Territoriality in a river specialist: the Blue Duck

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Introduction

The Blue Duck Hymenolaimus malacorhynchos is one of four anatid river specialists that inhabit mountain streams around the world. Other specialists include the Torrent Duck Merganetta armata of South America, the African Black Duck Anas sparsa and Salvadori's Duck Anas waigiuensis of New Guinea. Although these species are not closely related (Woolfenden 1961; Brush 1976; Bottjer 1983), they share a variety of social, physical, and ecological characteristics (Kear 1975; McKinney et al. 1978). Some of these traits, for example, long term pair bonds and year-round cooperative defence of territory are unusual among Anatidae and may be influenced by a predictable and defensible food resources in rivers (Johnsgard 1966; Siegfried 1968; Kear & Burton 1971; Ball et al. 1978; McKinney et al. 1978).

The fast, clean mountain streams preferred by anatid river specialists, are similar in physical characteristics and invertebrate fauna throughout the world (Hynes 1970a, 1970b). Kear and Burton (1971) found that Blue Ducks consume aquatic larvae of Tricoptera, Plecoptera, Ephemeroptera, and Diptera. These invertebrates occur in cold, highly oxygenated mountain streams throughout the world and are predictably most abundant in boulder strewn rapids (McLay 1968; Hynes 1970a, 1970b). In this paper, it is proposed that territorial behaviour in Blue Ducks may also be related to a predictable pattern of invertebrate activity. Stream invertebrates are most active during evening hours and are washed off rocks in the downstream movement known as invertebrate drift (Waters 1965, 1969, 1972). From a predator's perspective, invertebrate drift results in a consistent diurnal pattern of resource renewal. The invertebrates consumed by Blue Ducks figure strongly in drift samples taken in New Zealand (McLay 1968).

When a food resource is economically defensible and renewing, a diel pattern in territorial behaviour can be expected (Brown 1964; Davies 1980). In species defending a renewing resource, territorial individuals often have an advantage over intruders because they can pattern their return time to match the rate of renewal. Non-territorial individuals foraging on a territory are less efficient because they may forage in areas already depleted or at inappropriate times (Gill & Wolf 1977; Davies 1980).

The purpose of this paper is to report on the activities and social interactions of territorial Blue Ducks with special emphasis on diel patterns in their territorial behaviour.

Methods

My study was conducted on the Manganui a te ao River near Tongariro National Park on the North Island of New Zealand. The Manganui originates in the snow fields of Mt. Ruapehu and is characterised by swift, highly oxygenated, clear water that moves over a substratum of rocks, stones, or gravel with only limited areas of sand and silt.

I studied three pairs of Blue Ducks intensively from 1 January through to 15 February 1978, and recorded their activities and locations from specific observation posts during four time periods: 05.00 to 09.00 (period 1), 11.00 to 12.00 (period 2), 14.00 to 15.00 (period 3) and 18.00 to 21.00 (period 4). At minute intervals I recorded bird presence and participation in eight activities: sleeping, standing, moving (i.e., swimming, walking, flying) preening, dabbling, diving, and reproductive interaction. Every 15 to 30 minutes I recorded the locations of birds under observation. Time budget data collection was usually stopped when an interaction began and information specific to the interaction was gathered. Additional notes and observations were recorded by cassette tape recorder and photography.

During the first week of the study, I walked the river all night to capture and net birds. Sightings of birds on the river decreased rapidly after 21.00 and then birds were usually found sleeping on boulders beside the stream.

Six individuals, four adults and two fully fledged juveniles, were captured by mist 123

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netting, or night-lighting and marked with coloured leg bands during the first week in January. Subsequent observations were made primarily on these individuals. The four adults were territorial members of three pairs including both male and female of Green pair, and the females of Red and Blue pairs. The unmarked pair males were identified by their association with the marked females. Two juveniles of the Red pair were also marked and followed.

Results

This paper is based on 486.7 hours of observation on the river. Of this times, 22980 minutes (383 hours) were recorded as time budget data (Tables 1 and 2). Ducks were present and visible on the river for 51% of the time budget hours or a total of 11676 minutes (194.6 hours).

