Dumbell 1996; Barker 1999), also had some birds present throughout the breeding period (July-October).

Annually in April-June, before breeding started, teal feeding at night in seeps and hollows in the pastoral areas or who were residing in the creek during the day, were caught using hand nets and mist nets respectively. Over the 3 years of study, 95

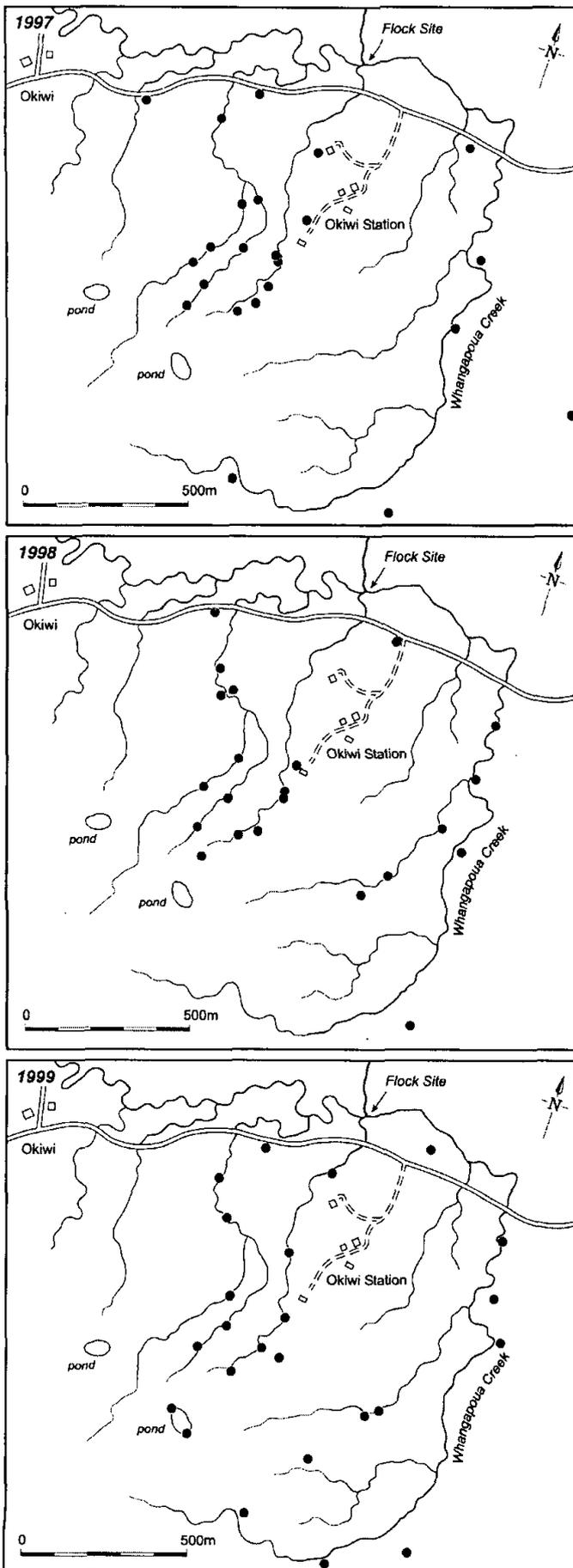


Fig. 1 The Okiwi Station study area for brown teal (*Anas chlorotis*) showing the location of Whangapoua Creek flock site and the dispersion of nests in 1997, 1998, and 1999.

teal were caught and leg-banded with individual combinations of coloured plastic bands and a numbered metal band. Radio transmitters (tx) were fitted to 7 females in 1997, 14 in 1998, and 17 in 1999. The 31 females who remained within the study area and whose transmitters remained active were monitored, at night and at day, at least once-weekly throughout the ensuing breeding periods. They comprised the sample upon which the proportion attempting nesting was determined.

Nests were located each year using a pointing dog (German short-haired pointer) or by monitoring daytime locations of tx females and subsequently inspecting the places they used regularly. To minimize desertions, females were not disturbed at the time of nest location but the nests were visited later when the females were absent, or immediately after hatching. Clutch size was determined by counting the number of eggs present or the number of eggshell membranes remaining immediately after hatching. In a successful nest, 1 or more eggs hatched. Unhatched eggs in successful nests were broken open to determine their fertility and state of development.

