Social and demographic characteristics of Blue Duck *Hymenolaimus malacorhynchos*

MURRAY WILLIAMS

A population of Blue Ducks inhabiting the Manganuiateao River in central North Island, New Zealand was studied over 1980-89. The birds were dispersed as pairs throughout the year with each pair occupying and defending territories which were similar in extent and location between years. Unpaired individuals also occupied territories throughout a breeding season. Pair associations persisted for up to 81 months (seven breeding seasons) and pair changes resulted mostly from challenges by bereaved neighbours.

Only territorial pairs attempted breeding. Nests were in caves or amongst enveloping riverside vegetation within the territory and the same nest site was sometimes used in successive years. Mean egg size was 64.5 x 44.8 mm, mean clutch was 6.0, and eggs were laid at two-day intervals. Only the female incubated (for about 35 days) and 10% of nest failures were followed by a repeat laying. Both parents contributed parental care throughout the 70-80 day fledging period.

Within the 9.3 km study area the number of territories occupied increased from four to ten over ten years. Fifty-eight breeding attempts produced 73 fledglings (mean 1.3 per breeding pair per year). Some individuals were more productive than others both in terms of the numbers fledged per breeding attempt and the numbers recruited into the breeding population. Annual survival of territory holders was 0.86, and that of juveniles in their 1st year 0.44. Recruitment into the breeding component of the population was 0.25 fledglings per breeding individual per year, twice that needed to replace lost adults. Productivity within the study area was higher than that on a neighbouring and deeply incised 6.7 km section of the river in which territorial density also increased.

Fledglings of both sex were highly philopatric, some establishing their territories immediately adjacent to their natal range. Nineteen of 26 birds which settled in the study area over the ten years were progeny of resident pairs and resulted in neighbouring territory holders being closely related to each other. Two sibling pairings persisted through a breeding season and there were two other examples of direct inbreeding (adult-grandchild).

The Blue Duck social system is similar to that of other southern hemisphere riverine ducks and it is argued that their population dynamics and structure will also exhibit striking similarities.

Few species of waterfowl occupy such a specialised habitat as Blue Duck *Hymenolaimus malacorhynchos*. A territorial, year-round and long-term resident of fast-flowing rivers and streams in New Zealand (Kear 1972), the Blue Duck shares these biological and environmental characteristics with three other southern hemisphere species, Salvadori's Duck *Anas waigiuensis* of New Guinea, Torrent Duck *Merganetta armata* of South America, and African Black Duck *Anas sparsa* of southern Africa. Harlequin Duck *Histrionicus histrionicus* is a summer occupant of Arctic rivers.

Knowledge of Blue Duck biology was well summarised by Kear (1972) who drew upon the writings of many of New Zealand's early naturalists (e.g. Buller 1888, Guthrie-Smith 1927) and on anecdotes in the contemporary literature to complement her brief field observations. As she noted, little of detail was known about the species' social and mating systems, family life, and the ways by which Blue Duck density, dispersion and productivity were related to the ecological characteristics of fast-flowing waters. Indeed, at the time of her review, these comments applied to all of the riverine waterfowl, which as a group were then perhaps the least known of all ducks. Bengtson's (1972) contribution on Harlequin Duck breeding, Kear's (1975) review of Salvadori's Duck, and particularly the studies of McKinney *et al.* (1978) and Ball *et al.* (1978) on the behavioural adaptations and territoriality of African Black Duck have since filled some of the gaps in knowledge.

The study reported here provides a population perspective to the biology of a riverine waterfowl while at the same time adding detail to many of the topics covered in Kear's (1972) review. In addition, it complements Kear & Steel's (1971) report of social behaviour and Eldridge's (1985, 1986b) studies of Blue Duck displays and territoriality.

The stimulus for the work arose from a conservation imperative. The species is classified as "threatened" (Bell 1986) for it presently occupies only a small portion of its former range (Bull *et al.* 1985). Nationally, its distribution is disjunctive with numerous small population isolates. Furthermore, the New Zealand Government's policy in the late 1970s of encouraging the harnessing of small headwater rivers for electricity generation placed additional pressure upon the bird's dwindling habitat.

The objectives of the study were:

(i) to monitor short and long-term changes in the population by measuring annual duckling production, survival, dispersal and recruitment of juveniles, longevity of adults and changes in breeding density;

(ii) to determine what factors influence breeding density by measuring territory size and seasonal variation in the use of territories, and by relating the pattern of territory use to the distribution, abundance and availability of food; and

(iii) to determine how many and how frequently birds may be removed (for liberation elsewhere into presently unoccupied habitat) without long-term prejudice to the population.

Several studies addressing parts of the first two objectives continue or are reported elsewhere (Veltman & Williams 1990, Triggs *et al.* 1991 in press, Collier in press, Collier & Lyon 1991). This paper reports some findings arising from the monitoring of the population prior to it being affected by experimental removals and manipulation.

Study Area

The Manganuiateao River (Fig. 1) drains the western slopes of an active volcano, Mt Ruapehu, in central North Island, New Zealand. It flows southwest for approximately 80 km to its confluence with the Wanganui River and has a total catchment of about 620 km^2 (Cudby & Strickland 1986).

The headwaters of the Manganuiateao River and those of its principal tributaries, the Makatote River and Waimarino Stream, descend steeply from the high mountain slopes, across the Erua Plain to coalesce at 650 m above sea level. For the next 8.3 km the river descends approximately 150 m through a series of 57 pool (areas of smooth surfaced water) and riffle (all areas of broken water) systems; this is the upper gorge in which the river channel is confined by sheer walls up to 30 m high, on top of which are extensive tracts of indigenous forest.

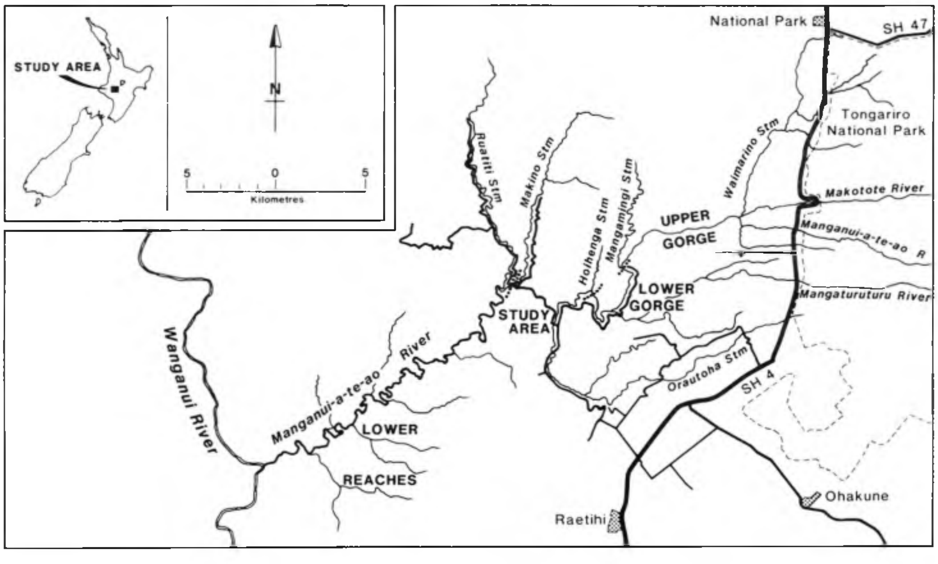

Figure 1. Manganuiateao River catchment and sections of the river referred to in the text.

The gorge widens below the river's confluence with the Mangamingi Stream and the river's gradient eases. For the next 6.7 km (to its confluence with the Hoihenga Stream) the river descends approximately 100 m through 43 pool/riffle systems. This is the lower gorge characterised in places by sheer walls seldom more than 15 m high, and by steeply sloping and heavily vegetated banks. The surrounding land is mostly pastoral with scattered pockets of regenerating scrub. It is into this section that the acidic waters of the Mangaturuturu River, uninhabited by Blue Ducks, enter (see below).

The next physically distinct section of river is the study area which extends for 9.3 km to the Ruatiti road bridge at the confluence of the Makino Stream. Within this section the river descends about 90 m through 48 pool/riffle systems. Low cliffs and riverflats flank the river and, apart from an almost continuous but narrow riparian forest of both indigenous and exotic trees, the surrounding land is pastoral.

The remainder of the river, the lower reaches, extends for 29 km over a gentle gradient. There are 108 pool/riffle systems as it descends 160 m to the Wanganui River. The river is initially flanked by farmland and has extensive river flats as it meanders within a widening valley. However, for its last 7 km the valley narrows and steep hills and cliffs flank the river.

An outstanding feature of the river is its morphological stability. Its bed comprises mostly large rounded boulders of volcanic origin interspersed with finer materials. Even during high floods there is little movement of boulders, ensuring that pools and riffles are almost permanent fixtures.

The mean annual water flow (at Ruatiti) is 18.2 m^3/sec (data for years 1962-1979 supplied by Rangitikei-Wanganui Catchment Board), but this belies its erratic nature. There is a marked seasonal variation, the mean monthly winter flow being three times that of late summer. In addition there are frequent brief floods or freshes resulting from heavy rain on the mountain slopes; in some months the 15% flow frequency is twice that of the 50% flow. During 1962-1979 the maximum flood flow was 463 m^3/sec and the mean annual flood flow was 321 m^3/sec (Cudby & Strickland 1986).

Water quality is uniformly high and comparable with that of smaller streams in undeveloped forest catchments. The river's mean annual sediment discharge of 58 t is very low and mostly originates as run-off from pastoral land within the lower reaches.

Because of its deep gorges and extensive shading by riverside trees, water temperature remains equable even during hot summers. The mean annual temperature is 11.3°C (S.E. 2.3°C), being highest in January and February (16°C) and lowest in July and August (7°C).

