Diurnal use of time and space by breeding Blue Duck *Hymenolaimus malacorhynchos*

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The diurnal time-activity budgets of two territorial pairs of Blue Duck were measured during the breeding season in New Zealand from August to December 1986. Morning and evening peaks of foraging behaviour characterised pre-incubation time budgets but their absence during and after the incubation phase indicated that Blue Duck activity was not determined by temporal variations in prey availability. Foraging accounted for less than 20% of the males' active day during all phases of the breeding cycle, except when moulting, whereas females spent over half their day feeding prior to laying. Males and females invested equal time in the major activity classes when ducklings were present. Home ranges contracted around the nest site during incubation and moulting, but encompassed the entire territory when ducklings were present. Blue Ducks predominantly used the river's edge and varied their behaviour in relation to other physical characteristics of the river. We conclude that defence of a food supply is not the primary function of year-round territoriality in Blue Ducks.

Blue Ducks *Hymenolaimus malacorhynchos* are river specialists endemic to New Zealand. Presently the species is dispersed in small, non-interacting remnant populations in widely scattered locations in North and South Island (Bull *et al.* 1985) and is accorded the conservation status of 'vulnerable' (Bell 1986).

Permanent, year-round territories are defended by Blue Duck pairs. This behaviour is unusual among ducks (Tribe Anatini) (Kear 1972) and is apparently restricted to species living year-round on rivers (McKinney 1985). In addition, Blue Ducks are strongly philopatric and their limited dispersal has major implications for Blue Duck conservation and management. Knowledge of territorial dynamics and habitat use is therefore crucial in the conservation of Blue Duck populations.

Eldridge (1986) studied the summer time-activity budgets of three pairs of Blue Ducks and observed that foraging was concentrated in a 4 h period after dawn and a 3 h period before dusk. She hypothesized that the birds were exploiting an invertebrate resource whose availability varied diurnally and which was continuously recolonising denuded areas. Since the common benthic invertebrates in New Zealand lotic ecosystems do not exhibit strongly seasonal life cycles (Winterbourn *et al.* 1981), and there is no evidence of seasonal reductions in drift biomass (McLay 1968), the hypothesis predicts diurnality of Blue Duck foraging activity throughout the year.

To explore this prediction in another season, and to quantify the use of riverine habitat defended by Blue Ducks, we monitored the daytime activities of two territorial pairs during the spring breeding period. When one of the breeding attempts failed we were able additionally to compare the time-activity budgets of adults with and without dependent offspring.

Methods

Study area

Several pairs of Blue Ducks resided on a 9.3 km stretch of the Manganuiateao River from its confluence with the Hoihenga stream to that with the Ruatiti stream (Fig. 1). The river originates on the western slopes of an active volcano, Mt. Ruapehu, in the centre of North Island, New Zealand, and is a major tributary of the Wanganui River. The river has mean annual flow of 18.2 m^3sec^{-1}, and a mean annual water temperature of 11.3°C. An alternating series of pools and riffles characterise the morphology of the river - for descriptive purposes these have been numbered consecutively from the downstream limit of the study area (Fig. 1).

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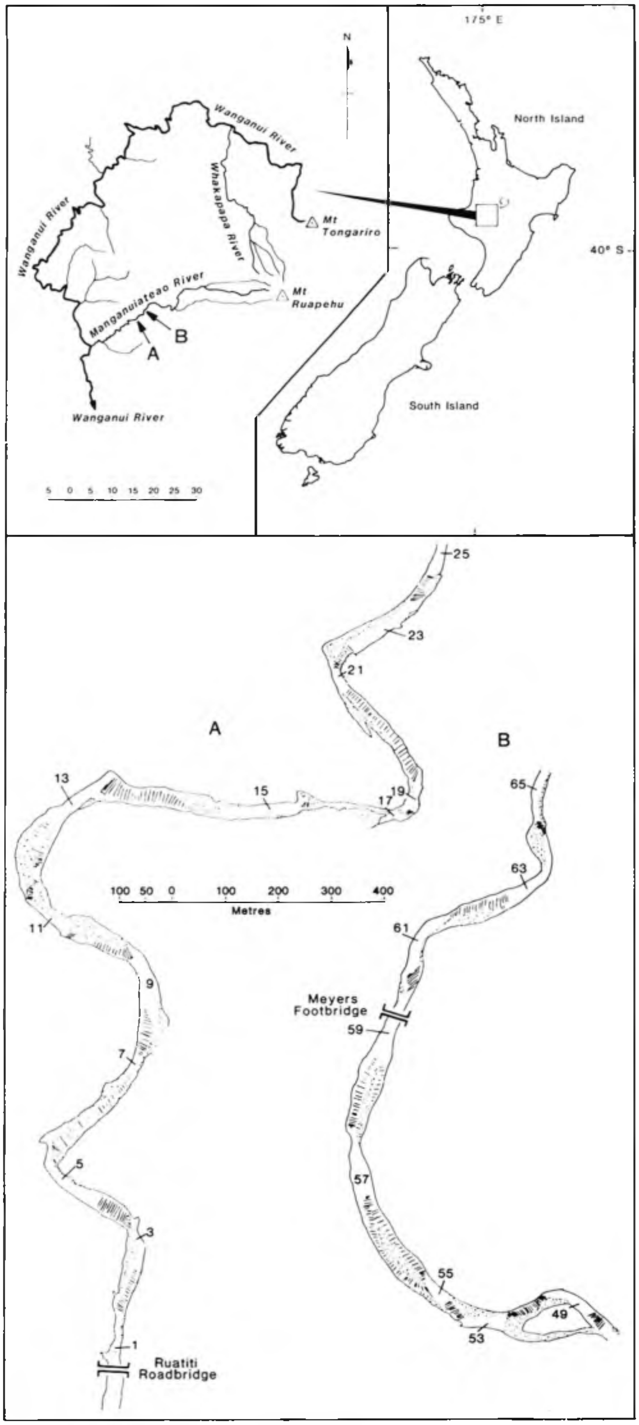


Figure 1. The Manganuiateao River showing the sequence of pools and riffles. Pair 1 occupied areas 10-23, pair 2 occupied areas 55-59.

