Observations on a pair of Torrent Ducks

JAN L. ELDRIDGE

Introduction

Torrent Ducks of the southern subspecies, *Merganetta armata armata*, are widely distributed throughout the lake district of Chile but are ecologically limited to torrential mountain streams (Johnsgard 1966). Their river habitat is characterised by swift, highly oxygenated, clear, cold water that moves over a substratum of rock, stones, and gravel with only limited areas of sand and silt (Hynes 1970a). They feed primarily on insect larvae that cling to boulders in streams. Their narrow, flexible bills and large, forward set eyes facilitate foraging for invertebrates among rocky crevices (Johnsgard 1966; Kear 1975).

Torrent Ducks are found in pairs throughout the year and are thought to be monogamous (Scott 1954; Johnson 1963; Johnsgard 1966; Moffett 1970). They nest in a variety of locations including trees, rocky ledges and crevices and holes in river banks (Johnson 1963; Moffett 1970). Nesting areas are used repeatedly, incubation periods are unusually long compared to other ducks and both sexes cooperate with brood rearing (Johnson 1963; Cecil 1969; Moffett 1970). They are highly territorial and both sexes cooperate in territorial defence with similar displays (Moffett 1970; Eldridge 1979).

Year-round territoriality and long term pair bonds are unusual traits in Anatidae but are present in three other anatid river specialists: the African Black Duck *Anas sparsa* (Ball *et al.* 1978; McKinney *et al.* 1978), Salvadori's Duck *Anas waigiuensis* (Kear 1975), and the Blue Duck *Hymenolaimus malacorhynchos* (Kear & Steel 1971; Kear 1972; Eldridge 1985). These species are not closely related (Woolfenden 1961; Brush 1976; Bottjer 1983) and the similarities have probably evolved independently in response to the fast water stream environment.

The purpose of this paper is to report observations on one pair of Torrent Ducks during a single breeding season on Rio Nalcus, Chile. Special emphasis is placed on how the pair responded to limits in the stream environment.

Study area

Rio Nalcus begins in the snow fields of Volcan Puntiagudo and drains about 27 km² before emptying into Lago Rupanco. My study area included the lower 2600 m of the river between a major 50 m waterfall and the lake. The pair I observed defended the lower stretch of about 1700 m and a second pair defended a small stretch of about 900 m between the downriver territory and the falls. The gradient was milder in the downriver territory and the river channel was less than one metre deep. Wide, shallow riffles with reduced current and numerous exposed rocks alternated with deep, fast, unbroken channels or pools. In several places the river branched through a network of small, stony islands covered with brush and beached logs. In most areas the stream was contained in a channel of rounded rocks and boulders but in some areas it cut into gravel banks. Much of the downriver territory was bordered by 15–20 m cliffs with pasture in the surrounding uplands. In contrast, the smaller upriver territory had a steep gradient, a strong, unbroken current, and was bordered by cliffs with dense, overhanging native vegetation which made observation on the upriver pair almost impossible.

Methods

During daylight hours I recorded the following eight activities at one minute intervals when birds were in view: dabbling, diving, preening, sleeping, moving, standing, aggression, and reproductive activities (including nest searching, copulation, and incubation). Terminology for displays follows Eldridge (1979). I mapped the pair's daily movements and supplemented my field notes with tape recorded notes and Super 8 mm films. I did not try regular observation periods from specific locations during the day because the birds were too mobile and often were difficult to locate and follow.

The birds were not marked but the male could be distinguished from other males by

variation in the black and white feather pattern of the head and neck region. Individual females could be identified by gaps in the rectrices which are molted periodically throughout the year (Weller 1968).

Results

I watched the downriver pair from September 14 through November 26, 1975. During this time they remained strongly bonded, they nested and the female laid three eggs and incubated them until the nest was destroyed by a flood. The pair then prepared to renest. This study can be divided into four time periods based on the pair's breeding chronology: prelaying, 14 September – 13 October; laying, 14–25 October; incubation, 26 October – 16 November; and renesting, 16–26 November.

Prelaying

During the month before egg laying began, the male and female were together almost constantly (Fig. 1). They moved throughout their 1700 m territory but they concentrated their activities on particular areas of the river (Fig. 2). Although they fed throughout the territory, they preferred the wide, shallow riffles probably because stream riffles contain greater invertebrate abundance (Hynes 1970b). For analysis, the river was divided into 68 segments, each 25 m long but varying in width depending on the river channel. During 29 days of observation I recorded 102 feeding locations. They used particular riffles on a regular basis but only once did they return to the same 25 m area in one day.