Thus, the Manganuiateao River, within the gorges and study area sections is highly stable, carrying cool, high quality water bank to bank within a narrow channel. Its morphological stability contrasts with a highly variable flow regime in which floods and freshes may reach high peaks but be of short duration.

Occasionally, the river is affected by volcanic activity. The Mangaturuturu River, a major tributary, drains a glacier from near the summit of Mt Ruapehu. In 1969 and 1975 vigorous activity within the crater spilled water and debris onto the glacier and the resultant sludge was transported down to the Manganuiateao River. The 1975 lahar was particularly damaging as vast quantities of heavy grey mud and forest debris carpeted the river channel, completely filling all pools and burying rocks in all but the steepest riffles and runs. It was almost two years before the mud washed away completely and during this time the lower reaches, study area and 4 km of the lower gorge below the Mangaturuturu confluence were uninhabitable by Blue Ducks. Some displaced pairs survived in side streams (two-three pairs in the Orautoha Stream, where birds have not resided during this study) but the fate of others went unreported. My period of study coincided with birds recolonising the previously degraded sections of river.

Population within the Manganuiateao catchment

Several surveys of all or parts of the Manganuiateao catchment were undertaken between 1979 and 1989 to determine numbers of Blue Duck present and the trend of their population. All surveys of the upper and lower gorge and lower reaches were conducted by floating down the river on car tubes or rafts. Provided the observers (usually four per party) remained prone on their tubes, or partly submerged, the birds showed little fear and could be approached to within 20 m. This was sufficiently close to identify colour banded birds and to discriminate adults and newly-fledged young, the latter by their grey bill, grey eye and sparse chestnut spotting on the breast. Surveys

Table 1. Numbers of Blue Ducks seen on different sections within the Manganuiateao River catchment. (pr = resident pair, ad = adult, juv = fledgling; January 1979 survey from Armstrong (1979)).

Survey date	Tributaries	Upper gorge	Lower gorge	Study area	Lower reaches
Jan 1979	12 pr	7 pr 5 ad	4 pr 2 ad	2 pr	1 pr 1 ad
Jan 1980		8 pr 2 ad			
Feb 1981		9 pr 13 ad/juv		4 pr 3 juv	
Feb 1982					1 pr 1 ad
Apr 1984	3 pr		6 pr 2 ad	6 pr 2 juv	
May 1985		10 pr 15 juv	7 pr 8 juv	5 pr 12 juv	
Dec 1986			8 pr	6 pr 1 ad	
Mar 1987	12 pr 14 ad/juv	25 ad 9 juv	11 pr 4 juv	6 pr 9 ad/juv	2 juv

of headwaters and study area were conducted on foot.

Resident territorial pairs and transients were distinguished by their behaviour. Territory holders initially moved downriver ahead of the observers but, after moving 1-2 pools would turn and fly back. Transients moved much further, often well downriver, bunching up with other pairs or individuals. They often then flew upriver as a group. Obviously there was room for some mis-identification, but the locations at which all birds were encountered was recorded, thus allowing retrospective interpretation of pair density.

Timing of surveys and results

Surveys were conducted in:

1. January 1979; The whole river from approximately 6 km above State Highway 4 (Fig. 1), including Waimarino Stream and Makatote River for a similar distance above the highway (Armstrong 1979).
2. January 1980; upper gorge.
3. February 1981; upper gorge, study area.
4. February 1982; lower reaches.
5. April 1984; Makatote and Manganuiateao Rivers between State Highway 4 and their confluence, lower gorge, study area.
6. May 1985; upper and lower gorge, study area.
7. December 1986; lower gorge, study area.
8. March 1987; as for January 1979 but not including Waimarino Stream.

The results are presented in Table 1.

Survey interpretation

Data from these surveys are consistent with there being a slowly increasing population. They indicate that, in 1987, approximately 36 pairs were resident within the catchment, and it is likely that further pairs, perhaps 6-8, live beyond the surveyed sections of the upper tributaries. The Manganuiateao River and its headwaters thus comprise one of the largest breeding populations of Blue Duck in North Island.

Although the tributary rivers were not surveyed frequently enough to confirm whether the apparently similar numbers in 1979 and 1987 indicates a stable population there, data from the upper gorge are more conclusive. All surveys are consistent with 8-10 pairs resident in this section at a density of one pair per 0.8-0.9 km and with each pair's range encompassing 5-6 pool/riffle systems.

Within the lower gorge, a steady increase in numbers was apparent. The 1979 survey recorded three pairs in that section above the Mangaturuturu confluence (Fig. 1) where Eldridge (1986b) recorded four the previous year. All three pre-1987 surveys of this section also recorded four pairs, the remainder being downriver of the Mangaturuturu confluence. In March 1987, 11 pairs were observed in the lower gorge. Monthly surveys during the 1987, 1988 and 1989 breeding seasons (not recorded in Table 1) found seven, eight and seven pairs respectively above the confluence and four, six and five pairs below, indicating a substan-

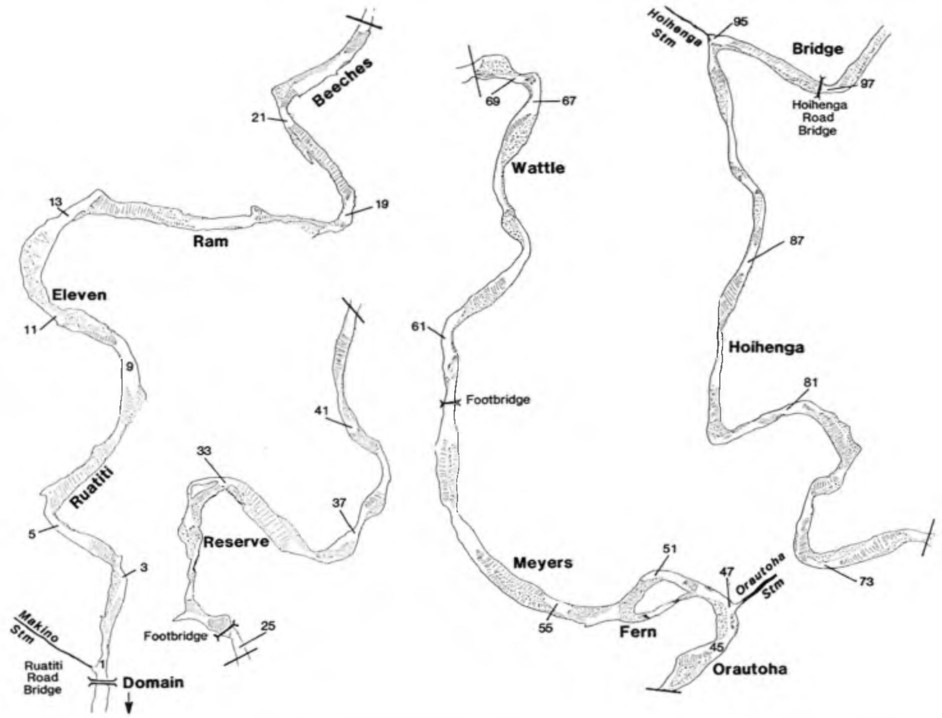

Figure 2. Topography of the Manganuiateao River within the study area and the locations of named sections of the river. Numerals indicate pool and riffle areas. Each segment of river is a continuation of that to its left.

tial increase in pair density throughout the entire lower gorge. The 12 pairs in 1989 occurred at an overall density of one pair per 0.6 km with each territory on average, embracing 3-4 pool/riffle systems.

The number of territorial pairs present within the study area also steadily increased. Four pairs were resident during the 1980 breeding season; by 1987 this had increased to nine, and to ten occupied territories in 1989. Their density was approximately one pair per km and each territory, on average, covered 4-5 pool/riffle systems.

The lower reaches remained uncolonised: birds encountered during three surveys were not present throughout a breeding season. In 1989 a young pair persisted for eight months near the confluence of Ruatiti Stream, less than 0.5 km below the lowermost pair within the study area, but by late November, abandoned that range and wandered upriver.

Thus, within the catchment of the Manganuiateao River during the 10-year period of the study, the Blue Duck population increased; this increase occurred within, or close to that section of the river devastated by the volcanic lahar in 1975.

Breeding biology

Methods

To investigate the breeding biology and population characteristics of Blue Duck, observations were restricted to the most accessible section of river, the study area, which was the downriver limit of the bird's range on the Manganuiateao River. Both banks within this area were accessible on foot and crossing was facilitated by four bridges. In addition, almost 40% of the river within the study area could be viewed from a road. All birds living within or traversing this 9.3 km section of river were the focus of study.

Visits to the river from August 1980 to December 1989 were usually of three-four days duration in every January/February, April, June/July and in each month August to December. All resident adult ducks were caught using mist nets suspended above and into the river (Williams 1988) and banded with numbered metal and darvic colour bands. All but four fledglings raised within the study area were banded also.

During each visit the entire study area was traversed several times and the identity, location and behaviour of all birds noted. Details were plotted onto 1:5000 scale field maps on which all pools were illustrated and sequentially numbered (Fig.2). Field observations were restricted to daytime and mostly during early morning and late evening in response to the birds' tendency to rest up and hide during the middle of each day.

To assist discussion and identification, sections of the river and the pairs resident therein were named. These, and the approximate numbers of pools and riffles (Fig. 2) to which they refer, are: Ruatiti (1-10), Eleven (10-12), Ram (12-20), Beeches (21-25), Reserve (26-37), Orautoha (40-47), Fern (50-54), Meyers (54-60), Wattle (62-72), Hoihenga (80-97) and Bridge (96 and above). Domain refers to eight pools and riffles immediately downriver of Rautiti.