In 1997 and 1998, broods of ducklings were encountered during regular thrice-weekly night-time searches throughout the study area. The number of ducklings in each brood was recorded and classified according to plumage characteristics. Whenever possible the identities of accompanying adults (if banded) were determined. In 1999, only broods of the tx females were followed, by locating each female at night every 2nd day from hatching until their broods either attained plumage class IV or disappeared.

Plumage classes were defined as follows: Class I (C.I) – duckling newly hatched, body rounded, neck/tail not discernible, appears as small fluffy ball, 1-7 days old; C.II – duckling completely down-covered, head and neck obvious, body shape long and oval, no contour feathers, 8-24 days old; C.III – first feathers appear on flank, then on shoulders, other contour feathers and secondaries develop, face remains down-covered, 20-40 days old; C.IV – face loses down cover, remaining down on nape and rump gradually disappears, predominantly feathered but not capable of flight, 35-50 days old; C.V – young able to fly but still aggregated as a brood. (Williams 1974, unpubl. data).

RESULTS

Breeding attempt

In 1997, 5 females carried active transmitters throughout the breeding season and the nests of 4 were found. For the 5th female, all 25 daytime radio fixes during July–October were from the

flock site on Whangapoua Creek. She was observed on 14 nights while feeding in pastoral areas, when twice she was accompanied by a male, but during none of the observations did she appear to have a distended abdomen typical of a gravid female.

In 1998, 10 females carried active transmitters throughout the breeding season and the nesting attempts of 8 were detected. Both females for whom no evidence of nesting was obtained nested in the previous year. One was located regularly in daytime in the same wetland in which she nested in 1997, and at night, often accompanied by a male, at the same feeding site used previously. Despite concentrated searches using the dog, no nest was located. The 2nd female was apparently displaced from her nesting and feeding areas of the previous year and spent most time in another small pastoral seep where never, during 16 observations at night over 41 days, was she seen accompanied by a male.

In 1999, 12 (75%) of 16 females carrying active transmitters were confirmed as having established a nest, laid, and commenced incubation. Of those that were not:

(1) 44 daytime radio fixes were obtained on a female that showed a pattern of strong site fidelity over a 2-week period in early August, typical of a nesting bird. However, she shifted her daytime haunts in late August and thereafter became a consistent daytime occupant of the Whangapoua Creek flock site. Searches with the dog failed to locate any form of nest at the locality where she was consistently recorded. In early August, she was also observed 5 times at night and on 2 of these occasions was accompanied by a male. However, in none of 6 night sightings in July and 5 in September was any consorting male observed.

(2) a breeder in 1998, this female was located in a pastoral seep 5 times during daytime over 12 days in late July but all 17 daytime radio fixes during August and September were at the Whangapoua Creek flock site. None of 18 night sightings during July-September recorded her being accompanied by a male and all sightings were in areas she did not frequent in the previous breeding season.

(3) 2 females were consistently recorded at distant locations within the study area throughout July-September but searches using the dog failed to confirm nesting. One of these females remained deep within the fringing kanuka forest throughout July-September but travelled at night to the pasture to feed where, on 5 of 9 sightings, she was accompanied by a male. For the other, 15 daytime radio fixes during July-September were from within a raupo (*Typha orientalis*) swamp while all 6 night sightings on pasture were of the female alone.

Thus, over the 3 years, nesting attempts were not confirmed for 7 (23%) of 31 monitored females.

Table 1 Nesting statistics for brown teal (*Anas chlorotis*) at Okiwi, Great Barrier Island 1997-99. *, no significant difference between years.

	1997	1998	1999
Nests found	23	22	16
Nests of known clutch size	15	19	13
Mean clutch (\pm SD)*	5.4 (0.6)	5.4 (1.1)	5.3 (1.0)
Nests of known fate	17	19	14
Percentage of			
nests successful *	12 (71%)	15 (79%)	10 (71%)
Nests of known clutch			
size and fate	14	17	12
Eggs	69	93	64
Percentage of			
eggs hatching *	44 (64%)	62 (67%)	44 (69%)

Nesting

In all, 69 nests were located, site details being recorded for 61, clutch size being determined in 47, and the nesting outcome known for 50. There were 1, 6, 16, 21, 2, and 1 nests containing clutches of 3, 4, 5, 6, 7, and 8 eggs, respectively. Overall, mean (\pm SD) clutch size was 5.4 (0.9) and there was no significant difference in clutch size between years (Table 1). Second clutches of 3 females were of 4, 6 and 6 eggs.