The birds used two feeding methods, dabbling and diving. I did not see them up-

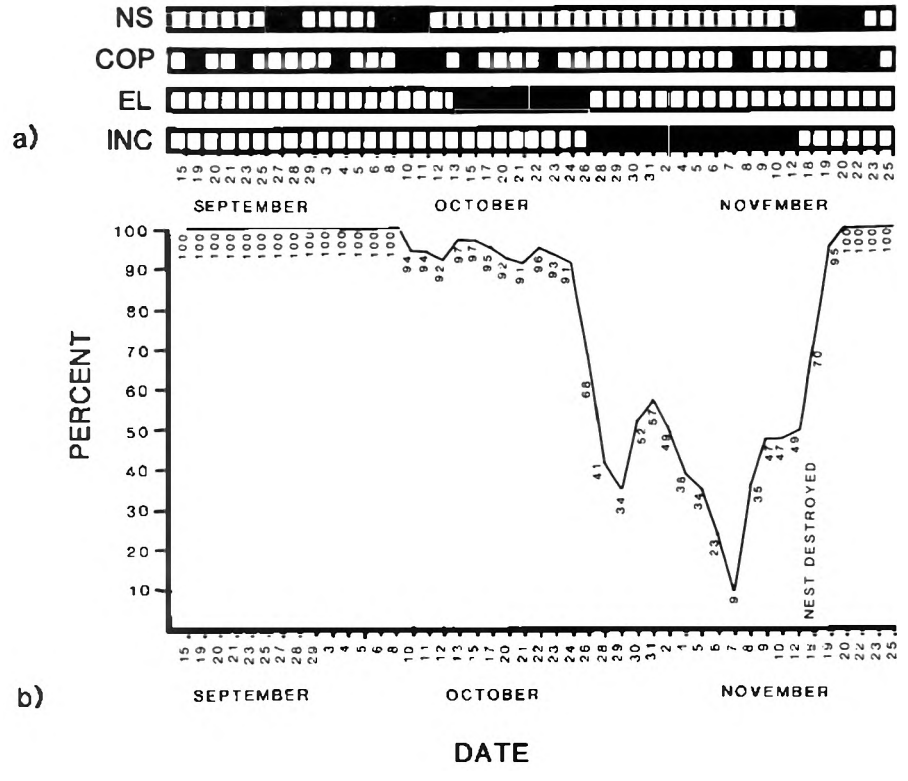

Figure 1. a) Occurrence of nest searching (NS), copulation (COP), egg laying (EL), and incubation (INC) during each day of the study. b) Time the male spent with the female as a percentage of daily observations.

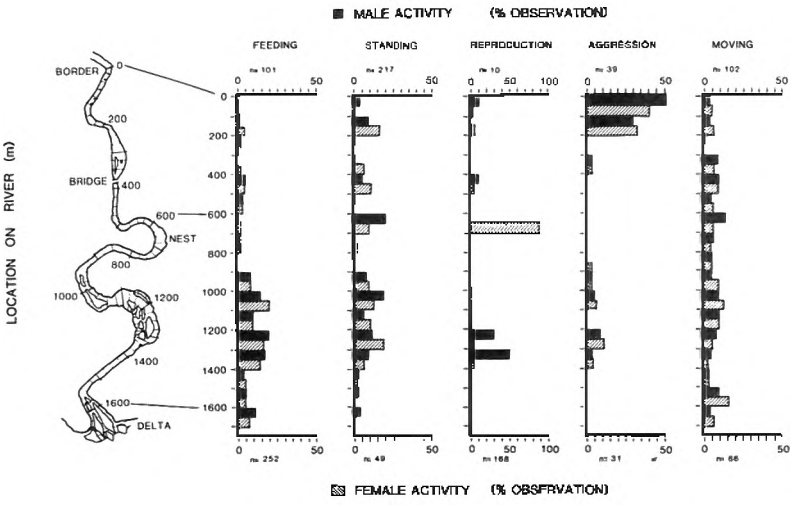

Figure 2. Location of various activities on the river, expressed in 100 metre increments as a percent of observed locations.

end, a feeding method typical of many dabbling ducks *Anas sp.* They dabbled in shallow water (0.1 to 0.2 m) along the stream edge or in wide, shallow riffles. They walked or swam in the shallows and probed around submerged rocks. Occasionally, a bird dabbled on exposed rocks in deeper water but usually feeding in the central part of the stream was accomplished by diving. Dives were clean and arched with wings held firmly to the body. Birds often dove upstream from a rock, fed along the bottom 2 to 3 m upstream and surfaced as the current carried them back to the rock. They also dove in eddies behind rocks and fed from eddy to eddy. With both types of feeding, the birds methodically probed the rocky substrate foraging for invertebrates, but on rare occasions they dashed after small fish that were 5 to 10 cm long.