Dispersion of pairs

In August 1980, when observations commenced, four pairs were in residence; by December 1989, eight pairs and a solitary male were present with another pair (Domain) immediately downriver of the study area. Their dispersion during each breeding season is illustrated in Figure 3. Data were derived from a minimum of eight sightings of each pair in each season and Figure 3 illustrates the extremities of each pair's range and the location at which they were most frequently seen.

With but one major exception the ranges of pairs were similar from year to year, even when there was a change in pair composition or when both members of a pair were replaced. For example:

(i) Ruatiti pair was not seen above riffle 10, other than once in 1986, and in every year most sightings were at pool 5 or riffle 6. A change of female occurred in 1984 and 1988, and the original male was replaced in 1989.

(ii) Meyers pair, the same two birds from 1981-1987 were most often at pool 57 or the adjacent riffles. Their range extended downriver only during brood-rearing.

(iii) In every year Ram pair were seen most frequently at the same pool and riffle. A change of female occurred in 1983 and of male in 1989.

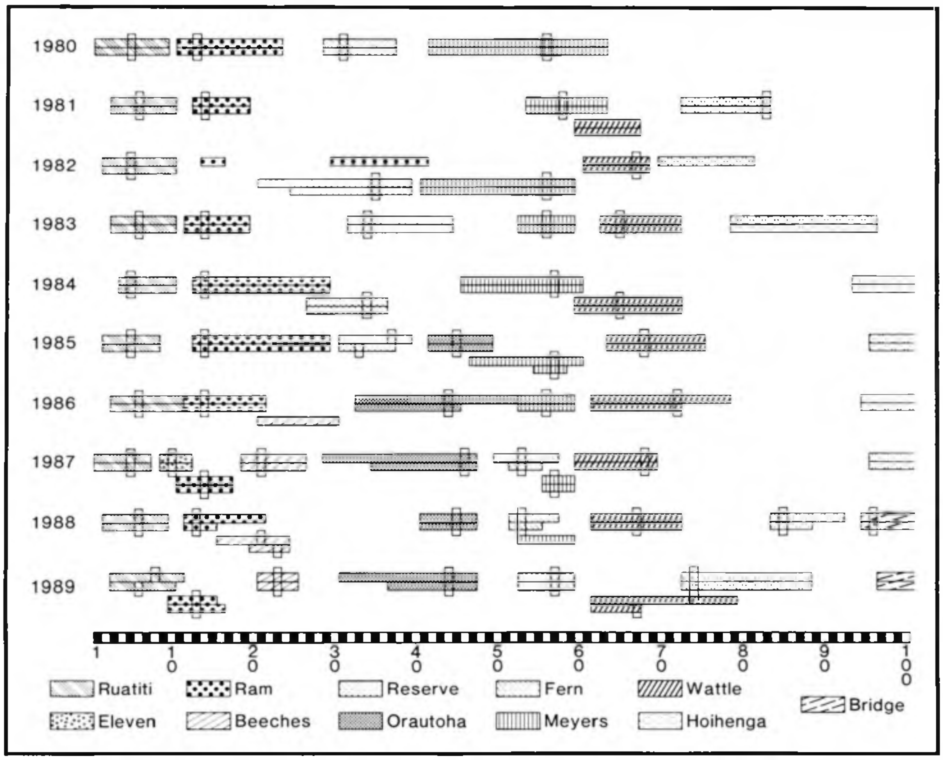

Figure 3. The annual dispersion of Blue Duck pairs within the study area of the Manganuiateao River. Bars show the range of each pair during the breeding season and the locations at which the male (upper line) and female (lower line) were encountered most frequently.

(iv) Reserve pair were shot in early 1981. A replacement pair appeared 12 months later and occupied the same general area, even though there were numerous unoccupied pools and riffles between them and their upriver and downriver neighbours.

The principal exception was Hoihenga pair in 1988. After five years at the upper extremity of the study area, they shifted their range almost 0.7 km downriver to where the male had resided seven years previously. They moved a further 0.5 km downriver in 1989 to abut the range of their downstream neighbours. From 1988, a new pair (Bridge) occupied most of Hoihenga pair's vacated range.

During the initial years of study, ranges of pairs were not in close contiguity. Nor, when Reserve pair disappeared in early 1981, did adjacent pairs extend their range to encompass the vacant section of river. Instead, ranges of pairs appeared to be more or less fixed, with the most frequently-used sections of those ranges being the same each year and being near nest sites.

There were, however, examples of shifts in location by bereaved males:

(i) Ram male, in 1982, supplanted his immediate neighbour (Reserve) and bred for one season with his female. After breeding, and while moulting, Ram male was evicted by Reserve male and returned to his original range.

(ii) Reserve male in 1986, Beeches male in 1988, and Wattle male in 1989 all supplanted their immediate neighbours to consort with the females. Return challenges were successfully repelled and the new pairings occupied the female's range.

(iii) Hoihenga male shifted his range considerably upriver consequent upon attracting a new female in 1983.

Only one female, apart from Hoihenga female in 1988 and 1989, changed her location. Eleven pair were siblings, who, throughout 1987, occupied a very restricted range between two long-established pairs (Ruatiti and Ram). When Rautiti female died during her moult, and in response to incursions by Rautiti male, Eleven female abandoned her partner thereafter to reside with Rautiti male within his territory.

Pair associations

Members of pairs remained in close association with each other throughout the year and it was rare, at any time, to find them separated by more than a few metres. Pairings persisted for up to 81 months (Fig. 4) and the relationship may best be described as long-term and constant. No resident female had more than two partners during the period of study: four of six extant females were with their second partner, the other two with their first; four of another ten females had two partners during their lifetime. Males, by virtue of their greater lifespan (see later) had more partners: of four males, one had four partners and another three, both over a period of almost ten years life, while the other two each had a single partner. Of nine extant resident males, one was with his third partner, five with their second and three with their first.

Although pair relationships were long-term they were regularly tested. Members were challenged by newly-fledged juveniles, bereaved neighbours, or non-resident adults, and some challenges persisted beyond one season (e.g. Meyers and Fern males, Fig. 4). Challenges all involved like sexes; a challenge by a male was met by the resident male while the resident female simply watched, as Eldridge (1986b) reported. When a challenge succeeded the victor became the female's close consort, and, if the new relationship endured, her new breeding partner.

Over a period of 64 pair-years, seven changes in pair composition resulted from death of one partner (a new partner taking up residence in an existing territory) and nine as the direct result of a male-male challenge. Four of the displaced males disappeared and were never seen again; the Ram-Reserve male challenges (Fig. 4) resulted in both birds re-establishing on their original ranges; the Meyers-Fern male conflicts resulted in Meyers male living furtively in a sidestream for over 12 months before disappearing; and the dispossessed Hoihenga male remained alone on his usual range (as at December 1989).

The breeding attempt

With but six exceptions over a total of 64 pair-years, each pair occupying and defending a section of river during all or most of a breeding season (August-December) made an attempt to breed (determined by one or more observations of either copulation, an obviously gravid female, the male regularly seen alone, nest found, or pair with ducklings). No detected breeding attempt was made by paired siblings (Eleven pair in 1987), paired one-year-olds (Domain 1989), in two instances when males with previous breeding histories were newly partnered by one-year-old females (Hoihenga pair 1983, Wattle 1987), when a newly established

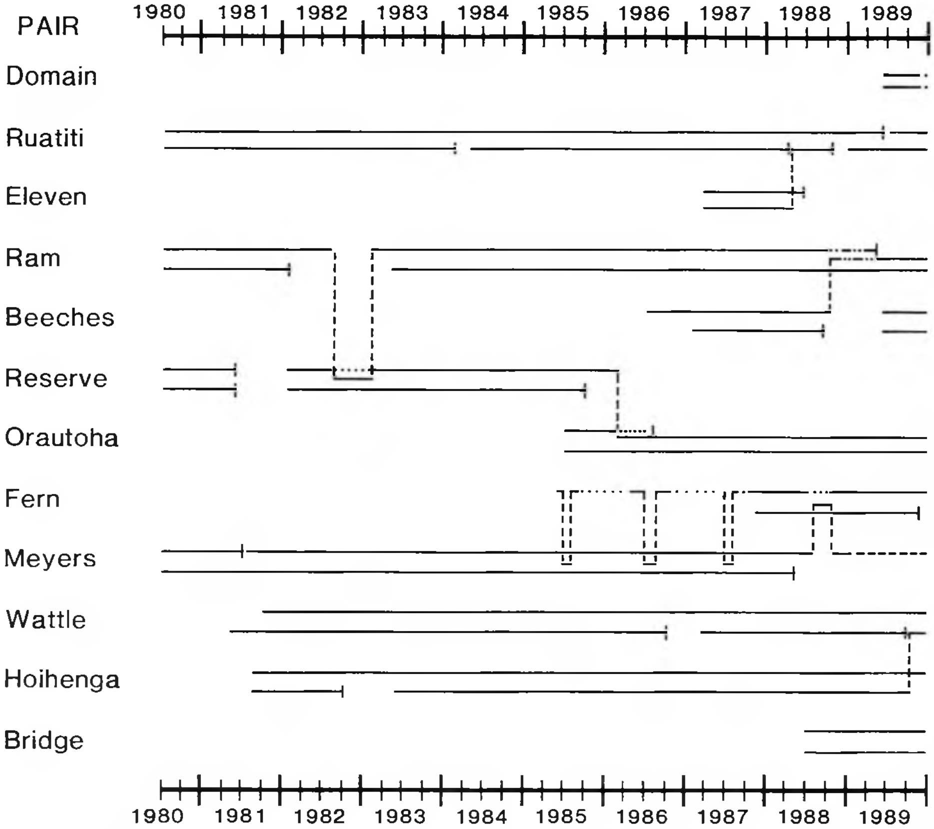

Figure 4. The chronology of Blue Duck pair associations (male upper line, female lower line) over the 10 years 1980-1989.

one-year-old female was partnered late in the season by a male of unknown age and origin (Wattle 1981), and by a pair (Fern 1987) which formed in October and the female of which was a one-year-old. Although, in most years, unpaired birds were occasionally seen moving about the study area, no unpaired female was seen with young, nor did territorial pairs tolerate unpaired females within their territories during the breeding season. Unpaired or recently bereaved males occupying a territory during a breeding season (Ram 1981, Beeches 1988, Wattle 1989, Fern 1985-88; Fig. 4) attempted to displace their paired neighbour then; two pair changes occurred when the female was gravid, one during incubation and another during brood-rearing. Thus, breeding attempts were made solely by territorial pairs.