The dispersion of nests is indicated in Fig. 1. Most nests were sited in dense vegetation and were well obscured from above. Of 61 nests: 5 were located within the kanuka forest, mostly beneath fallen fern fronds; 2 were within raupo swamps; 6 were on the banks along Whangapoua Creek and beneath a mat of kikuyu grass; 32 were within the pastoral seeps mostly within clumps of *Carex* and *Cyperus*; 5 were in kikuyu grass or beneath fallen branches along the roadside; 4 were in *Juncus* or *Carex* clumps in grazed pasture; and 7 were deep in kikuyu grass in pasture long rested from grazing. In both 1998 and 1999, 2 females were found nesting at precisely the same sites used the previous year. One such female lost her 1st nest in each year and established her 2nd nest within 10 m of the first.

All of the nests monitored were active during August or September. Gravid females were first observed, while feeding, in late June and the earliest recorded hatching was on 5 August. Hatching extended to mid October, the 2 latest nests being 2nd nesting attempts. Five females established a 2nd nest 21-30 days after the loss of their initial clutch or hatchlings.

Successful nests comprised 74% of 50 nests of known fate and this success rate did not differ between years. Of the 13 unsuccessful nests, eggs were preyed upon in 4, flooding affected 2 creek-side and 1 pastoral seep nest and our field activity definitely caused 2 females to abandon. However,

Table 2 Productivity of female brown teal (*Anas chlorotis*) nesting at Okiwi, Great Barrier Island, 1997-99.

	1997	1998	1999
Females monitored	5	10	16
Females confirmed nesting	4	8	12
Nesting attempts	5	9	15
Mean(\pm SD) ducklings fledged nesting female ⁻¹	0	0.1 (0.3)	1.2 (1.9)
Mean(\pm SD) ducklings fledged monitored female ⁻¹	0	0.1 (0.3)	0.9 (1.7)

causes of failure were not immediately apparent for 4 nests that were deserted. Hatching rate (percentage of eggs that hatched) averaged 66% over the 3 years and did not differ significantly between years (Table 1). In 1997, 13 of 37 eggs in 7 successful nests failed to hatch; 2 of these eggs contained full-term embryos, 2 contained early-term embryos, 1 appeared freshly laid, and 8 were rotten. In 1998, 13 of 41 eggs failed to hatch in 8 successful nests; 9 eggs were rotten, 1 appeared freshly laid, and 4 contained embryos almost half-developed. In 1999, 7 of 29 eggs failed to hatch in 5 successful nests; 5 were rotten, and 2 contained early-term embryos.

Duckling rearing and survival

Ducklings generally remained hidden throughout the day but, under cover of darkness, they and their attendant females were encountered feeding in damp pastoral areas. Males were observed on 33% of 54 occasions accompanying a female and brood. Females generally took their broods to the same feeding areas each evening where tall *Juncus* spp. rushes afforded shelter and provided a visual barrier from other teal.

In 1997, there were only 15 observations of 12 different broods within the study area. Five observations were of young C.I broods (mean size 2.0 ducklings, range 1-4), 7 of C.II (mean 3.3, range 1-4) and 3 of C.III (mean 3.0, range 1-4). Only 2 broods were seen more than once. There was a high loss of entire broods immediately after hatching. For example, 9 of 11 banded females known to have nested successfully, were observed within 10 days of their estimated or known hatching dates without ducklings.

In 1998, there were 43 observations of broods within the study area. The number of different broods observed is unknown as positive identification of the attendant female was made on only 7 occasions. Eleven observations were of young C.I broods (mean size 3.1 ducklings, range 2-5), 12 of C.II (mean 2.75, range 1-5), and 20 of C.III and C.IV (mean 3.25, range 1-5). The high loss of entire broods immediately after hatching, was nearly at the same as in 1997; 8 of 11 banded females, known to have nested successfully, were

observed without ducklings within 10 days of their estimated or known hatching dates.

In 1999, only those broods emerging from the nesting attempts of the 16 tx females were followed. Ducklings emerged from 10 nests but 6 (60%) of these broods disappeared entirely within 1-3 days of hatching. In each of the remaining 4 broods, ducklings were raised to C.IV age (mean 3.5, range 1-5).