 Table 1.
 Total observation time (29,201 minutes or 486.7 hours in a total of 174 observation sessions).

 Time is expressed in minutes and observation sessions in parenthesis.

Territory		Time	period	
	1	2	3	4
GREEN	3625	1740	583	2614
RED	(18) 2820	(11) 2321	(4) 1395	(14) 2326
KED	(16)	(16)	(16)	(22)
BLUE	3385	2491	2247	3654
	(19)	(16)	(16)	(22)

Table 2. Time budget observations (a subset of total observation time). Duck presence and activities were recorded at minute intervals for a total of 22980 minutes (383 hours).

Territory		Time	neriod	
rennery	1	2	3	4
GREEN	2700	1080	360	2460
RED	2340	1800	960	1980
BLUE	2880	1560	1440	3420

Case histories

Three pairs, Blue, Red, and Green maintained territories on two kilometres of stream that were 470, 500, and 640 metres in length respectively. A fourth pair was sighted repeatedly in a portion of stream present and visible on the river for 51% of the time budget hours or a total of 11676 minutes (194.6 hours) (Table 3).

Table 3. Duck presence. Minutes during time budget observations when one or more ducks, regardless of territorial status, were present for a total of 11676 minutes (194.6 hours).

Territory		Time	period	
	1	2	3	4
GREEN	1382	292	115	932
RED	1277	969	399	952
BLUE	1857	863	653	1985

separating Green and Red territories but this area was inaccessible for observation. Two additional pairs were sighted infrequently both up and downstream from the study area.

Each territory consisted of alternating pools and white-water rapids. The territorial pairs spent most of their time on the areas they defended but they also made regular forays into adjacent portions of stream. Each territory was bordered by an undefended area that included pools, channels, and rapids. Dispersing juveniles and unpaired adults congregated in these uncontested areas and regularly intruded into neighbouring territories. The group's composition changed daily and observations on marked individuals suggested that these unpaired, non-territorial birds were highly mobile.

The Red pair was the only one of the three that was obviously reproductively successful at the start of the study. Four juveniles in the brood were fully fledged and two marked juvenile males continued peacefully to associate with the pair but aggressively confronted were bv neighbouring territorial pairs when they began to disperse. One marked juvenile moved downstream into Green territory for a period of days, and was never seen again. The second marked juvenile stayed on the Red pair's territory or associated with other juveniles and lone adults in the pool separating Blue and Red territories.

After the Red brood began to disperse, the Red pair moulted synchronously. During this period, pair mates rarely defended their territory and they hid together in caves and hollow logs at the side of the stream. Intruders usually foraged uncontested on the territory, although one marked juvenile remained on the territory and occasionally confronted intruders with the "whio" call and aggressive Headbobbing (Eldridge 1985).

The Blue pair apparently did not have a brood and the female was flightless when the study began. She hid in a log while moulting and was separated from the male for long periods of time. The Blue male defended the territory in her absence but after she completed her moult, Blue female began a liaison with a lone male who established a territory in the uncontested area downstream between Blue and Red territories. The two territories were directly adjacent and non-overlapping but the female moved freely between them and behaved like a territorial female with both males. She assisted in ousting intruders and participated in pre-copulatory displays with both males (Eldridge 1985).

When the males encountered each other as the female moved between the territories, intense confrontations and aerial chases resulted. Five times these confrontations escalated into combat as each male grasped the opponent with its bill and pummeled with its wings (Fig. 1). The fights lasted two to four minutes and in all five

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fights, the Blue male appeared the loser; he tired and was driven deeper in the water and broke from the fight first. With each fight, the downriver male claimed more territory but did not completely displace the Blue male. By the end of the study Blue female was still returning in the evenings to Blue male but she was spending most of the day with the downriver male.

When the study began, Green male and female were without a brood but they appeared strongly bonded; one was never observed without the other and they cooperated in territorial defence. Several weeks into the study an unpaired male with melanistically patterned legs intruded repeatedly. He interacted aggresively with Green male with aerial chases and displacement. These chases usually ended out of sight and no fights were observed. Within a week Green male was displaced and Green female and the new male appeared bonded. They remained together, aggressively confronted intruders and were observed copulating twice.