Age of first breeding

Both males and females bred as one-year-olds. Ten one-year-old females were members of territorial pairs throughout a breeding season and five nested (two successfully). Five males occupied territories as one-year-olds and three participated in a breeding attempt (one successfully). There were four instances where both members of the pair were one-year-olds (Orautoha 1985, Eleven 1987, Ruatiti 1989, Domain 1989); two attempted breeding, both successfully. One male and four females bred first as two-year-olds after having territories in the previous year; one male was first recruited into the study population as a three-year-old and bred in that year; and Fern male, raised in 1984, did not attempt breeding until the spring of 1988.

Nest sites

Thirty-two nests of 14 females were located, all at or within 30 m of the river edge. The most frequently-located site was a riverside cave; wherever a cave was present within a territory it was used as the nest site. Eighteen nests were established in caves and eggs hatched in 15 of these. The three unsuccessful nests were all established in the same cave by the same female and were flooded during spring freshes.

The 14 non-cave nests comprised five in holes or on ledges on the immediate riverbank (up to 10 m above river level), two amongst vegetation on a cliff face 10-15 m above the river, five on the ground in riparian scrub, and two amongst vegetation on the exposed river bed. Six of these nests were unsuccessful, three as a result of mustelid predation, one when eggs chilled following a change in pairing, and two from unknown causes. The general location of five other nests was determined; two were amongst vegetation on a small island (one flooded, one female predated), and three amongst river-bank vegetation (one successful).

Some females used the same nest site in consecutive years. For example, Meyers female nested in the same cave in four consecutive years, including the year after her nest was flooded then successfully nested in a hole in the river bank only to return again to the cave in each of the next two years, being flooded out both times. Ram female nested successfully in the same cave in seven consecutive years, the same location used by the female who occupied the territory before her. Ruatiti female nested successfully in the same cave over two years but changed to another cave for her third nesting attempt. Three females returned to a previous year's site amongst riverside vegetation.

Nest

In all cases, the nest bowl was a shallow depression amongst debris on the cave floor or ground. Some breast feathers and down provided a scant cover over the eggs in the female's absence, and, during the course of incubation, these feathers eventually carpeted the floor of the nest bowl. Occasionally grass or soft twigs become incorporated into the nest bowl. All non-cave nests had dense overhead cover ensuring the nest and sitting bird were invisible from above and, apart from the female's single point of entry and egress, virtually invisible from all sides.

Eggs

These were ovoid and white and those within a single clutch were usually similar in size and shape. The dimensions of 55 eggs from nine clutches ranged from 59.0-70.9 mm (mean 64.5 mm, SD 2.4 mm) in length and 40.8-46.7 mm (mean 44.8 mm, SD 1.3 mm) in width. Eggs within complete clutches, on average, varied by up to 3.2 mm in length and by 1.9 mm in width. The mean fresh weight of 25 eggs whose average dimensions were 60.7 x 43.2 mm was 62.3 gms.

Clutch size

The mean size of 23 clutches was 6.0; eight, nine, four, one and one nests contained seven, six, five, four and three eggs respectively. The clutches of three females nesting as one-year-olds were three, four and six.

Laying interval

The interval between successive eggs of a clutch exceeded 24 hours; field observations recorded a female laying her first egg overnight, sometime between 1720 h and 0730 h, her second egg between 1315 and 1736 h the following day, missing one day and laying her third egg between 0810 and 1012 h on the next. (One clutch of five eggs laid in captivity had an interval of two full days between each of the first four eggs and almost three days between the fourth and fifth). In two cases, the duration of laying is known; a clutch of five was laid over eight days, and a clutch of six between 9-10 days.

Incubation and incubation behaviour

Only females incubated eggs. While their mates were on the nest males spent most time (68-81% of daylight hours, Veltman & Williams 1990) inactive and inconspicuous on the river edge, usually directly opposite the nest site. The incubation period exceeded 30 days but was not determined precisely. One female who laid the first of her six eggs on 10 September and was still laying on 18 September appeared with ducklings on 27 October, suggesting an incubation period of about 35 days. Another female, known to be laying during 5-9 October and whose clutch of five contained a pipping egg on 15 November appeared with ducklings on 18 November, a minimum incubation period of 33 days. Males were observed alone on their territories while their females were at the nest for periods up to 42 days, which also implies the incubation period exceeds 30 days.

Females left the nest to feed at about the same times each day, usually during the first two hours of morning and again during the last three-four hours of daylight. The mean of 11 morning recesses was 48 min (range 30-96

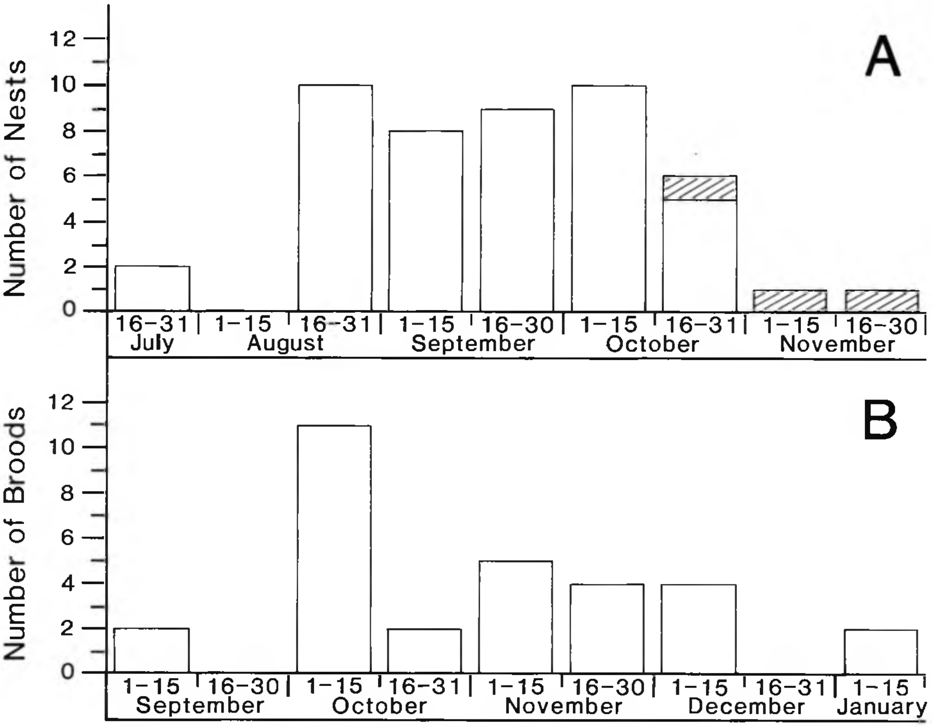

Figure 5. A - The distributions of laying dates for Blue Ducks (data for all years 1980-1989 combined; renests shaded), B - timing of brood emergence (data for all years 1980-1989 combined).

min), that of nine evening recesses was 37 min (range 20-65 min). Three females were not seen to leave their nests in the 48 hours immediately prior to bringing their ducklings to the river. When returning to the nest after feeding the female was usually unaccompanied by the male. In most cases the female flew, walked or swam directly to the nest from a regularly-used roosting spot, at which the male remained.

Timing of laying and brood emergence

The timing of 47 nesting attempts (Fig. 5a) were determined by one, or a combination of (i) backdating from the timing of brood emergence (35 days incubation plus twice the clutch size or brood size for the laying period; $n = 30$); (ii) direct observations of laying hens ($n = 20$); and (iii) from the first sightings of males alone on their territories ($n = 36$). The latter dates were used on their own for two unsuccessful nests for which there were no observations of laying females.

With the exception of two nests in 1987, no nesting attempts commenced before the latter half of August, and those initiated after October were re-nests following the failure of the first attempt. The timing of individual females' nesting attempts varied considerably between years. For example:

(i) Meyers female nested in late August (1984), early September (1982, 87), late September (1980) and early October (1981, 83, 85, 86);
(ii) Ram female nested in late July (1987), late August (1984, 85, 89), early September (1988) and late September (1983, 86);
(iii) Wattle female nested in late August (1984), late September (1985, 86) and late October (1983).

This variability extended to a two-month difference in the timing of successive nesting attempts by three females, two months for one female and one month for two females. Extremes of this variability occurred in 1983 (late nesting) and 1987 (early nesting), years of contrasting winter weather caused by southern oscillation (El Nino) weather events. With the exception of two nests in 1987, ducklings were never observed on the river before October, while the latest a newly-hatched brood from a first nesting attempt reached the river was 14 December (1983) (Fig. 5b).