Ducks

The study concentrated on two pairs, both of whom defended a number of consecutive pools and riffles (Fig. 1). A fifth individual, an unattached male, was included in the study while he attempted to displace one of the territory residents (see below).

The female of Pair 1 settled on the territory as a recently-fledged juvenile in April 1984 and commenced breeding successfully with the resident male whose previous partner died early in 1983. The male was a breeder of unknown age in 1980.

Pair 2 formed in August 1981 when the male, then aged ten months, ousted the resident male. From 1985 the male of Pair 2 was frequently challenged by a 1984 fledgling; in August 1985 and 1986 the pairing was disrupted for up to a week, but on both occasions the resident male re-established his dominance. Our initial observations on 6 August 1986 coincided with the intruder associating with the female and our second visit followed the successful return challenge of the resident male but with the intruder in close attendance. The challenger was not seen on subsequent visits. The female was of unknown age when the pair formed in 1981.

Both pairs had near neighbours. Downriver of Pair 1, a pair ranged up as far as area 10 while the upriver neighbours occupied areas 33-52 concentrating most of their activity about areas 40-46 (Fig. 1). Late during the study, a juvenile male became a furtive resident of areas 21-30.

The upriver neighbours of Pair 2 lived between areas 61-75 with the focal point of their activities being at area 71. Downriver were the two birds described above as upstream neighbours of Pair 1.

In the years before and since this study, both females nested in caves; Pair 1 at pool 13 and Pair 2 at pool 57.

Data collection

Data were collected during nine visits made at two-weekly intervals, commencing 5 August 1986 (Table 1). Each pair of ducks was followed for the equivalent of a full day on every visit (usually midday to dusk on one day and then dawn to midday on the next); no night watches were attempted. Focal animal sampling (Altmann 1974) at one-minute intervals was employed, and data were gathered simultaneously on both members of a pair. Data were recorded directly onto 22 column score sheets for later computer entry.

Table 1. The four phases of the breeding cycle of each Blue Duck study pair as referred to throughout the text, and dates of visits to the study area.

Breeding phase	Pair 1	Pair 2
Pre-breeding	Visits 1 and 2	Visits 2 and 3
Pre-laying,laying	Visits 3 and 4	Visits 4 and 5
Incubation	Visits 5 and 6	Visit 6
Post-breeding	Visits 7,8,9	Visits 7,8,9

Dates of visits: 1: 5-7 August; 2: 21-22 August; 3: 6-7 September, 4: 17-19 September; 5: 4-6 October; 6: 24-25 October; 7: 13-15 November; 8: 21-22 November; 9: 8-9 December.

Eleven categories of behaviour were scored in relation to two locations and three other categories describing the duck's orientation to the river flow. Five foraging behaviour patterns were distinguished: (i) up-end - in which the head, breast and nape were immersed while the remainder of the body was above water and oriented vertically; (ii) head dip - only the head and bill were immersed; (iii) dive -the duck removed invertebrates from rocks by swimming under water; (iv) graze -the duck stood on or swam near a rock and gleaned invertebrates from the surface, its head remaining above the water; and (v) peck - a swimming duck darted over the water, snatching prey from the surface of the water. Other behaviour patterns were fly, preen, stand, sleep, flight and swim.

Location was scored as pool or riffle number (see Fig. 1), and then as top (the upstream end), middle or bottom (the downstream end) within each. The duck's lateral position on the river was categorised as: shore, edge (within 3 m of the shore), side (lateral third of river width), and centre (central third of river). Characteristics of water flow where the duck was active were based on water surface appearance and defined as smooth (slow flow, unbroken surface), ripply but unbroken, ripply and white (the surface sufficiently disturbed so as to appear white), bubbly and white (fast water), and savage (very fast and turbulent). The other obvious characteristic of the river was the presence or absence of exposed rocks within 1 m of the duck. The relative sizes of the exposed rocks were defined as: none, at water-level, half-duck height, 1, 1-2, 2-3, and 3+ ducks in height.

Because the ducks were sometimes briefly hidden from view, the number of observations of each individual in each hour of the day did not always total 60. We therefore used 3-point running means (i.e. the mean percentage of time spent in a behavioural state in that hour and the previous and subsequent hours) in our presentation of the time-activity budget data in Figures 2-5.

Throughout the analysis, it was assumed that the time devoted to each activity by the ducks was equal to the percentage of total scores in which the activity was recorded.

Variations in the intensity with which birds foraged and stood were measured in terms of bout length. The onset of foraging or standing bouts was defined as two consecutive observations of the same activity, and the bout terminated with four consecutive observations not of that activity. This may have occasionally generated overlapping foraging and standing bouts, if the criterion to start a standing bout, for example, was met before the criterion to end a foraging bout. Sleeping bouts began with two consecutive sleeping scores and ended prior to a sequence of six consecutive non-sleeping scores. This was because long periods of sleep were briefly punctuated by other non-foraging activities. We then compared the length of bouts between phases of the breeding cycle and between ducks of either sex.

Results

Scope of the data

A total of 18,035 one-minute focal animal observations was made. Fewer observations were obtained for females because of their absence while incubating. The predominant activities were four of the five foraging patterns (excluding pecking), and preening, standing and sleeping (Table 2).