Figure 1. Aggressive confrontations occasionally escalated into combat in the Blue territory. The male participants pummel each other with wings armed by bony spurs as the territorial female watches.



After being displaced, Green male was seen repeatedly upriver in Blue territory and on several occasions he approached Blue female but was displaced by Blue male. Most of the time he was seen with lone males and dispersing juveniles in the pools separating territories.

Pair bond summary

The only pair (Red pair) observed with a brood was also the only one to moult synchronously and remain paired during this study. Blue female made a gradual shift between males and Green female shifted rapidly when Green male was displaced (Fig. 2). These differences suggest three factors in pair bond maintenance: first, unsuccessful pairs may seek new mates; second, separation caused by asynchronous moult may weaken pair bonds; and third, lone individuals can acquire territories and mates through a variety of means. These results are consistent with those of another river specialist, the African Black Duck (Ball et al. 1978; McKinney et al. 1978).

Location summary

Variation in pair stability is reflected in the

location data (Fig. 3). The Red pair remained paired and individual ranges overlap. Blue female occupied more stream than either Blue or the downriver male by using the non-overlapping territories of both males. Unlike Blue male, Green male was rapidly displaced and he lost both the territory and the female. Green male then wandered across all territories as an intruding lone adult.

Lone adults and juveniles were observed throughout the study area but concentrated in the pool and riffle area between Blue and Red territories before the downriver male displaced them.

Time budget

Territorial birds were visible (present) more in the mornings and evenings. Nonterritorial birds were present erratically but with a tendency to be visible more at midday. This tendency is revealed in the total minutes present over the entire study as a percent of time observed (Fig. 4).

When territorial or non-territorial birds were present, they were usually feeding (Fig. 5). Both territorial and non-territorial birds fed in the morning and evenings



Figure 2. Proportion of time spent with the primary or secondary male by marked territorial females in eight periods, each five days long.



Figure 3. Location of territorial and non-territorial birds on the river. The rapids are marked in black on the map. The range (extreme sightings) are represented by the vertical line, the box delineates the first and third quartiles divided by the median location for territorial and intruding birds.

(periods 1 and 4). But, considering total feeding over the entire study as a percent of time observed, territorial birds fed relatively less in the middle of the day (periods 2 and 3) while non-territorial birds fed more (Fig. 6).

Mates fed together and often in the same rapids, in fairly close proximity. They fed primarily by dabbling in the riffles and rapids of their territories or among the smaller rocks and boulders along the stream edge. Birds rarely dabbled with the bill at the surface or up-ended, both of which are common feeding methods of Anatini; instead, they scoured the rocks, often with heads submerged, making dabbling motions with their bills. In the rapids they often stood on one rock and dabbled along the downstream side of nearby rocks. Much less frequently, they drove underwater below rapids and in pools and scoured the downstream sides of submerged rocks. They dove with their wings partially open and swan submerged in the turbulence of the stream floor.

Dabbling in the rapids was the most common foraging method. Territorial males

and females both dabbled 96%, intruding adults 89% and juveniles 86% of time observed feeding. Dabbling decreased relatively during midday and diving in the pools increased (Fig. 7).

Aggressive interactions

During 29,200 minutes (486.7 hours) of observation on three territories, 119 interactions were observed between territorial and intruding birds. Intruder status could be identified for 114 interactions and almost half of these occurred in the morning (period 1, Table 4). Eighty interactions involved intruding adults and the remainder

Table 4.Number of aggressive interactions oneach territory during each time period.

Territory		Time	period	
,	1	2	3	4
GREEN	19	5	2	12
RED	8	4	6	9
BLUE	25	11	9	9





Figure 4. Cumulative presence of territorial and non-territorial ducks on each territory as a percent of total time observed.

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Figure 5. Relative frequency of total time present spent in various activities on each territory. Territorial females are represented by black bars, juveniles by dashed bars and adult males by clear bars. Time budget for Blue and Green territories include primary male (M1) and secondary male (M2). Activities include feeding (F), standing (ST), preening (PR), sleeping (SL) and moving (M).