Nest and hatching success

Of 61 nesting attempts (including three renests), 33 (54%) successfully hatched ducklings. Early nests tended to be more successful; of 29 layings prior to October, 21 (72%) were successful compared with only nine (50%) of 18 later nests. Known causes of nest failure were flooding (6), mustelid predation (3), human disturbance (1), and interference caused by a mate change (1). Six females disappeared while nesting, one of whom was killed by a cat *Felis catus*. Hatching success was determined from 13 nests, in nine of which all eggs hatched; one egg remained unhatched in three nests, and three eggs in another. In all, 67(92%) of 73 eggs hatched.

The brood

From the nest ducklings were taken direct to the river where they immediately commenced foraging amongst the stones on the margins. Both male and female guarded the ducklings throughout their development, the male's role appearing to be primarily one of vigilance, the female's mostly of maintaining brood cohesion. The effect of dual parental care was apparent when, in 1989, Fern female disappeared when her four ducklings were about ten days old. Fern male reared the brood successfully but when feeding the ducklings were often widely scattered up to 100 m apart, a distinct contrast with the tight grouping when a female was present. Young ducklings were brooded only during their first few days, and only by the female. Thereafter, ducklings rested and slept on rock tops as a tight bunch with the attendant adults close by.

a) Growth rate:

The fledging period, defined as the interval during which the young could not fly, varied from 70 to 82 days (n = 14). At fledging ducklings were about 100 gms lighter than mean adult weights (males: 903 g, SD 60 g, n = 20; females 767 g, SD 61 g, n = 20). Growth rate data (Fig. 6; obtained when banding ducklings of known age) while too few to show differences between broods reared in different territories, illustrate that, after five weeks, males grew faster than females. By 55 days, males were about 100 g heavier. Three of five ducklings who raised themselves in isolation after having become separated from their parents and siblings were caught and weighed; all were light. One female weighed 400 g at the same time her two sisters who remained with the parents weighed 610 g and 630 g. Two others, a male and female separated at 40 days from their parents and each other weighed 655 g and 545 g respectively at 65 days, each about 100 g lighter than other ducklings of the same age. Three ducklings raised as singletons for more than half of their fledging period were of similar weights to those of the same age reared in the company of siblings.

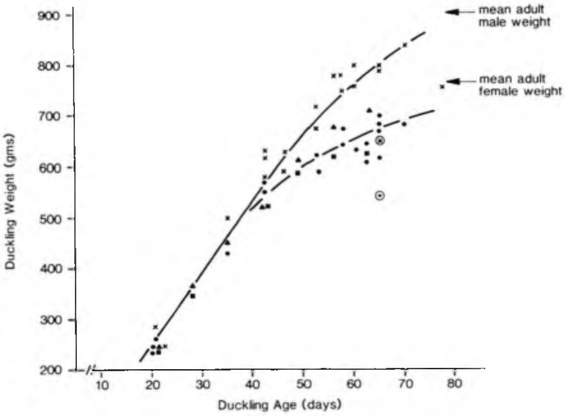

Figure 6. Growth rate of Blue Duck ducklings. Circled points are for ducklings who became separated from their parents and survived alone for most of the fledging period. (Symbols: cross = males, dots = females, triangles = captive males, squares = captive females, the latter two are data from Pengelly & Kear 1970).

After 40 days there was little or no further growth of the tarsus and the average adult tarsal length (males: 51.2 mm, SD 1.5 mm, n = 16; females: 47.3 mm, SD 1.3 mm, n = 15) was reached in 35-40 days by ducklings of both sexes. The culmen grew more slowly; at 70 days males had a culmen 1.0-1.5 mm longer than females but those of both sexes were 1.5-2.0 mm less than the mean adult length (male: 45.6 mm, SD 1.2 mm, n = 16; females: 44.1 mm, SD 1.1 mm, n = 15)

(b) Survival:

Only in four (12%) of 33 broods did all ducklings perish before fledging, three being in 1983 and one, the result of Black-backed Gull *Larus dominicanus* predation in 1989. Survival of ducklings throughout their growth was determined by allocating each duckling, whenever sighted, to one of four plumage classes, a modification of Mosby's (1963) scheme as used by Williams (1974, 1979). Ducklings from 28 broods spent approximately 8-10 days in Class I (C.I), 15-20 days in C.II, 17-20 days in C.III and about 30 days in C.IV before fledging.

Forty-one (75%) of 55 ducklings in 14 broods survived C.I, 71 (83.5%) of 85 ducklings in 27 broods survived C.II, of which 64 (90%) survived C.III and all but one (98%) which reached C.IV, fledged. Thirty-three (60%) of 55 ducklings first seen on the river immediately after hatching eventually fledged. However, there were losses between hatching and first sighting; combined data from seven nests indicate that only 28 (78%) of 36 hatchlings were observed on the water.

Causes of duckling death were not identified; no predators other than the gull were seen catching ducklings and no bodies were found. One C.IV duckling was found, obviously ill, bearing small puncture marks on the back of the head, perhaps indicating an unsuccessful mustelid attack. Five ducklings lost contact with their parents and siblings when 20-40 days old but survived to fledging; this may indicate brood fragmentation as a possible source of mortality. Visits to the study area were not frequent enough to relate the timing of duckling disappearance to periods of river freshes or prolonged bad weather.

Survival data provided consistent evidence of differences in duckling survival between territories. For example, Ruatiti pair raised 11(42%) of 26 ducklings they brought to the river and in no year fledged more than 60% of their initial number of ducklings; Meyers pair raised 13(65%) of 20 ducklings and on two of four occasions raised all ducklings which reached the river; Ram pair raised 22(61%) of 36 ducklings losing one or two ducklings only each year, except in one year when five of six disappeared overnight; Wattle female's three rearing attempts resulted in four (31%) of 13 ducklings fledging.

c) Brood fragmentation:

The break-up of the brood and cessation of parental interest appeared gradual. The initial signs were when adults ceased to keep close company with their young and their activities were no longer synchronous. Over two-three weeks the ducklings became increasingly independent of their parents and the adults spent more time preening as their body moult progressed. By the time they became flightless, adults had virtually no contact with the young who, by then, had commenced short forays up and down the river. Cessation of parental interest usually was not obvious until the ducklings had fledged. However, three sets of parents became flightless before their ducklings could fly and had contact with them only towards evening and during the night. Although three broods retained cohesion for four to five weeks after cessation of parental interest, most quickly fragmented when the young journeyed beyond the natal range. However, it was not uncommon to find siblings together even three to four months after fledging, and in two cases, they acted as a pair to occupy an apparently unclaimed section of river adjacent to their natal range.

Population characteristics

Population density

At the commencement of the study in August 1980, four pairs resided within the study area. In seven of the following nine years the number of discrete sections of river occupied by pairs or singletons increased with nine pairs being resident in 1987, and a 10th pair (Domain) establishing in 1989 immediately downriver of the study area (Fig. 3). The two years in which no increase in population density occurred were 1984 and 1988, immediately following the least productive years of the decade of study (Table 2).

Birds were recruited into the resident

Table 2. Fledglings/breeding pair.

	Resident pairs *n*	Single males *n*	Pairs breeding *n*	Pairs fledging young *n*	Total fledged *n*	Fledglings breeding pair
1980	4	0	4	3	6	1.5
1981	5	0	4	2	4	1.0
1982	4	2	4	3	9	2.25
1983	6	0	5	0	0	0
1984	6	0	6	4	11	1.8
1985	7	1	7	4	7	1.0
1986	6	2	6	4	16	2.7
1987	9	0	6	2	5	0.8
1988	8	1	8	5	8	1.0
1989	9	1	8	3	7	0.9
Total	64	7	58	30	73	1.3

population by:

(i) An unpaired bird staking claim to an unoccupied section of river and thereafter attracting a partner (Wattle female 1981/male 1981, Beeches male 1986/female 1987, Fern male 1985/female 1987).

(ii) Two birds acting as a pair claiming unoccupied space (Reserve 1982, Hoihenga 1981, Eleven 1987, Bridge 1988, Beeches 1989, Domain 199). In two cases (Eleven, Domain) the pair did not attempt breeding and the partnership ceased when other pairing opportunities arose.

(iii) Pairing with a recently bereaved resident on its territory (Ram female 1983, Ruatiti females 1984, 1989, Wattle female 1987, Hoihenga female 1983, Ruatiti male 1989).

(iv) Challenging and supplanting a resident adult (Meyers male 1981).

Most recruits to the resident population were of local origin; of 27 birds which established territories after 1980 (Fig. 4), 19 were known progeny of resident pairs (17 of which established in their first year of life.)

Annual productivity

Over ten years, 58 breeding attempts resulted in 73 young fledging (Table 2), an average production of 1.3 fledglings per attempt. Annual productivity was erratic with, for the first eight years, a curious alternation between good and poor years. The inconsistency of production is emphasised by the facts that 28(48%) of all breeding attempts failed to produce a single fledging, there was total breeding failure in 1983, a season which followed a major and prolonged El Nino event, and there were high failure rates in 1987 and 1989, also years in which weather was dominated by the southern oscillation. Only in two years did production exceed two young per breeding pair while in six years production equated to one fledgling per pair or less.

Individual productivity

Some pairs with long breeding histories averaged in excess of two fledglings per year while others failed to average one (Table 3). These differences appear to be unrelated to the duration of pair relationships. For example:

- Ruatiti male, resident in 1980, had three partners over nine years, raising four young from four attempts with his first female, seven in four attempts with his second, and none in the single attempt with his third;
- Ram male, resident in 1980, had three partners, raising five in two attempts with his first, two in one attempt with his second (Reserve female) and 14 in six attempts with his third. His third female has so far raised 15 young from seven attempts, the last partnered by Beeches male of 1986-88 (Fig. 4);
- Orautoha male made three breeding attempts with Reserve female (1983-85 inclusive) but raised no young. His parentage of seven fledglings was solely with Orautoha female, his partner of four seasons;
- Orautoha female had one partner in her first year with whom she raised two young. Thereafter her partner has been Orautoha male;
- Meyers male and female bred together for eight seasons, 1981-1988 raising 13 young. The female was resident in 1980 and that year raised one youngster with her then partner;
- Wattle male has had two partners, raising four in five attempts with his first and none from two attempts with his second;
- Hoihenga male has had two partners, being unsuccessful at two attempts with his first, and raising two from six attempts with his second.