Productivity

Many ($n=25$) of the nests located and most ($n=48$, 1997 + 1998) of the broods observed represented the breeding efforts of unmarked females or females whose identities could not always be confirmed. Therefore, productivity estimates have been derived solely from the sample of females who carried active radio transmitters and who were located and seen regularly within the study area throughout the breeding periods.

Over the 3 years, 31 females were monitored with sufficient frequency to determine conclusively the outcome of their breeding activities. For 7 (23%) of these females, the nesting attempts, if made, were not confirmed. Collectively, the 31 monitored females fledged 15 ducklings, a mean (\pm SD) productivity of 0.5 (1.3) ducklings female⁻¹. The 95% confidence intervals for this overall productivity estimate, and for those for 1998 and 1999 (Table 2) were ± 0.5 , ± 0.2 , and ± 0.9 respectively. Only 5 (16%) of the 31 females successfully raised ducklings; 1 of 10 in 1998 and 4 of 16 in 1999.

DISCUSSION

Productivity is one of the essential parameters that characterise the demographic status of a population. A population's intrinsic reproductive ability, measured as offspring female⁻¹ of reproductive age, is the sole means by which numbers may increase in populations, which, like Great Barrier Island's brown teal, are beyond the support of immigration from other populations.

The several components that contribute to overall reproductive output – breeding incidence (proportion of females of reproductive age that attempt breeding), clutch size, nest and egg success, and survival of ducklings – are each influenced by different factors and any or all of these may vary annually. They may also vary within any single breeding season and across the range of habitats occupied (Johnson *et al.* 1992). In providing our description of reproductive performance of brown teal at Okiwi, we are conscious that we have left most of these factors unassessed, a consequence of small sample sizes, narrow study focus, and the inherent difficulty of working with such a cryptic species.

Do all females attempt to breed?

We could not confirm nesting by 7 (23%) of 31 females we monitored closely. We concede that the nesting of some could have been so brief that the prolonged site attachment which typifies known nesting females was not observed. However, we consider that the 3 females who remained at the flock site during daytime and were never observed accompanied by a male when seen at night feeding in pasture did not attempt to nest. Similarly, we consider 2 females whose breeding season ranges differed from that occupied in the previous year, when they nested, and who were not seen with male company at any time during the breeding season, did not make a nesting attempt.

Brown teal can breed in their 1st year (Reid & Roderick 1973) so every female alive at the start of a breeding season may be regarded as a potential breeder. Although there is a distinct breeding season (July-October), broods of brown teal have been recorded in most months of the year (Marchant & Higgins 1990). Nevertheless, a female fledged in late January has been found nesting 7 months later (MW unpubl. data).

Breeding incidence depends on obtaining both mate and breeding site. At breeding time, we found brown teal dispersed as territory-holding pairs along the creek, at ponds, alongside old drains and in wet areas of *Juncus*-dominated pasture. Each pair fed and raised their brood within restricted ranges in which they challenged other individuals, pairs, or broods they encountered. Members of these pairs retained close contact throughout breeding, the males guarding their females during her feeding forays and accompanying the female and ducklings. However, we also identified pairs using the Whangapoua Creek flock site for daytime refuge and specific pastoral areas for feeding at night. Females of these latter pairs established nests in pastoral seeps, along the roadside or in other isolated pastoral sites. Once incubation commenced, these females were often seen feeding alone at night, and most sightings of these females with their broods did not include their male consorts.

We found 2 females, breeders of the previous year, living in pastoral seeps during the breeding season apparently without male companions. Whereas another 8 females with known breeding histories all re-occupied their previous season's nesting and feeding ranges and attempted breeding, these females did not. Their former ranges were occupied by other pairs. If there is competition for nesting and feeding ranges, perhaps displacement is sufficient to disrupt breeding ambition. Identities of their former male partners were not known so we were unable to determine whether displacement was the result of pair bond disruption or eviction.

Barker (1998, 1999) recorded the sex ratio of birds at 2 flock sites within the Whangapoua basin July 1997-June 1999. During the 2 breeding seasons (July-October) he never recorded females comprising fewer than 32% of birds present. Even allowing for females rejoining flocks after early nest failures, we consider these observations indicate the presence of a significant non-breeding female component in the population in addition to the non-breeding females we identified in our pastoral study area. Specific investigation of these individuals may reveal breeding constraints for reasons that are presently unsuspected.