Breeding cycle of study pairs

In presenting our data we matched the breeding cycles of the two pairs as shown on Table 1. The female of Pair 1 was incubating during our October visits (numbers 5 and 6, Table 1) and her clutch of six eggs hatched on 27 October. Allowing 35 days for incubation and a laying period of approximately ten days, this female probably commenced egg-laying on or about 12 September and incubation on 22 September.

The female of Pair 2 visited her nest site for 4.5 hours during visit 4 but did not appear

Table 2. Percent distribution of the four commonest activities of study Blue Ducks in each phase of the breeding cycle.

Breeding Phase	Activity	Pr1 male	Pr1 female	Pr2 male	Pr2 female
Pre-breeding	Foraging	14.6	43.5	15.9	14.6
	Preening	4.9	5.4	11.9	6.5
	Standing	31.8	5.1	12.2	1.5
	Sleeping	32.5	33.7	8.8	70.3
	Other	16.2	12.3	11.2	7.1
Total scores		711	710	1056	1199
Pre-laying	Foraging	18.4	53.0	15.9	58.1
	Preening	8.2	5.5	10.0	9.6
	Standing	39.0	2.8	10.1	6.4
	Sleeping	21.4	30.6	58.1	20.0
	Other	13.0	8.2	5.9	5.9
Total scores		146	1103	1184	932
Incubation	Foraging	4.7		9.9	
	Preening	7.5		11.5	
	Standing	49.9		26.5	
	Sleeping	31.5		41.2	
	Other	6.4		10.9	
Total scores		1056	21	405	18
Post-breeding	Foraging	11.2	5.1	32.2	39.3
	Preening	8.6	8.8	23.2	30.6
	Standing	38.4	32.4	15.8	3.3
	Sleeping	25.7	25.4	24.3	24.7
	Other	16.1	18.3	4.4	2.1
Total scores		2139	2136	2160	2059

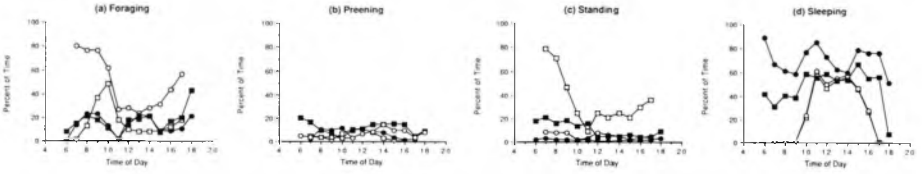


Figure 2. The percentage of time during each daylight hour of the pre-breeding phase which each Blue Duck spent (a) foraging, (b) preening, (c) standing, (d) sleeping. Key: Filled square - male of Pair 1; Filled circle - female of Pair 1; Open square - male of Pair 2; Open circle - female of Pair 2.

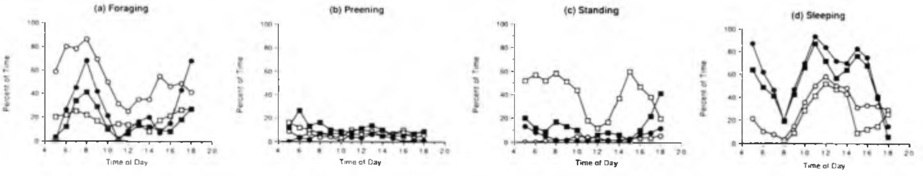


Figure 3. The percentage of time during each daylight hour of the pre-laying phase which each Blue Duck spent (a) foraging, (b) preening, (c) standing, (d) sleeping. Key as for Figure 2.

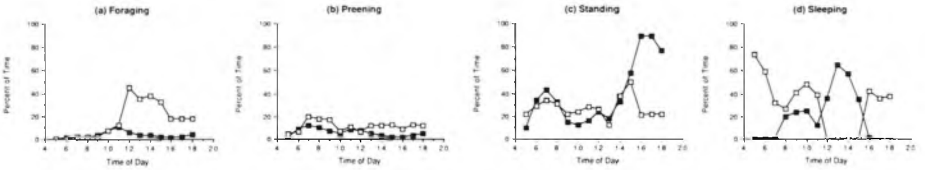


Figure 4. The percentage of time during each daylight hour of the incubation phase which each male Blue Duck spent (a) foraging, (b) preening, (c) standing, (d) sleeping. Key as for Figure 2.

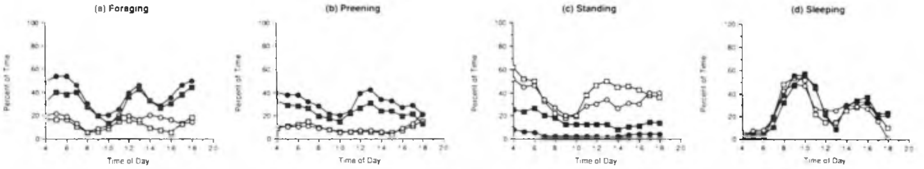


Figure 5. The percentage of time during each daylight hour of the post-breeding phase which each Blue Duck spent (a) foraging, (b) preening, (c) standing, (d) sleeping. Key as for Figure 2.

gravid. She was not recorded at the nest or separated from the male during visit 5 (5-6 October) but had commenced incubating her five-egg clutch by visit 6 (24-25 October). However, the nesting attempt failed before visit 7 (13 November).

Seasonal and daily time budget

Comparison between phases of the breeding cycle

The most obvious feature of the pre-breeding phase was the difference between birds in the amount and periodicity of sleeping and foraging behaviour (Figs 2a-d). During the pre-laying phase, the principal difference was between the behaviour of the sexes (Figs 3a-d); both females foraged more than their mates as egg-laying approached, this effect being more marked in Pair 1 (Table 2).