Four females passed through the population leaving no descendants (Eleven 1987, Beeches 1987-88, Hoihenga 1981-82, Wattle 1987-89)

Table 3. Productivity of individual Blue Ducks.

	Breeding attempts *n*	Total fledglings	Mean
Ruatiti male 1980-88	9	11	1.2
Ram male 1980-88	9	21	2.3
Orautoha male 1982-89	7	9	1.3
Orautoha female 1985-89	5	11	2.2
Meyers male 1981-88	8	13	1.6
Meyers female 1980-88	9	15	1.7
Wattle male 1981-89	7	4	0.6
Hoihenga male 1981-89	8	2	0.25

Table 4. Number of progeny of individual Blue Ducks which, by the 1989 breeding season had established territories.

	Progeny *n*	Progeny on territory	% on territory
Ruatiti male 1980-88	11	4	36
Ram male 1980-88	21	9	43
Ram female 1983-88	14	8	57
Orautoha male 1982-88	7	7	100
Orautoha female 1985-88	9	8	89
Meyers male 1981-88	13	8	62
Meyers female 1980-88	15	9	60
Wattle male 1981-88	4	1	25
Hoihenga male 1981-88	2	1	50
Hoihenga female 1983-88	2	1	50

whereas all territorial males with the exception of Eleven male (a yearling who paired with his sibling for one season) have produced fledglings.

Another measure of individual or pair productivity is the number of their fledglings which established territories within the study area or further upriver (by 31 December 1989) (Table 4). These data indicate that fledglings from Meyers and Orautoha pairs have been more successful than others at establishing on the river. What is of particular interest in this regard is that Orautoha female is a fledgling of the Meyers pair (see later discussion on genetic relationships).

Survival

a) Adults

Once birds occupied and defended sections of river they became year-round residents there. The disappearance of a member of an established pair resulted from death or supplanting. With but two exceptions the 18 adults which disappeared during the ten years were never seen again; the exceptions were: Orautoha male (1985) seen near his former territory five months after having been displaced, but not subsequently, and Meyers male who, for 15 months after being supplanted lived furtively in a sidestream and periodically appeared on his old range. If a bird disappeared from its territory and was not seen over the subsequent six months it was considered as dead.

Annual survival of territorial adults has been calculated for the year 1 August to 31 July, i.e. from the commencement of one breeding season to the next (Table 5). The rate of disappearance was similar in all years except 1980-81 when a pair was shot. On average, approximately seven of every eight territory holders present one year were alive the next, suggesting approximately one-quarter of them may survive for ten years, and a mean lifespan upon becoming a territory holder of 6.75 years.

Table 5. Annual survival of territorial adult Blue Ducks.

	Birds alive *n*	Alive next year *n*	% surviving
1980-8	8	5	62.5
1981-82	10	9	90.0
1982-83	11	10	90.9
1983-84	12	11	91.7
1984-85	12	12	100.0
1985-86	15	13	86.6
1986-87	14	13	92.9
1987-88	17	14	82.4
1988-89	17	13	76.5
Total	116	100	86.2

Twelve females disappeared during the study, three during the January-March period of the annual moult, six while nesting, one shot, one in April after failing to regain weight after moulting, and one while attending ducklings. Only six resident males disappeared; one shot, three following displacement, one in winter (cause unknown) and one following his female's association with a neighbouring male. The higher mean annual survival of males (0.92, Table 5) is emphasised by all four males who occupied territories in 1981 being still present in 1988; the last of the four 1981 females died in March 1988. Mean annual survival of females was 0.80 (Table 5).

b) Juveniles

Estimates of juvenile survival (Table 6) were determined from sightings (to December 1989) of 50 birds banded as ducklings within the study area between 1980 and 1987. During 1980-1985, 29 ducklings were banded at fledging; 16 (55%) of these survived their first 12 months, of which 13 (81%) remained alive at the end of the second year. A further 16 ducklings were banded in

Table 6. Number of Blue Ducks marked as fledglings alive 6-24 months later and the percentage survival in each six month interval.

Time elapsed	Male (n = 29)	Female (n = 21)	Total (n = 50)
6 months	17 (59%)	14 (67%)	31 (62%)
12 months	9 (31%)	13 (62%)	22 (71%)
18 months	9 (100%)	13 (100%)	22 (100%)
24 months	8 (89%)	12 (92%)	20 (91%)

Survival over first 12 months = 44%, over second 12 months = 91%

1986; nine (56%) were alive after 12 months, of which seven (78%) remained alive at the end of the following year. None of the five ducklings which fledged in 1987 have been sighted subsequently. Not included in Table 6 are six 1988 fledglings, five of whom were alive 12 months later. Higher survival estimates were obtained for females than males (Table 6). These data may indicate a lower probability of resighting males particularly during their second six months of life when a major change in juvenile dispersion occurred (see below).

Juvenile dispersal and settlement

During their initial six months most fledglings remained within or close to their natal range and kept company with some of their siblings. Juvenile intruders appeared to be tolerated by neighbouring pairs and allowed to feed unmolested except when in close proximity to the pair. As a consequence, juveniles became familiar with their natal range and habitat nearby.

By June, adults became more defensive and actively harrassed transgressing juveniles. This forced juveniles to disperse more widely up and down the river and small groups of two-six birds, sometimes comprising siblings, were commonly seen in June and July. As they ranged more widely on the river juveniles were observed contesting with established pairs or attempting to occupy pools and riffles between the territories of existing pairs. Dispersal and settlement histories of 30 juveniles (16 females, 14 males) banded within the study area were recorded (Table 7). Most (67%) birds dispersed and settled up-river and most (63%) settled close to their natal territory, separated from it at the time of settlement by two pairs or fewer.

One male fledgling dispersed outwith the Manganuiateao catchment to settle and breed on the adjacent Whakapapa River, the first authenticated record of inter-catchment dispersal by Blue Ducks. Assuming this bird initially flew upriver, less than 7 km separates the headwaters of the two rivers on the lower slopes of Mt Ruapehu. Nineteen (ten females, nine males) of the remaining 29 fledglings dispersed and settled upriver of their natal range. Although there were few observations of these birds prior to settlement, especially of those that eventually resided within the lower gorge, only three birds were seen prospecting areas downriver of 'home' three months or later after fledging.

There was a (non-significant) tendency for females to settle closer to their natal range than did males; seven of 14 males settled at a location where they were separated from their natal range by four or fewer pairs compared with 13 of 16 females ($\chi^2 = 3.28, 0.05<P<0.1$). Overall, two-thirds of the fledglings were separated from their parent(s) by two or fewer pairs at settlement, and five birds established immediately alongside their natal range.

Genetic relationships

As a consequence of the high individual productivity of some long-lived males, the limited dispersal of juveniles, and the increase in population density, many territorial birds were related to each other. Assuming ducklings were, in all cases, the progeny of their guardian adults (see Triggs *et al.* 1991), Figure 7 illustrates the known relationships amongst members of all study pairs.

Table 7. Number of Blue Duck fledglings whose eventual location of settlement was separated from their natal territory by one or more resident pairs. One male settled in a neighbouring catchment.

		Number of intervening pairs							
		0	1	2	3	4	5	6-10	11+
Males	(n = 14)	2	2	3	0	0	1	5	0
Females	(n = 16)	3	3	6	0	1	0	2	1

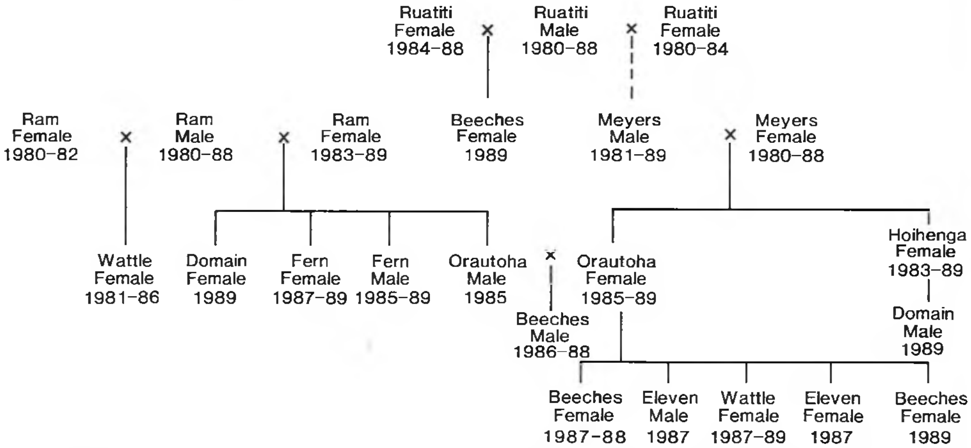

Figure 7. Genetic relationships of territorial Blue Ducks within the Manganuiateao River study area. (Based on the assumption that ducklings are the progeny of their guardian adult - see Triggs *et al.* 1991).

The principal conclusions from Figure 7 are:

(i) Meyers pair had descendants occupying the two ranges immediately upriver of them (Wattles, Hoihenga), the two immediately downriver (Orautoha, Beeches) and two other descendants as a pair further downriver (Eleven). In 1987 they and their descendants were present on six of the nine territories occupied within the study area.