Influences on nesting outcomes

We found no significant annual variation in either clutch size, nest success, or egg success (Table 1) and our nesting statistics were similar to those previously recorded. For example, almost 79% of clutches were of 5 or 6 eggs, confirming Marchant & Higgins' (1990) summary of clutches of 5 and 6 being the most common. Dumbell (1987) followed the fate of 22 teal nests at Awana and recorded 77% nest success and 63% hatching of eggs, almost identical with our results.

Predation and flooding were identified as causes of nest failure, the same causes that appear to influence nest success in most species of waterfowl (Johnson *et al.* 1992; Sargent & Raveling 1992). We did not identify the predators however, but found broken eggs in nests at both wet and dry sites, including kanuka forest (1), pastoral seeps (2), and raupo swamp (1).

We suspect females other than the nesting duck visited some nests. We found freshly-laid eggs, and eggs with undecayed embryos at a younger state of development than all others, in 8 of 20 successful nests in which unhatched eggs remained. We interpret this as evidence of parasitic egg laying and speculate this may have contributed to the failure of some of the 4 nests found abandoned without obvious cause. Although parasitic egg laying is uncommon in dabbling ducks (Sayler 1992) except in cavity nesting species, such as grey teal (*Anas gracilis*) (Frith 1977), it may be present in other *Anas* species when they nest under crowded conditions (Titman & Lowther 1976; Sayler 1992).

In each year of our study, nests in the pastoral seeps were closer to each other than, for example, those established by contiguous pairs along Whangapoua Creek (Fig. 1) or those of teal pairs which occupied similar stream territories in 2 Northland populations, Clendon Cove and Tutaematai (Williams 2001, unpubl. data). Whereas nests within territories of stream-dwelling pairs have protection afforded by the persistent vigilance of resident males, the mates of some pastoral-nesting females spent time away at the Whangapoua

Creek flock site. Five of the 8 successful nests in which unhatched eggs remained, and 2 of the 4 abandoned nests were in pastoral seeps.

We speculate that parasitic egg-laying and the crowding of nests into pastoral seeps is evidence of breeding habitat being limited. As such, the small area of wetland in the pastoral environment may be a factor that serves to limit breeding opportunity and influence nesting outcome.

Influences on duckling survival

A significant finding of our study was the demise of most broods soon after hatching. Over the 3 years of study, 23 (72%) of 32 females that nested successfully were seen without ducklings 1-10 days after hatching. For at least 12 of these females, the brood was lost within 3 days of hatching.

We obtained little direct evidence for the cause of duckling deaths. However, most waterfowl studies identify predation as the important cause of duckling mortality, with exposure to adverse weather, starvation, and attacks from other ducks also listed as other causes (Johnson *et al.* 1992). Combinations of these factors may also apply. For example, Mendenhall & Milne (1985) observed predation to be more severe on eider (*Somateria mollissima*) ducklings when adverse weather forced them to feed farther from the attendant females.

Predation is likely to be a significant cause of loss of brown teal ducklings. Cat and pukeko, both known predators of birds, were observed hunting and foraging at night in the same pastoral habitats as teal broods, and, during daytime, pukeko were often flushed from clumps of *Carex* and *Cyperus* in which teal had previously been found. Barker (1998, 1999) examined stomach contents of 83 cats from throughout Great Barrier Island, finding avian remains in 7 and identifying rabbit and rat as the predominant food remains. He did not observe cat predation of teal. Pukeko, although primarily herbivorous, have been observed feeding on a wide variety of wetland animals including young ducks and duck eggs (McKenzie 1967; Marchant & Higgins 1993). During this study, 2 pukeko were observed together chasing a female brown teal and brood and carrying off 1 of the C.I ducklings. Experimental reductions in pukeko numbers and density could provide a helpful test of the nature and intensity of interaction between pukeko and brown teal families.

We have no direct evidence of any effect of weather on duckling mortality other than noting the differences in weather and brood persistence in 1997 and 1998. Barker (1998) considered that the persistent strong winds which blew during the 1997 breeding season made communication between ducklings and their attendant female difficult and to have caused brood fragmentation. He found young ducklings dead with no signs of predation.

Belligerent interactions between parents of broods attempting to feed simultaneously in the same damp pastoral sites was a conspicuous feature of brown teal ecology at Clendon Cove in Northland (Williams 2001). This behaviour, while not observed in pasture at Okiwi, was seen on one of the ponds and we suggest it was likely to have occurred also amongst pairs nesting or feeding within the confines of the narrow pastoral seeps. Newly-hatched young may use the nest, or its immediate environs, as a daytime refuge, thus ensuring that they are active close to other nesting females, or broods. Males accompanying their broods can be expected to be belligerent toward any teal they encounter nearby.