The temporal patterns of activity of the two pairs were similar during these initial phases of the breeding cycle (Figs 2 and 3). After foraging in the early morning, the ducks slept through to late afternoon when they commenced foraging again. The prolonged period of rest was broken during the early afternoon by standing, preening, and some foraging activity.

Figures 4a-d illustrate incubation phase time-budgets for males only since females were out of sight on their nests. The behaviour of both males was similar in that they were inactive (standing or sleeping) for long periods. Foraging amounted to less than 10% of the day concentrated in the early afternoon, contrasting with the midday peak of inactivity during earlier phases. Each female was observed to leave her nest on one occasion, for 17 minutes and 18 minutes respectively. The female of Pair 1 foraged for half of her nest relief, and stood or swam for the remainder. The Pair 2 female foraged for 22% of the time she was off the nest, and preened and swam for the remainder.

The contrasting time-budgets of the pairs during the post-breeding phase (Figs 5a-d) results from the failure of the breeding attempt by Pair 2. Apart from a period of rest during the late morning, the adults of Pair 1 spent a similar proportion of each daylight hour foraging in company with their ducklings. However, the dominant activity at this time was standing which we interpret as alert behaviour associated with parental care. Pair 2 preened consistently throughout the day indicating that moulting had begun. Foraging occupied more time compared with Pair 1, but both pairs were inactive for a similar period in late morning.

Synchrony of behaviour within each pair

There was a high degree of synchrony between the members of each pair, ranging from 62% of 1717 observations when both birds in Pair 2 were visible during the moult to 81% of 875 observations for the same pair in the pre-laying phase.

Duration of foraging, standing and sleeping bouts

The four focal animals generated 325 foraging bouts, summarised on Table 3. Females tended to forage in longer bouts than males.

Table 3. Length (minutes) of Blue Duck foraging bouts for both sexes in each phase.

Phase	Males			Females		
	n	$\bar{x}$	s.e. of mean	*n*	$\bar{x}$	s.e. of mean
Pre-breed	23	10.61	2.18	29	15.72	3.14
Pre-lay	43	7.95	1.50	32	21.25	3.28
Incubation	12	4.42	0.74	2	4.50	0.50
Post-breeding;						
Pair 1	34	4.53	0.46	37	5.64	0.82
Pair 2	62	8.87	1.11	51	13.45	1.78

Table 4 summarises standing bout lengths. In contrast to females, males stood for extended periods in the weeks before incubation commenced.

Only 106 bouts of sleeping behaviour were extracted from the data. Overall, mean male sleeping bout length was 33 minutes ($n = 50$, SE = 1.12) and 33 minutes for females ($n = 62$, SE = 1.14). During the incubation phase, the two males slept in bouts averaging 45 minutes ($n = 9$, SE = 23.75).

Table 4. Length (minutes) of Blue Duck standing bouts for both sexes in each phase.

Phase	Males			Females		
	n	$\bar{x}$	s.e. of mean	*n*	$\bar{x}$	s.e. of mean
Pre-breed	31	10.35	1.96	9	3.89	0.86
Pre-lay	49	10.02	1.56	7	4.00	0.87
Post-breeding;						
Pair 1	57	10.96	1.71	60	8.52	1.17
Pair 2	44	4.86	0.73	5	6.4	2.94

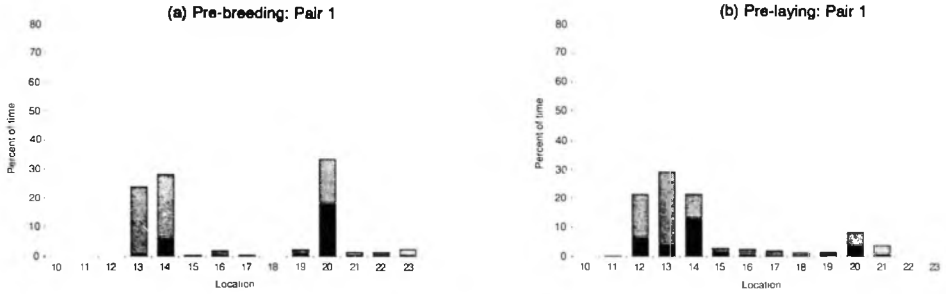
Use of pools and riffles by each pair

Pools and riffles within the ranges of each pair were not used with equal intensity, for feeding tended to be concentrated at particular riffles while selected pools and riffles were used for non-foraging behaviour (Figs 6 and 7). In addition, patterns of use varied with each phase of the breeding cycle.

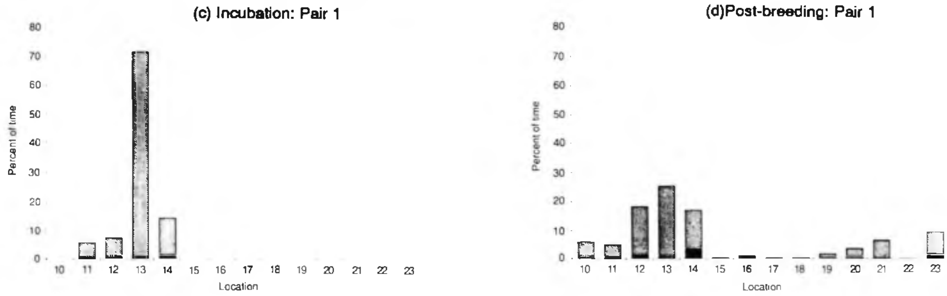
As incubation approached, both pairs changed their foraging locations to nearer the nest sites. For example, up to one month prior to laying almost 66% of Pair 1's foraging took place in riffle 20 with a further 21% in riffle 14. But close to and at egg-laying, feeding was concentrated at the two riffles and pool adjacent to the nest site in a cave at pool 13. The female of Pair 2 nested in a cave at pool 57, around which the pair foraged.