(ii) Meyers male was initially captured in 1980 as a newly-fledged juvenile on the Ruatiti range and was thought to be the progeny of Ruatiti male. If this is so, then Ruatiti male had descendants on all but two of the study area territories in 1987 (see Triggs *et al.* 1991).

(iii) Two sibling pairs established. Fern pair were 1984 and 1986 siblings, and Eleven pair were progeny of the same clutch in 1986. In addition, Beeches male (1986-88) was a half- brother to his mate of 1987-88.

(iv) Eleven pair broke up in April 1988 following the death of Ruatiti female (1984-88). Ruatiti male then paired with Eleven female, probably his great-grand-daughter.

(v) Beeches female died at the nest in September 1988. Subsequently, Beeches male challenged and ousted his downstream neighbour, Ram male, while Ram pair were with young ducklings. After a series of alternating pairings and challenges, Ram male was permanently ousted and disappeared, allowing Beeches male (1986-88) to breed in 1989 with his paternal grandmother.

The genetic relationships of study area birds are more extensive than reported here. Nothing is known of the origins or relationships of key individuals, e.g. Meyers female, Ram male and his two females, Ruatiti male and his two pre-1987 partners, and the two males long resident at Wattles and Hoihenga (Fig. 4). Triggs *et al.* (in press) used DNA fingerprinting to determine genetic relationships amongst all study area birds and those elsewhere on the Manganuiateao River.

Discussion

This study was the first modem investigation to record the year-round characteristics of Blue Duck. It builds on the pioneering observations of Buller (1888) and Guthrie-Smith (1927) and provides substance to some of the predictions about pair associations and residency of recent investigators (Kear 1972, Kear & Burton 1971, Kear & Steel 1971, Eldridge 1986b) whose short-term studies were restricted to a month or two during or immediately after the breeding season. Blue Ducks do indeed associate as pairs throughout the year; pairings are, by and large, maintained over several years; and pairs hold and defend territories throughout the year.

This study monitored Blue Duck density on a single river over several years. Although much has been written about changes in the species' range since European colonisation of New Zealand (e.g. Williams 1964, Kear & Burton 1971) it is apparent that densities on the Manganuiateao River are similar to those reported by some early observers (Guthrie-Smith 1927, Pascoe 1957), despite the presence of introduced salmonid fishes, potential dietary competitors.

Details of Blue Duck productivity and breeding rate within a single population and over several years are presented. Records of clutch size have been compiled before (Oliver 1930, 1955, Falla, Sibson & Turbott 1966, Kear 1972) but not details of nesting success and that of the breeding effort. Blue Ducks have many of the characteristics of other species endemic to New Zealand - they are long-lived with low reproductive rates and irregular breeding success.

This study also appears to be the first long-term investigation of riverine waterfowl in which details of reproductive output, population dynamics and population structure, and long-term social relationships are highlighted. McKinney *et al.* (1978) and Ball *et al.* (1978) highlighted social and territorial behaviour in *Anas sparsa* and its behavioural adaptations to life on southern African rivers; Moffett (1970) and Eldridge (1986a) provided accounts of the breeding and family life of Torrent Ducks; and Bengtson (1966, 1972) summarised Harlequin Duck nest and brood statistics. None of these studies investigated reproduction over several seasons nor examined social interactions within the framework of population dynamics, both critical to understanding the ecology of these 'specialised' waterfowl.

Blue Duck social system

Oring & Sayler (1991) have identified three components to a social system: spatial organisation, mating relationships, and the nature of parental care. As they point out, these components are closely inter-related, selective forces acting on one induce changes in the others. Simply put in the case of Blue Duck, the riverine habitat, with its ever-present potential to sweep away and decimate broods, demands an attentive male role in the caring of the young. This requirement effectively limits breeding opportunity to one mate and imposes a strictly monogamous mating system. The breeding effort requires close male-female cooperation, an intimate knowledge of the breeding habitat, and a certainty of access to its resources. These in turn select for year-round association as pairs and year-round occupancy and defence of the habitat and its resources.

a) Spatial organisation

That Blue Ducks were dispersed as pairs throughout the year was implicit in the writings of early naturalists (e.g. Buller 1888, Guthrie-Smith 1927, Douglas, in Pascoe 1957). Douglas's observation that "every pair of ducks kept two or three hundred yards of river to themselves...." and his report of 13 pairs and their young on four miles of a small river implied a social system in which pairs were spaced serially along the linear riverine habitat but the report left unanswered the fate of each year's crop of juveniles and how they in turn became established occupants of that river. Potts (1870) reported "flocks of moderate numbers in winter" which implies a non-paired, non-residental or non-breeding component.

On the Manganuiateao River pairs serially occupied suitable riverine habitat but the presence of unpaired birds (males in all but one case) occupying a fixed range interspersed between breeding pairs indicates that the occupation and defence of that space is an important behavioural requirement for both individual survival and the opportunity to breed. And with this year-round residency goes an intimate knowledge of the environment; individual birds resided on the same section of river all of their breeding lives. In many cases this embraced the area with which the bird was familiar soon after fledging, or was reared on or near. Small shifts in location during a lifetime were restricted to no more than movement to the adjacent territory, and no bird occupied two more distant ranges as a breeder. Bereaved birds of both sexes remained on their territories or attempted to get a new partner by challenging their immediate neighbours. Displaced birds returned the challenge but if this failed they simply disappeared.

Although there was a period of widespread movement by some fledglings up and down the river, and some birds were seen several kilometres from their eventual point of settlement, all juveniles appeared to have settled by the start of each breeding season. Yet some, as pairs, occupied space through a season and did not breed. Eleven pair in 1987 and Domain pair in 1989 were birds of the year which had a very fixed range during the breeding season but their pairing dissolved in the new year and the females moved to other territories with new partners. Perhaps these were temporary liaisons with the express purpose of keeping an eye out for other pairing options including challenging a neighbour while at the same time gaining familiarity with the surroundings. Sibling pairs were observed both in autumn and winter with many of these associations persisting for several weeks; co-operation may provide the best chance of obtaining space, and it is also a way of mate-testing.

A noticeable difference between the spatial organisation of Blue Duck and that of the other well-studied riverine duck, African Black Duck (Ball *et al.* 1978) was that young birds of the latter species reportedly spent considerable time in habitat beyond the river and their pre-breeding survival was probably enhanced by food resources beyond the river. In the case of Blue Duck, only the river was exploited, imposing a great necessity for young of any year to secure residential space as soon as possible.

Both Ball *et al.*'s study and this, however, describe rather special circumstances, leaving unrecorded important details about juvenile settlement. In this study, the Manganuiateao population was recovering from the destabilising effects of recent volcanic lahars; Ball *et al.*'s study was located where supplementary food was available beyond the watercourse, perhaps atypical over much of the African Black Duck's range. The unanswered question is how do fledglings behave when the resident adult population is at or close to the carrying capacity of the river and they are dependant solely on the resources of the river? Are they more dispersive than this study has recorded? Do they form small flocks as Potts (1870) reported?

Ranges of most adult pairs were fixed; only rarely did they exploit other than a few core riffles and pools (Veltman & Williams 1990), even though at low population density many pairs had large sections of suitable habitat between them and their neighbours. Indeed, it appeared that even between contiguous pairs there were buffer zones, mostly one pool and riffle, into which neither pair normally ventured. It was into these zones that juveniles first attempted residency. A conspicuous feature of the use of territory was that the range of the adults often increased markedly when with young (see Fig. 3). In these circumstances I had the impression that ducklings were dictating movements and that the parents, ever vigilant, went with them until real conflict with a neighbour eventuated. Examples of this were Ram and Meyers pairs, the former ranging well upstream, the latter ranging well downstream with their young into areas in which they were not observed at any other time of year. Again, perhaps these extended movements were more a reflection of low population density because from about 1987 when these extended portions of range became occupied, Ram and Meyers pairs confined all of their activities and brood-rearing to their respective core areas.

b) Mating relationships

Mating relationships in Blue Ducks appear, in the short-term, similar to those of African Black Ducks (McKinney *et al.* 1978). Liaisons between members of neighbouring pairs of Blue Ducks during the moult were recorded by Eldridge (1986b), temporary liaisons between non-resident birds were observed as they attempted to claim space, and established territorial pairs were always at risk from challenges by non-resident birds or bereaved neighbours. Perhaps the major difference with African Black Duck was in the greater frequency and intensity of challenges reported by McKinney *et al.* (1978), again possibly a reflection of the dynamics of the two populations under investigation. Also, judging from data presented by Ball *et al.* (1978), pair bonds may persist for longer amongst territorial Blue Duck pairs. However, this conclusion too could be influenced by the differing population densities of the two species, that of *A. sparsa* may have been much closer to the carrying capacity of the habitat than that of the Blue Ducks.

In this Blue Duck population, most changes in pair associations were the direct or indirect result of death of a member of a territorial pair. Seven pair changes took place when a bereaved bird attracted a new mate to its territory. In one case this involved the relocation of a neighbouring female on to the male's territory (Eleven female 1988); all other new partners were previously unestablished birds. In five cases a bereaved male displaced his immediate neighbour, but in two of these instances the dispossessed neighbour successfully re-established his old pairing after a period of several weeks or months. There was only one example of a successful challenge by an unestablished bird against a territory holder (Meyers male 1981) while the feud between Fern male and Meyers male over three years did not lead to a permanent severing of the Meyers pairing, despite separations of up to six weeks. Thus, the principal threat to an existing pairing was not an unestablished juvenile but a bereaved neighbour.

c) Parental care

Male Blue Ducks, like males of Torrent Duck (Johnsgard 1966, Moffett 1970) and Salvadori's Duck (Kear 1975) assist with raising the brood. Although the impression was of different roles for the two sexes (vigilance by the male, brood cohesion by the female), Veltman & Williams (1990) found no significant differences in the time-activity budgets of one set of parents. However, during the study one female disappeared early during brood rearing. Her male successfully reared all four young but in so doing spent less time guarding the chicks while they were at rest than would have been the case with two attendant adults (unpubl. data) and when feeding the brood was widely scattered. Broods being reared by solo parents were reported last century by Douglas (in Pascoe 1957).