Productivity

We recorded a mean annual productivity that is only 25% of that recorded in 2 Northland populations (Williams 2001) and c. 50% of that recorded by Dumbell (1987) in the neighbouring Awana catchment of Great Barrier Island.

Our findings indicated that teal productivity in the pastoral environment at Okiwi was well below population replacement rate, unless mean annual adult survival exceeded 76%, there were no deaths of juveniles during their 1st year of life, and all females attempted to breed. But there was clearly further mortality before recruitment. For example, Barker (1999) fitted radio transmitters to 9 fledglings in 1998 and recovered 8 dead within 5 months; 2 killed by cars on a nearby road, and 2 dead amongst wetland vegetation without obvious sign of injury. The others were found as scavenged cadavers in pasture.

The population of teal at Okiwi and throughout the Whangapoua basin has declined at an average rate of 5% year⁻¹ since 1986, based on annual counts of birds at flock sites during summer (Barker 1998, 1999). Assuming annual survival of adults and juveniles of 65% and 50% respectively — based on Dumbell's (1987) estimate of 63% annual adult survival ($n=90$), and table 14-1 in Johnson *et al.* (1992) — our productivity estimate, if applied throughout this 14-year period would have the population declining by 80-100%. We conclude that the estimated productivity of our sample of the Whangapoua population simply cannot be typical of the whole.

Constraints on productivity

We have identified breeding incidence and brood survival as 2 obvious constraints on annual reproductive output in Okiwi's pastoral environment. We see both as being wholly, or in part, consequences of the limited extent of wetland habitat within the study area. However, we caution against assuming that these constraints will be the same in other habitats occupied by brown teal on

Great Barrier Island, or elsewhere in its current national range. Where nesting is more dispersed than at Okiwi and pairs maintain a continuous presence in exclusive feeding and brood-rearing areas, other productivity parameters, including nest success, may be more important. We speculate that the productivity of pairs dispersed for breeding either as contiguous territorial pairs along watercourses, or as pairs exclusively occupying isolated small wetlands, as is typical in Northland (Williams 2001), or along Whangapoua Creek in the present study (Fig. 1; see also Barker 1998, 1999), will be higher than pairs sharing wetlands as nesting and brood-rearing habitat and in which males are not always present continuously.

Primary constraints on productivity may be identified by following the approach of Johnson *et al.* (1992). They presented a productivity model based on the interaction of breeding incidence, likelihood of re-nesting after failure (nesting intensity), clutch size, incidence of dump nesting, nest success, survival rate of eggs in successful nests, and survival of broods. They quantified their model's parameters for 3 waterfowl species with divergent life histories (mallard *Anas platyrhynchos*; wood duck *Aix sponsa*; snow goose *Anser caerulescens*), and compared the relative importance of each parameter using regression analysis relating reproduction to each parameter. For all 3 species, nest success and brood survival were the 2 factors that influenced annual productivity the most. Breeding incidence was the next most influential factor for the 2 ducks. We suggest that working towards quantifying the various components of Johnson *et al.*'s (1992) productivity model would provide a useful focus for any future research on brown teal that seeks to underpin the management of this increasingly threatened species.

Wetland habitat conditions

Johnson *et al.* (1992) noted that predation was the single-most important factor which influenced the key productivity parameters for all 3 of the species they modelled. Weather, wetland habitat conditions and density-dependence were each identified as a secondarily important factor for 1 of the 3 species. We have highlighted our suspicions about the role of predation, weather, and nest and brood density affecting brown teal productivity but have not considered the condition of the wetland habitat. The 1st year of our study coincided with an intensive El Niño phase of the El Niño-southern oscillation (ENSO) weather pattern which typically brings cold and windy springs, summer-autumn droughts and subsequent low water tables to northern and eastern New Zealand (Brenstrum 1999). The subsequent 2 breeding

seasons, during which broods persisted for longer than in 1997, experienced more benign warm and moist La Niña conditions. High intensity El Niño events have been suggested as a major factor promoting the decline of brown teal and the loss of their habitat in the pastoral lowlands of Northland (Parrish & Williams 2000; Williams 2001). During periods of drought, we suspect that nesting and feeding in the pastoral environment may also be severely constrained, an influence mediated as much by the grazing patterns and requirements of co-habiting cattle as through direct weather-induced changes in habitat quality or resource availability. Periods of drought-induced reproductive failure and low juvenile survival may add further to the apparent productivity woes of brown teal on Great Barrier Island.