These changes in feeding locations were accompanied by complementary changes in the locations of other activities (Figs 6 and 7).

While the females were incubating, the ranges of both males contracted dramatically, and almost all of their activities were restricted to the immediate vicinity of the nest cave. We did not see the males make any forays to the extremities of their territories, a feature of their behaviour at


(a) Pre-breeding: Pair 1

(b) Pre-laying: Pair 1


(c) Incubation: Pair 1

(d)Post-breeding: Pair 1

Figure 6. The percentage use of pools (odd numbers) and riffles (even numbers) within the range of the Blue Duck Pair 1 during (a) pre-breeding, (b) pre-laying, (c) incubation, (d) post-breeding phases of the breeding cycle. Key: light hatching - foraging; dark hatching - non-foraging activities.

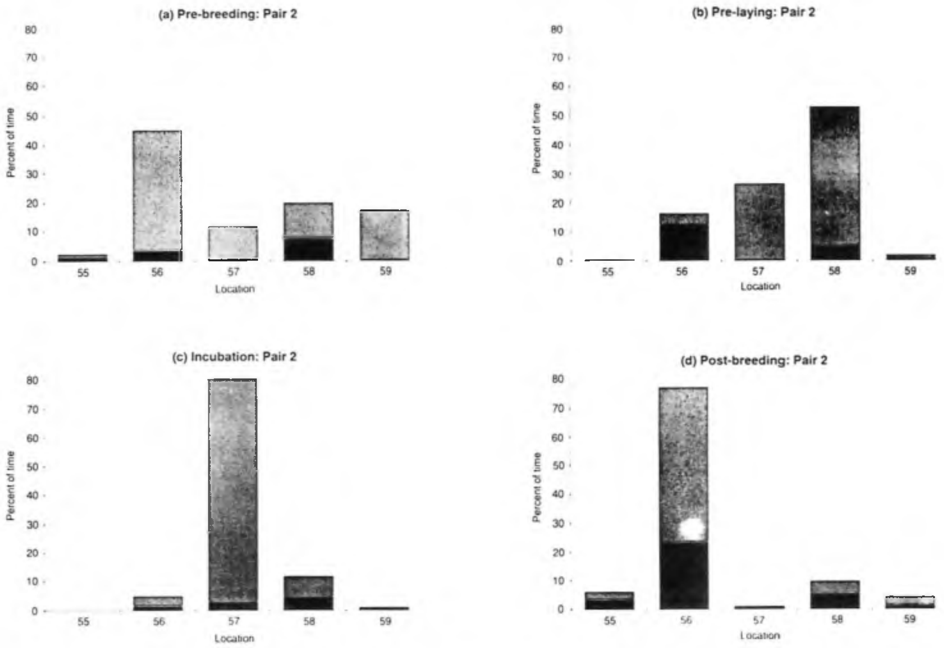


Figure 7. The percentage use of pools (odd numbers) and riffles (even numbers) within the range of Blue Duck Pair 2 during (a) pre-breeding, (b) pre-laying, (c) incubation, (d) post-breeding. Key as for Figure 6.

other times of the year.

Data from the post-incubation phase (Figs 6d and 7d) highlight the differences in breeding success of the pairs. The range of Pair 2 contracted progressively as their moult intensified and five weeks after the loss of their nest, almost all of their time was spent at riffle 56 where, for part of the time, they hid amongst a tangled pile of flood debris. In contrast, the range of Pair 1 expanded considerably when they were accompanied by ducklings.

Use of habitat during the predominant activities

Observations of all birds were combined and divided into two categories, foraging and non-foraging. The least frequently occurring patterns from each category are not illustrated, namely pecking (0.6% of all foraging observations), and fighting and flying (0.3% each of all non-foraging observations).

(i) Distribution of activities throughout pools and riffles

The distribution of foraging activities was significantly different in the three linear sections of pools ($\chi_6^2 = 55.67$, $P<0.001$) and riffles ($\chi_6^2 = 41.29$, $P<0.001$), reflecting the concentration of up-end feeding in the upstream reaches of both pools and riffles (Figs 8a and b), and the localisation of diving at the downstream interface of pools with riffles.

The four predominant non-foraging activities also varied significantly along the length of pools ($\chi_6^2 = 201.90$, $P<0.001$) and riffles ($\chi_6^2 = 374.4$, $P<0.001$). Whereas swimming behaviour was more-or-less evenly distributed in all linear zones of the river, the ducks were more often inactive (standing and sleeping) at the upstream end of pools and slept more frequently in the upstream section of a riffle.

Significant differences in foraging ($\chi_6^2 = 235.60$, $P<0.001$) and non-foraging ($\chi_6^2 = 1303.30$, $P<0.001$) occurred across the four lateral zones of the river channel. Most activity was confined to within 3 m of the river's shoreline (Figs 9 a, b) and even dive feeding most frequently took place there. We did not see Blue Ducks feeding beyond the main river channel, and only during aerial pursuit flights did we observe birds flying beyond the confines of the waterway.