Early in the study the pair dabbled and dove in equal proportions but as time passed the male spent less time feeding and dove more in the central portion of the stream while the female dabbled in the shallows along the edge (Fig. 3). While the female fed, the male followed closely and stood near her in an alert, watchful stance (Table 1). The female fed almost twice as much as the male (Fig. 4). While she fed, the female initiated most moves from one feeding area to another and if she moved out of sight the male actively called and searched for her.

They often fed by moving upriver against the current. They avoided the main force of the current by walking in the shallows along the stream edge or moving upriver in the eddies behind rocks. While following the female, many of the male's activities appeared precopulatory (Fig. 5). When the female paused on a rock, the male joined her in a hunched posture with body lowered, neck extended slightly and crest feathers depressed. When the female was in the water he approached in the hunched posture and performed repeated bill-dips

Table 1. Simultaneous observations of the male and female with row frequencies above column frequencies for the following activities: Standing (STD), Feeding (FED), Aggression (AGG), Reproduction (REP) and Other, which included sleeping, preening and moving. Based on a total of 5485 minutes of observation.

Male activity	Female activity				
	STD	FED	AGG	REP	OTHER
STD	.06	.54	0	.36	.04
	.38	.51	0	.38	.08
FED	.10	.78	0	.02	.06
	.33	.37	0	.01	.06
AGG	0	0	.90	.09	.01
	0	0	1.00	.01	0
REP	0	.10	0	.85	.05
	0	0	0	.02	0
OTHER	.04	.11	0	.49	.36
	.28	.12	0	.58	.85

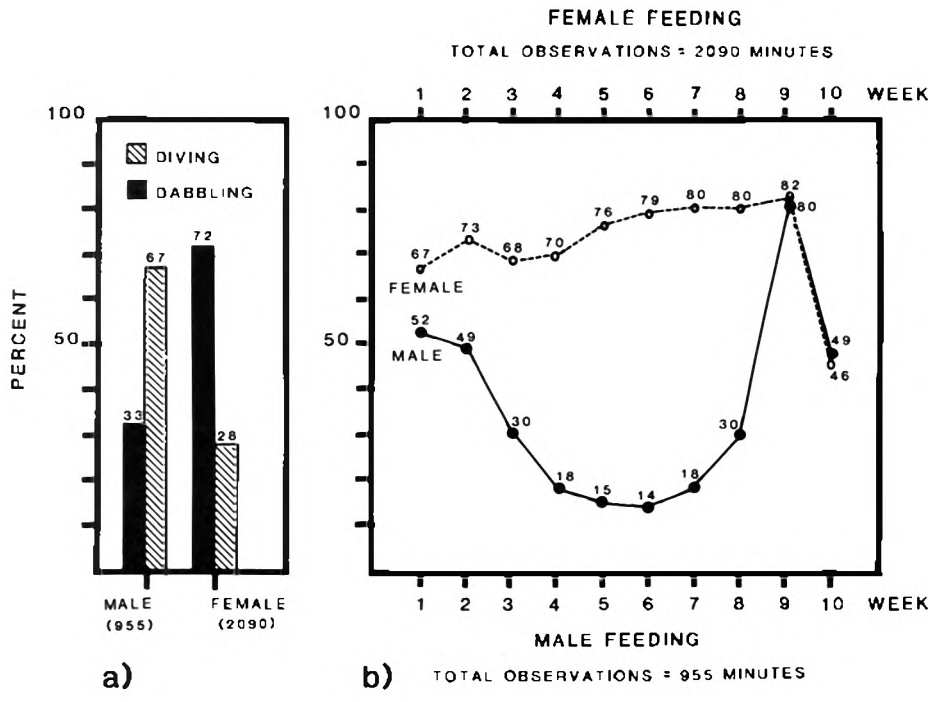

Figure 3. a) Foraging technique used by the territorial male and female, expressed as a percent of foraging time. b) Seasonal change in foraging by territorial male and female expressed as a percent of total observations each week.