Persistence in pastoral environments

The last refuges of brown teal in Northland and on Great Barrier Island are conspicuously different from the habitats in which this species was commonly reported in the late 19th and early 20th centuries. "This elegant little duck is distributed all over the country, being met with in every inland lake, and often in the deep freshwater streams which run into them, where the overhanging vegetation affords ready shelter and concealment" was how Buller (1888) summarised their distribution and habitat. His subsequent text makes much of the bird's daytime concealment "among the sedges and vegetation which usually fringe the inland watercourses and lagoons", and he and Oliver (1955), refer to the bird's widespread association with kahikatea (*Dacrycarpus dacrydioides*) swamp forests. Distribution of fossil remains (Atkinson & Millener 1991; Worthy & Holdaway 1993; Worthy 1997, 2002) indicates that brown teal were also present in a wide variety of forest environments and at elevated sites. For example, they were present in the humid podocarp/hardwood forests on karst terrain at Waitomo, in wet podocarp-hardwood forests and swampy riverflats at Punakaiki, in *Nothofagus* forest on Takaka Hill, in dry podocarp-hardwood forest on loess-covered hills and valleys of northern Canterbury, in grassland and shrubland communities of southern Canterbury, in the coastal dune forests of North Cape, and in the distinctive coastal akeake (*Olearia traversii*)-matipo (*Myrsine chathamica*)-karamu (*Coprosma chathamica*) forests of Chatham Island. The brown teal appears to have been a conspicuous member of both the aquatic and forest floor insectivore-omnivore guild throughout much of pre-human New Zealand and to have been associated with vegetation that provided it with abundant daytime cover to escape the attention of diurnally-active avian predators.

The last sites in Northland at which teal have lingered during the past 40-50 years (Hayes & Williams 1982), and from which they have now almost disappeared (Parrish & Williams 2001), have been the small coastal flats through which slow-flowing streams meander. These wet and low-lying areas seemingly provided teal with feeding and breeding habitat that had long since disappeared, or been alienated, in the hinterland. These flats have been gradually stripped of their forest or scrub cover and replaced by grass and pastoral farming, in the process most likely expanding feeding opportunities for brown teal. However, as the streams have become denuded of their riparian forest or ecotonal vegetation and have had their banks slumped by the hooves of cattle, and as the scattered swampy ground and ephemeral wetlands have been drained and heavily grazed and trampled, so the teal have disappeared. In the end, intensive pastoral farming on these flats has been a consistent and essential precursor to the eventual elimination of teal from the local biota (Guthrie Smith 1927; Hayes & Williams 1982; Williams 2001).

On Great Barrier Island, most teal now congregate for much of the year near the mouths of major streams (Dumbell 1987; Marchant & Higgins 1990). As in Northland, the land near the streams is flat and low-lying, and, when seasonally wet, the pastoral areas provide teal with significant feeding habitat. But as in Northland, the same gradual change in human use of these flats can be seen: drains have facilitated more intensive pastoral farming of the flats and nearby slopes and the flats become attractive sites for human dwellings. The tale of the brown teal's decline in Northland is being replayed on Great Barrier Island.

The results of this study can be interpreted as highlighting one of the processes contributing to the decline of remnant teal populations remaining in these pastoral environments. Diminution of wet areas, demonstrably favoured as nesting habitat, can serve to constrain the population's annual productivity, most likely with density-dependant effect. Whereas pairs may ordinarily seek to obtain and defend an exclusive breeding range, such as serially along streams (Williams 2001), the enforced concentration of nesting and brood-rearing in restricted remnant wetlands, as we have recorded, may simply cause such a high level of competitive interaction between pairs and families, and concentrate the attention of predators, so as to restrict breeding opportunity and depress breeding success. Persistence of brown teal in pastoral environments, the main habitat in which this species is now observed, concentrated and managed, will require extensive restoration of wetland habitat just as much as it

will involve concerted predator control (Hayes 1994) and mitigation, by adroit stock management, of the deleterious effects on wetlands and teal daytime refuges of intensive cattle farming (Guthrie Smith 1927; Williams 2001).

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