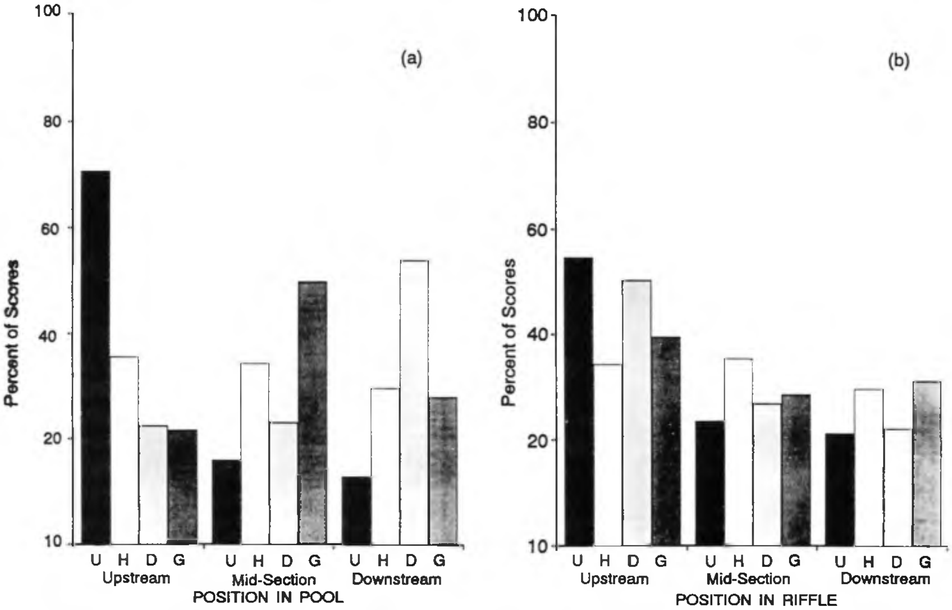


Figure 8. The distribution of foraging behaviour patterns of Blue Duck in the upstream, mid- and downstream sections of (a) pools and (b) riffles (data from all birds and all visits combined). The bars are labelled as follows: U up-end; H head-dip; D dive; G graze.

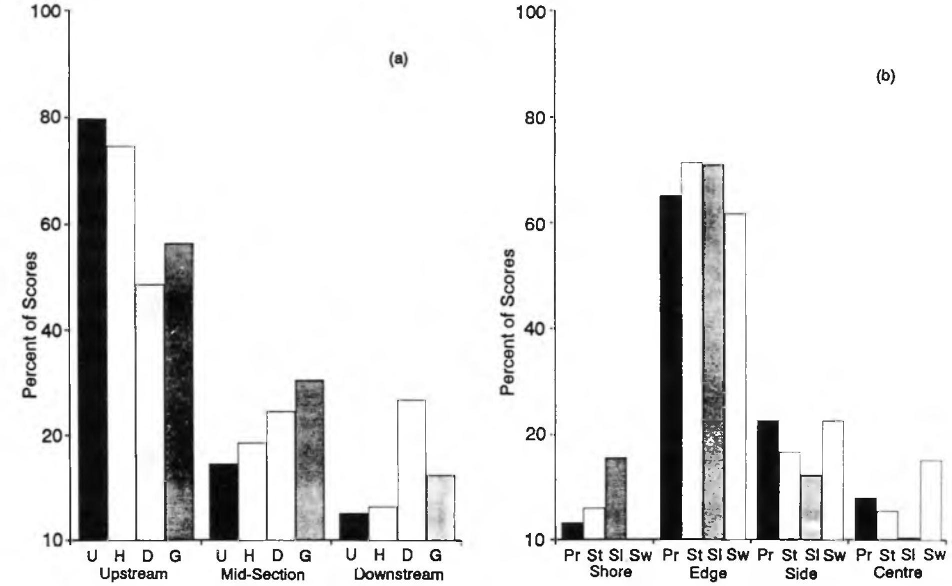


Figure 9. The distribution of (a) foraging (bars labelled as in Fig. 8.) and (b) non-foraging behaviour (bars labelled as follows: Pr preening; St standing; Sl sleeping; Sw swimming) by Blue Duck in relation to position within the river channel.

(ii) Distribution of activities in relation to water turbulence and exposed rocks

Water turbulence significantly influenced duck behaviour (χ^2_{16} = 257.26), $P<0.001$). Foraging activities were concentrated in ripply water (Fig. 10a) while non-foraging activity was also dependent on turbulence (χ^2_{12}= 504.60, $P<0.001$), but included relatively greater use of smooth water zones (Fig. 10b). Fast, white water was avoided by the birds and the few observations