TIME PERIODS

Figure 6. Diurnal pattern of feeding by territorial and intruding Blue Ducks as a percent of time present on the river. Territorial females are represented by black bars and males by clear bars.

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Presence as a Percent of Time Observed



Time Periods

Figure 7. Relative frequency of total time spent diving (minutes) during the four time periods of the day by territorial and intruding ducks.

were with juveniles.

Specific information for each interaction considered here includes territory, intruder status (adult or juvenile), interaction duration and intensity. Intensity was determined following a procedure adapted from Recher and Recher (1969). Interactions were scored 1 through 4 as follows: 1=swim-off (least intense), 2=feeding displacement, 3=feeding displacement and chase, and 4=fight.

In a swim-off (rank=1), territorial birds followed the intruder(s) and all swam slowly up or down stream. The intruder assumed a neutral pose and, in general, did not attempt to forage on the territory. Territorial birds kept intruders moving without obvious displacement. Often the group left the water and stood on emergent rocks, resembling a family more than belligerents. When the intruder left the rocks and returned to the water, the pair continued to follow.

Territorial birds confronted foraging intruders (rank=2) more aggressively with

displays (Head-low flight, Upright, Headbobbing, Siphon-feeding, and vocalisations, Eldridge 1985). Intruders reacted with a neutral posture or continued to feed. Territorial birds escorted the intruder off the territory or on to nearby rocks, often with bill pokes, displays and active displacement. Foraging displacements could escalate until the intruder was forced into flight and chased from the territory (rank=3).

The most intense type of confrontation resulted in violence (rank=4) between territorial males ad intruders. An attack was often preceded by display (Head-low flight, Upright, Head-bobbing, and vocalisations) and intruder assumed an aggressive Upright stance. (See fight description in Case Histories and Fig. 1).

Interaction summary

Interactions tended to be more common in the mornings (Table 4) and of longer duration in the mornings and/or evenings (Table 5) than in the middle of the day.

Time	Adult		Juvenile	
period	Intensity	Duration	Intensity	Duration
1	$2.4 \pm .2$ (32)	36.4 ± 6.2	$1.4 \pm .2$ (18)	50.2 ± 13.4
2	$2.7 \pm .4$ (13)	16.0 ± 4.4	1.0 ± 0 (6)	33.3 ± 12.5
3	$2.3 \pm .2$ (12)	14.6 ± 5.1	1.0 ± 0 (5)	20.2 ± 11.1
4	$2.3 \pm .2$ (19)	13.8 ± 3.6	1.0 ± 0 (9)	46.2 ± 14.0

 Table 5. Average intensity and duration of aggressive interactions with adult and juvenile intruders.

 Mean duration is expressed in minutes with standard error and sample size is in parenthesis.

Interactions with adults were equally intense during the day but longer in the mornings and interactions with juveniles were slightly more intense in the mornings and longer in the mornings and evenings than the rest of the day (Table 5). In general, interactions with adults were more numerous, more intense and shorter than interactions with juveniles (Table 6). Interactions were more intense on Blue and Green territories where the pairs were undergoing change (Table 6). These pairs were without broods and interactions with intruding juveniles were longer than on Red territory.

Both members of a pair seemed to cooperate in conflicts with mutual displays and calls (Eldridge 1985) but, the active involvement by each sex varied with intruder status. All of the intruding adults appeared to be males and the territorial male was most active in the confrontation. In contrast, the territorial female confronted intruding juveniles of both sexes.

In summary, most of the interactions observed involved intruding adult males actively confronted by the territorial male. These interactions occurred most frequently in the mornings and were relatively intense

and long, often leading to the expulsion of the intruder. Interactions with juveniles were less intense, often involving long swim-offs by the territorial female. Territorial pairs without young, in the process of splitting, were involved in more frequent and intense interactions than the more stable pair.

Vocalisations

Blue Ducks have a variety of highly variable vocalisations and the most common was the "whio" whistled by the male. It is given regardless of intruder presence and is often associated with the Extended-neck display (Eldridge 1985). This call is considered by previous investigators to be the main territorial call (Kear & Steel 1971; Kear 1972). Males vocalised far more commonly than females (88% of the recorded vocalisations were given by a male), usually with the "whio" call given in the morning (Fig. 8).