Fragmentation of broods is an ever-present hazard to life on fast flowing waters subjected to brief, and sometimes horrendous freshes. Although I recorded three examples (involving five ducklings) of separated ducklings surviving on their own, all ducklings were of lower weight than those reared in intact broods; they may have been the only fortunate ones to have survived separation given the disappearance without trace of so many ducklings. But is habitat hostility the sole or major factor inducing male parental care? Harlequin Duck breed on mountain rivers yet males do not contribute parental care, indeed they desert their mates when the latter begin incubation (Bengtson 1966). A conspicuous difference between this species and Blue, Torrent and Salvadori's Duck is that males are not territorial and pairs are only summer visitors to their breeding habitat. By comparison with the other riverine species, the habitat of African Black Duck is relatively tranquil. Males of this species are strongly territorial and although they do not contribute active parental care they maintain regular contact with the female and, therefore, her brood. McKinney *et al.* (1978) have suggested these characteristics are an adaptation to river life since they are not shown by African Black Duck's relatives. Perhaps in these riverine species male parental care is a bi-product of year-round territoriality and mate retention and that it is more highly developed in those species occupying rivers of steep gradient where the male role confers a selective advantage.

Breeding Rate

The reproductive rate of Blue Ducks is low by comparison with other anatids. Average clutch was six, eggs were large relative to the size of the female (each about 10% of the female's body weight), the usual interval between eggs of a clutch was two days and the incubation period at approximately 35 days considerably exceeds that of other New Zealand anatids. Renesting was rare (three examples following the failure of 28 nests) and the fledging period was about 11 weeks, also longer than that of other New Zealand ducks. Although breeding may occur in the first year, not all birds did so; five (50%) of ten females and three (60%) of five males occupying territory as a member of a pair in their first year attempted to breed.

These characteristics are entirely similar to those of other riverine waterfowl inhabiting similar headwater habitat: Moffett (1970) and Eldridge (1986a) reported an interval of seven days between each of the last three eggs of a four-egg clutch and an incubation period of 43-44 days for Torrent Ducks, and each egg is estimated to weigh 16% of the female's body weight (Lack 1968); Kear (1975) reported an average clutch of three-four for Salvadori's Duck, an egg being about 13% of the female's body weight, and an incubation period of "at least 28 days". Siegfreid (1968) recorded that the average clutch of African Black Duck as 5.9 (range 4-8), an egg weight equivalent to 7% of the female's body weight, an incubation period of about 30 days, frequent renesting, and a fledging period of nine weeks, all characteristics that place this species between the Mallard group from which it is derived (McKinney *et.al.* 1978) and the other three year-round river residents.

Population Dynamics

During this study the number of birds resident in the study area more than doubled. The majority of the new settlers were progeny of the study area and additionally one-third of the establishing fledglings settled beyond the study area. The population was producing and recruiting more young than required to replace annual losses from it.

a) Births and recruitment in relation to deaths
The average annual mortality of breeding birds was 0.14 (Table 5), the average annual productivity per breeding pair was 1.3 fledglings per year (Table 2) and juvenile survival in their first year was 0.44 (Table 6). Seventeen of 19 locally produced young which established territories within the study area did so as one-year-olds and half of them attempted to breed. By these data, the total recruitment into the **breeding** component of the population was approximately 0.25 fledglings per breeding individual per year, almost double that required to replace adult losses.

b) Annual variations in productivity
Perhaps the outstanding characteristic of Blue Duck breeding was its erratic nature. One year was a total failure, in five other years production was at or less than one fledgling per breeding pair and in only four years was production in excess of the 10-year mean. In the most productive year (1986) three times as many ducklings fledged as in the previous or following year.

Initially there was a curious alternation of good and bad years, this pattern being disrupted by low production in 1988. Although, because of the small number of pairs under observation, variation in annual productivity was not statistically significant, it would be wrong to conclude that it was simply the result of chance events. In two years (1983, 1987) weather in New Zealand was dominated by the southern oscillation. Its effect in 1983 was a very dry winter, during which virtually no freshes of consequence occurred in the river. The build-up of periphyton from the previous summer continued through the 1983 winter and spring, so that when ducklings reached the river algae covered all rocks and invertebrate density was extremely low. Adult birds were then ingesting large quantities of algae (the only occasion I observed this) and despite four of the five breeding pairs bringing ducklings to the water, no youngster survived beyond five weeks.

The winter of 1987 was mild and stimulated two females to commence nesting very early. The spring was warm and wet promoting early snow thaw on Mt Ruapehu. Numerous and prolonged floods followed causing the failure of all other nesting attempts; the two early nesters were the only birds able to fledge young in that year.

c) Representativeness of the study area

Nineteen (73%) of the 27 birds which established within the study area after 1980 were known progeny of resident pairs. There appeared to be little immigration from outwith the study area yet ten fledglings from the study area settled in the lower gorge immediately upriver. This suggests, either, that there was differing productivity of birds resident in the study area and the lower gorge, or, that the previously identified tendency for fledglings to settle upriver of their natal range applies more strongly than existing data indicate. Both the study area and much (4.0 of 6.7 km) of the lower gorge were depopulated by the volcanic lahar in 1975. But in both areas the resident population effectively doubled since between 1980 and 1989; from four to ten occupied territories in the study area and from about six to 12-14 pairs in the lower gorge.

Two surveys of the lower gorge in October and December 1987 encountered only one young brood (from 11 pairs) and these ducklings failed to fledge. Three surveys there in (late September, October and early December) 1988 encountered 14 pairs only one of which fledged ducklings. Further surveys in August, September, October and November in 1989 established that 12 pairs were resident, found the nest of one pair in a low cave, but encountered only one pair with young - the same who fledged young the previous year (and also in 1986). Productivity from within the lower gorge over those three years was almost nil.

Within both the upper and lower gorges the river is deeply incised with mostly vertical walls. At normal summer and winter flows the river spreads wall to wall at pools, but at riffles the river usually narrows and an exposed area of rock, aggregate and river debris persists. In the absence of caves these areas offer the only nest sites. But the frequent and sometimes horrendous freshes which characterise this river race wall to wall within most of the upper and lower gorges; conceivably the nesting attempts by pairs resident here are regularly savaged by these spring freshes. Perhaps it is significant that within the territory of the one successful pair in the lower gorge was a large accumulation of river aggregate and debris which remained above water during these freshes.

Production from within the study area alone was insufficient to account for the increase in pair density in both study area and lower gorge. This implies that not all years were as unproductive in the lower gorge as 1987-89. Nevertheless the study area may have been considerably more productive than the incised sections of the river; it assumes a particular importance in the overall dynamics and genetics of the river's Blue Duck population.

Genetic Relationships

Given the tendency of fledglings to settle so close to their natal range high levels of genetic relatedness amongst birds within the study area are expected. The extent to which this may be typical of Blue Duck populations or merely an artifact of the large number of opportunities for settlement which a recolonising population presents can only be determined by analysing genetic relationships in a variety of other Blue Duck populations with different densities, population histories and dynamics (see Triggs *et al.* in press). Nevertheless, the outcome for this population once it reaches its carrying capacity within the study area and lower gorge, is that a large number of contiguous territories will be held by closely-related individuals. If settlement close to home is a feature of Blue Duck biology, this clumping of closely-related birds will persist.

The settlement of progeny from the study area within the lower gorge is evidence of gene flow between sections of the river and may indicate that the high level of genetic relatedness extends over larger sections of the river than just the study area. Again however such interpretations are bedevilled by the present dynamics of the population - is this observation also the result of the larger number of settlement opportunities afforded a recolonising population?

True sibling pairings were observed, one pair breeding successfully over two seasons and raising five young. Two other totally inbred relationships were identified - Ruatiti male with his great grand-daughter (1988), and Ram female with her grandson (1989) but only the latter produced young; both of these pairings resulted from descendants settling alongside the long-established territories and pairing following death of one or other's partners.

Comparisons with other riverine waterfowl

All four Southern Hemisphere riverine waterfowl retain their pair associations year round and probably keep the same partners over several years, all defend their territories year round, and, with the exception of *Anas sparsa*, all have biparental care of the brood.

The resources of the riverine environment are probably more easily sequestered and defended than those exploited by other anatids; for a start there are only two points of conflict at the upper and lower extremities of the territory. Also, the annual variations in food abundance and availability are probably less in the riverine environment than in still waters or swampland subject to extensive drawdown or drying up; in New Zealand, stream invertebrates do not exhibit obvious seasonal cycles of abundance. Although freshes or prolonged floods may cause major reductions in invertebrate densities, their recolonisation and population recovery appears very rapid (Winterbourn 1978). Thus there are no seasonal impediments to year-round residency as, for example, would face Harlequin Duck in Arctic rivers.

The similarity of the riverine environment colonised by these waterfowl in different parts of the world has shaped the behaviour of the birds in similar ways. My prediction would be that their population dynamics and structure will prove similar also: birds on contiguous territories will be closely related to each other, juveniles of both sexes will attempt settlement close to their natal ranges, annual productivity will be highly variable, and territorial birds will be long-lived. The power of ecological factors to shape the individual and social behaviour of these birds, as McKinney *et al.* (1978) so elegantly demonstrated, will have a complementary effect on their population processes as well.

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Murray Williams, Department of Conservation, P.O. Box 10-420, Wellington, New Zealand.