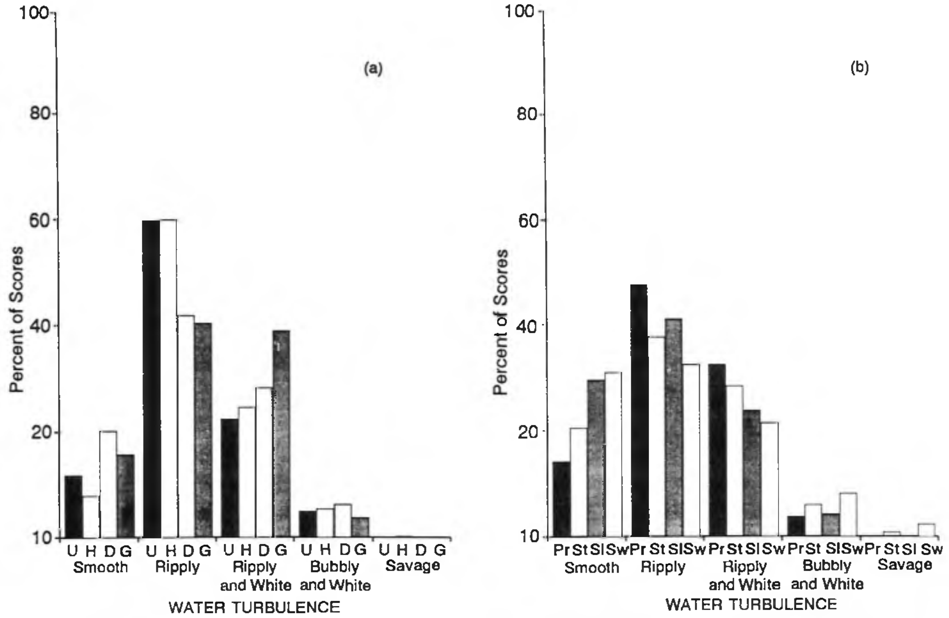


Figure 10. The distribution of (a) foraging (bars labelled as in Fig. 8) and (b) non-foraging behaviour (bars labelled as in Fig. 9) by Blue Duck in relation to water turbulence.

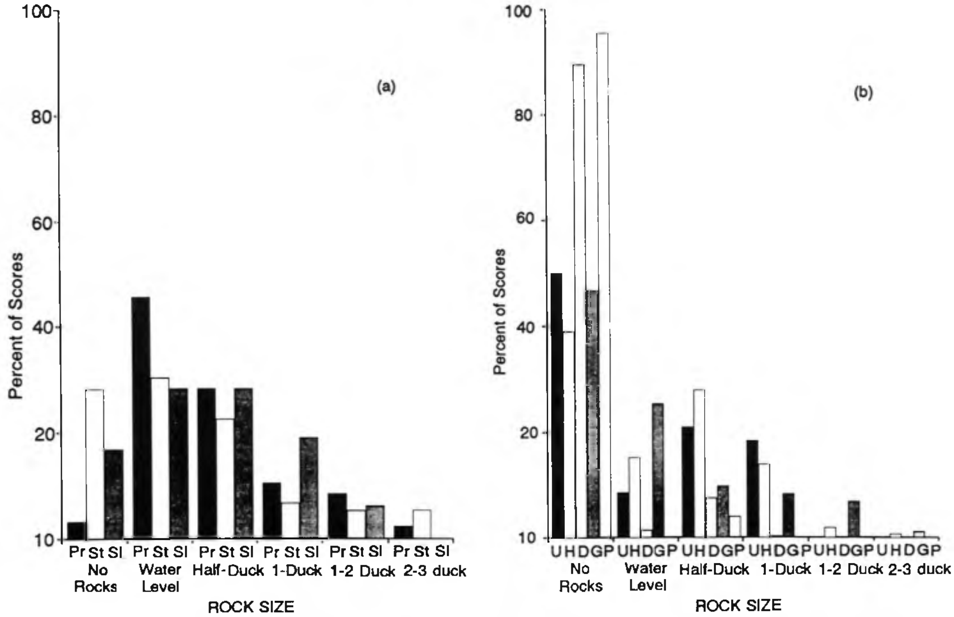


Figure 11. The distribution of (a) foraging (bars labelled as in Fig. 8, P peck) and (b) non-foraging behaviour (bars labelled as in Fig. 9) by Blue Duck in relation to the size of adjacent rocks.

we made of feeding or swimming activities in white water were usually of ducks tucked in behind exposed rocks.

The distribution of foraging behaviour varied significantly in relation to the size of exposed rocks (χ^2_{20} = 437.26, $P<0.001$). Most foraging occurred in relatively open water or in the vicinity of small rocks, i.e. those of lesser height than the swimming duck (Fig. 11a). The use of rocks by inactive ducks also varied with rock size ($\chi^2_{10} = 905$, $P<0.001$), the greatest use being made of rocks at water level or exposed to about half a duck in height (Fig. 11b).

Discussion

Year-round territoriality is a conspicuous feature of the biology of four riverine anatid species (Blue Duck, Torrent Duck *Merganetta armata* (Johnsgard 1966), Salvadori's Duck *Anas waigiuensis* (Kear 1975) and African Black Duck *Anas sparsa* (Ball *et al.* 1978, McKinney *et al.* 1978)). Territories are defended by pairs and presumed to encompass all the food and other resources required. Although no quantitative studies of the diets of these species exist, aquatic invertebrates apparently comprise a major food of each. Their year-round territoriality may reflect temporal stability and abundance of these prey populations.

(i) Feeding effort

A clue to prey availability and abundance is the time ducks spend feeding during the various phases of their annual cycle. Only three other time-activity budgets for riverine waterfowl have been published (Ball *et al.* 1978, Eldridge 1986, Inglis *et al.* 1989) and to our knowledge, the results presented here are the first to focus on the use of time and space of river-dwelling ducks during the breeding season.

We found that, prior to incubation, Blue Duck foraging was concentrated in early morning and late afternoon, consistent with the explanation that the birds were exploiting invertebrates active on rock surfaces and in the drift. However, when females were incubating, male foraging was concentrated in the early afternoon and adults with ducklings foraged throughout the day while the moulting pair exhibited three foraging peaks. At these times the birds must have been utilising non-drifting invertebrate prey, so we doubt that variations in the diurnal availability of invertebrates impose temporal restrictions on the foraging activity of Blue Ducks. Morning and evening peaks characterised the feeding activity of another riverine feeder, African Black Duck (Ball *et al.* 1978), even though acorns were a significant food. Bengston (1972) observed periodic foraging behaviour by Harlequin Duck *Histrionicus histrionicus*, in the aperiodic conditions of the arctic summer although Inglis *et al.* (1989) described more constant feeding activity during the pre-breeding season. Similar periodicity of activity has also been found in non-riverine waterfowl, e.g. Gadwall *Anas strepera* during the breeding season (Dwyer 1975) and non-breeding period (Paulus 1984) and non-breeding Green-winged Teal *Anas crecca carolinensis* (Quinlan & Baldassarre 1984) and may be typical of waterfowl in general.