Discussion

During the post-breeding period when

 Table 6.
 Average intensity and duration of aggressive interactions on each territory with adult and juvenile intruders. Mean values are included with standard error and sample size is in parenthesis.

Territory		Adult		Juvenile		
	Intensity	Duration	Intensity	Duration		
GREEN	$2.6 \pm .2$ (23)	31.9 ± 6.7	$1.2 \pm .2$ (23)	48.6 ± 14.1		
RED	$1.9 \pm .2$ (20)	22.0 ± 4.8	$1.2 \pm .2$ (6)	6.7 ± 3.0		
BLUE	$2.6 \pm .1$ (33)	19.3 ± 4.9	$1.2 \pm .1$ (20)	49.9 ± 10.8		



Figure 8. Diurnal pattern of vocalisations by territorial males expressed as a percent of total male

vocalisations.

territorial defence appeared closely tied to resource defensability may not provide a the food resource both in space and time. complete explanation for their territoriality. Territories centred around feeding rapids. Territories maintained after the breeding Borders were defended but large areas season and tied exclusively to the food between territories often were not. The resource are often defended by lone diurnal pattern of foraging and territorial individuals (c.f. Wolf 1969, 1975; Gill & defence in the mornings and evenings Wolf 1975, 1977; Davies & Houston 1981). matched expected patterns of invertebrate activity and redistribution known as inver- In this study, a lone male established a tebrate drift.

defended territories (fights and vocal- territory, he lost the Green female as well. isations) in the mornings and evenings but The well-developed mutual threat display non-territorial birds foraged on territories repertoire suggests the importance of coat midday – an inefficient time given inver- operative defence of the territory by paired tebrate activity and redistribution. They birds (Eldridge 1985). The most intense also foraged in the pools by diving interactions and physical fights occurred suggesting that they were consuming a between males in conflict over a female and slightly different diet than territorial birds territory. It seems territoriality is inexbecause stream invertebrates vary by tricably tied to pair formation and pair-bond habitat zone (Hynes 1970a).

In this post-breeding period, Blue Ducks may economise on defence by constricting with other river specialists (Ball et al. 1978; the size of territories to the most productive Eldridge 1978; McKinney et al. 1978). areas. It is quite possible that the territories Where studied, territorial owners confront expand during the breeding season and intruders of the same sex. In this study, birds with broods compete for bordering males confronted males but none of the pools.

broods were dispersing and pairs moulting, invertebrate abundance, the economics of

Territorial birds are almost always paired. territory but immediately attracted the Blue In this study, territorial birds foraged and female. When the Green male lost the maintenance.

> This is a trait Blue Ducks have in common adult intruders were positively identified as

In spite of the correlation between Blue female. It seems unusual that there were no Duck behaviour and expected patterns in lone females moving on the river and the

lack deserves further study. It could suggest an artificially skewed sex ratio caused by the laying female's vulnerability to introduced predators (c.f. Johnson & Sargeant 1977).

The results from this study suggest several approaches for future work. It would be interesting to tie foraging behaviour to diurnal and seasonal invertebrate change. Territory size and density may be correlated on a broad scale with invertebrate population levels but also may be related to the presence of other territorial Blue Ducks. Rivers vary in the number of rapids, degree of incline, and current velocity, and these factors must influence territory quality.

Presumably, Blue Duck density on a stream will correspond to these variations. Since trout have been introduced to many of the streams, the influence of competition for the invertebrate food resource may lead to larger Blue Duck territories and reduced populations.

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Summary

Territorial Blue Ducks *Hymenolaimus malacorhynchos* foraged on and defended territories more in the mornings and evenings than in the middle of the day. In contrast, intruding Blue Ducks foraged on territories more in the middle of the day. It is suggested that territorial birds are capitalising on a renewing invertebrate resource that varies in diurnal availability.

Pair bond maintenance was also an important aspect of territoriality. Differences between territorial pairs suggest three factors in pair bond maintenance: first, pairs that are reproductively unsuccessful may seek new mates; second, separation caused by a synchronous moult may weaken pair bonds; and third, lone individuals can acquire territories and mates through a variety of means.

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