Post-breeding Blue Ducks observed by Eldridge (1986) approximately 10 km upriver of our study area foraged for 27-29% of each day (from her Fig. 6) and apparently did not feed at night. This represents about 234-252 minutes of daily foraging (day length data from Nautical Almanac). At least three of Eldridge's six main study birds underwent full wing moult during her period of study, presumably imposing high metabolic demands and a consequent increased foraging effort. Her non-moulting pair (green) fed for 17-28% (147-243 mins) of each day.

Total feeding time of birds recorded in our study varied considerably, from as little as one hour per day for males during incubation to almost 400 minutes for females at or close to egg-laying. Our data most comparable with Eldridge (1986) are from the post-breeding phase where adults with chicks fed for 11.2-15.1% (98-132 minutes) of each day, and the moulting pair for 32.2-39.3% (282-345 minutes) of each day. In general, the results of the two studies are similar, even allowing for the greater likelihood of Eldridge observing feeding birds during her opportunistic sampling regime. There is clearly considerable variation in feeding effort at different phases of the annual cycle.

The time spent feeding by, during and after breeding is low compared with other waterfowl foraging for insects. For example, Blue-winged Teal *Anas discors* spent 40-70% of their time foraging during egg-laying (Stewart & Titman 1980) and Dwyer's (1975) study of breeding Gadwall reported them feeding for in excess of 70% of 16-17 h days (672-714 minutes). Seymour & Titman (1978) observed Black Duck *Anas rubripes* forage for 75-90% of the time in the pre-laying period.

The lower feeding effort by female Blue Ducks at or prior to laying compared with those of northern, migratory ducks probably results from the combined need of northern birds to replace reserves used up in migration and to produce larger clutches over short time periods (laying eggs daily compared with every two days for Blue Duck).

There are few comparative post-nesting data available. Gunn & Batt (1985) reported that Northern Pintail *Anas acuta* hens attending ducklings spent approximately 52% of each 16.5 h day feeding (= 514 minutes). In their study, the daily percentage feeding effort increased over 10% as the season progressed and as the females both recovered condition following incubation, and laid reserves for moult and migration. The lower feeding effort by Blue Ducks with young may reflect their sedentary life compared with northern migratory waterfowl and the longer fledging period of ducklings (70-80 days, Williams in prep.), thus allowing a longer period for recovery of body condition after incubation and the deposition of reserves for the more delayed period of body moult.

We offer four as yet untested explanations for the relatively small amount of time expended in foraging by the Blue Ducks we observed: (i) food was superabundant; (ii) the constraints imposed by the time required to digest prey; (iii) limited food requirements as a result of high levels of inactivity; and (iv) the birds also fed at night. Some of these explanations are now under investigation.

(ii) Use of space

Although the space used by Pair 2 contained half the number of pools and riffles found within the territory of Pair 1, both pairs nevertheless concentrated their activities to within 3 m of the river edge and contracted their home ranges prior to incubation. While females incubated, their mates stood and slept in the pool nearest the nest site. Every river variable we scored significantly affected the spatial distribution of foraging behaviour, indicating that riffles in particular were not homogeneous foraging sites. Varying use of entire pools and riffles and regions within them indicated that spatial heterogeneity rather than temporal variations in food availability affected the foraging patterns of Blue Ducks during breeding. The reduction in range at nesting time may be a behavioural response by the male to protect the nest site or his mate, or by the female to limit energy expenditure. That such a reduction in range can occur implies that the prey resource at the foraging location is either superabundant or recolonization is extremely rapid. We observed birds foraging repeatedly over the same sections of a riffle.

In contrast to the strong attachment to a single riffle exhibited by Pair 2 after failure of their breeding attempt, Pair 1 and their ducklings ranged widely throughout their territory and extended beyond the range over which the adults had been seen previously (Fig. 6). Since sleeping was not disrupted and standing constituted a large portion of the time-activity budget at this time, the greater range of Pair 1 was unlikely to be a response to food demands of the adults. This extensive movement appeared initiated by the foraging ducklings for the adults were invariably swimming behind them, particularly as they foraged upstream. The mobility was greatest when ducklings were youngest, and it is possible that as they became older and could forage in faster water, or developed relatively lower energy requirements, they had no need to cover such an extensive area in search of food.

(iii) Sexual differences

Despite sexually dimorphic vocalisation patterns (Eldridge 1985) and greater male involvement in boundary disputes (Eldridge 1986), we discovered no sex role differences after incubation during the breeding season. At that time, territoriality impacted equally on the time-activity budgets of males and females and even when with ducklings, the activities of the two adults were not significantly different (Table 2). Guardianship by both parents may enhance duckling survival in river habitats.

With the exception of the early brood rearing period, Blue Ducks occupy a range which appears to be considerably larger than is necessary for the living requirements of the birds. Throughout the egg-laying and incubation period, and also during the period of moult (this study and Eldridge 1986) activities were limited to a core 2-3 pools and riffles. Clearly, territory size is not determined by the abundance or availability of food for the adults during spring or summer months, nor, probably, winter since most common benthic invertebrates in New Zealand rivers have extensively overlapping life cycles (Winterbourn *et al.* 1981).

The large territories and small foraging times of Blue Ducks lead us to the conclusion that defence of a food supply is not the primary function of territoriality. However, year-round territoriality does appear to be related in some unknown way to life on fast flowing rivers, and the functional significance of this pattern remains to be discovered.

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