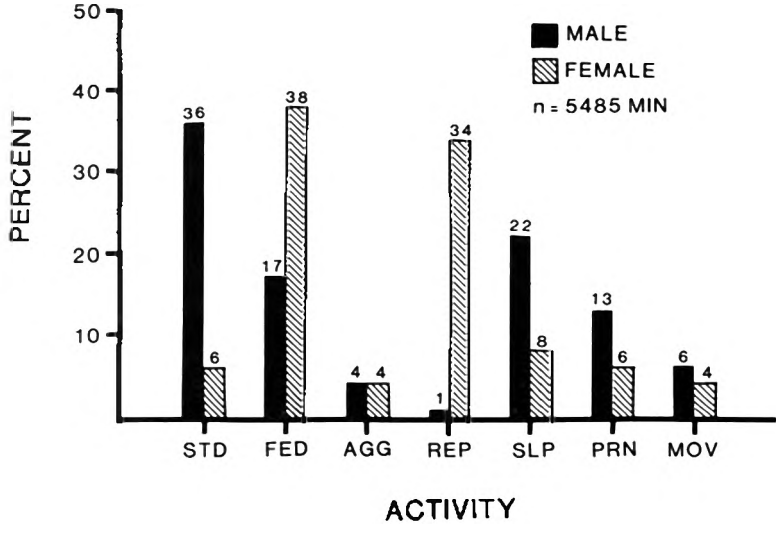

Figure 4. Time budget of the territorial pair while they were present on the river. Activities include standing (STD), feeding (FED), aggression (AGG), reproductive activities such as copulation, nest searching, and incubation (REP), sleeping (SLP), preening (PRN), and moving (MOV).

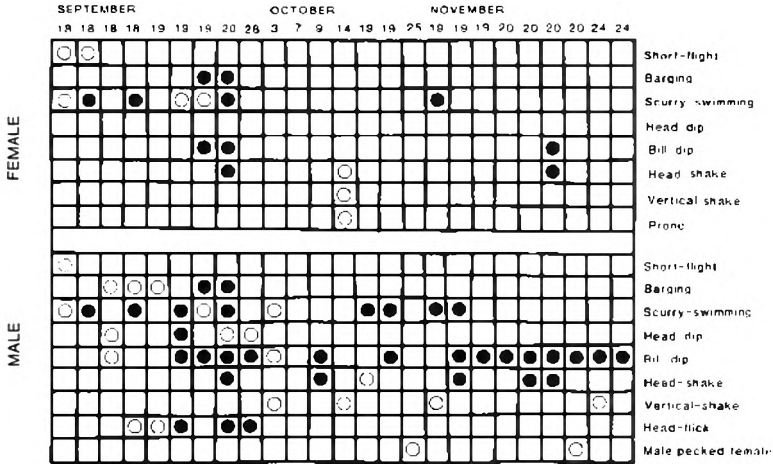

Figure 5. Chronology of laying as indicated by the dates of first egg.

○ Occurred 1 to 3 times
● Occurred many times

Figure 5. Interactions that appeared precopulatory during the study.

and head-shakes. At other times the male rapidly approached the female by scurrying over the surface of the water of flying a short distance, assuming the hunched position when he neared her.

Copulations usually followed when the female assumed a Prone position (Fig. 6). The male responded to the female's Prone with one or two Vertical-shakes followed by a low barge approach with bill angled down and crest erect. He mounted and dismounted with head held back and bill tucked. He followed three copulations with a partial Body-bend in the water beside the female.

The pair searched for a nest site during the month before egg laying began. They returned repeatedly to five holes that varied from 1 to 10 m above the water in the river bank. Nest searching involved an elaborate interaction between pair members while the female, and sometimes the male, investigated a site. Throughout each 5 to 15 minute investigation the pair tail-wagged and Pointed continuously and the male performed repeated Body-bends with "warble" call. Often during a search they encountered other hole nesting species such as the Chilean Cinclodes *Cinclodes patagonicus*, and the Huet-huet *Pteroptochos tarnii*. The smaller birds attacked the Torrent Ducks briefly and then left the hole to them.

Whenever the pair encountered other Torrent Ducks they aggressively confronted the intruders and both sexes performed a variety of displays described in Eldridge (1979). During the course of this study I observed 14 interactions with intruders. Most occurred at the border between the two territories (Fig. 1). Six interactions involved the upstream pair, six were with intruding lone females and two were with intruding males. Of these, I recorded displays performed in six interactions; two with intruding pairs, two with single males, and two with single females. For analysis, I considered the five most common discrete displays: Vertical-shake, Body-bend, Mule-kick, Wing-flap, and Shudder-shake. Average display intensity was determined subjectively and the displays were ranked by the apparent energy involved in their performance (Vertical-shake = 5 (most intense), Mule-kick = 4, Body-bend = 3, Wing-flap = 2, Shudder-shake = 1). In this system, adapted from Recher and Recher (1969) interaction intensity is determined by multiplying display rank by the number of times it was performed during the interaction and dividing by total displays performed. Intense interactions involved more Vertical-shakes and Mule-kicks (rank > 3.0) and less intense interactions had more Shudder-shakes and Wing-flaps (rank < 3.0). In general, interactions with pairs

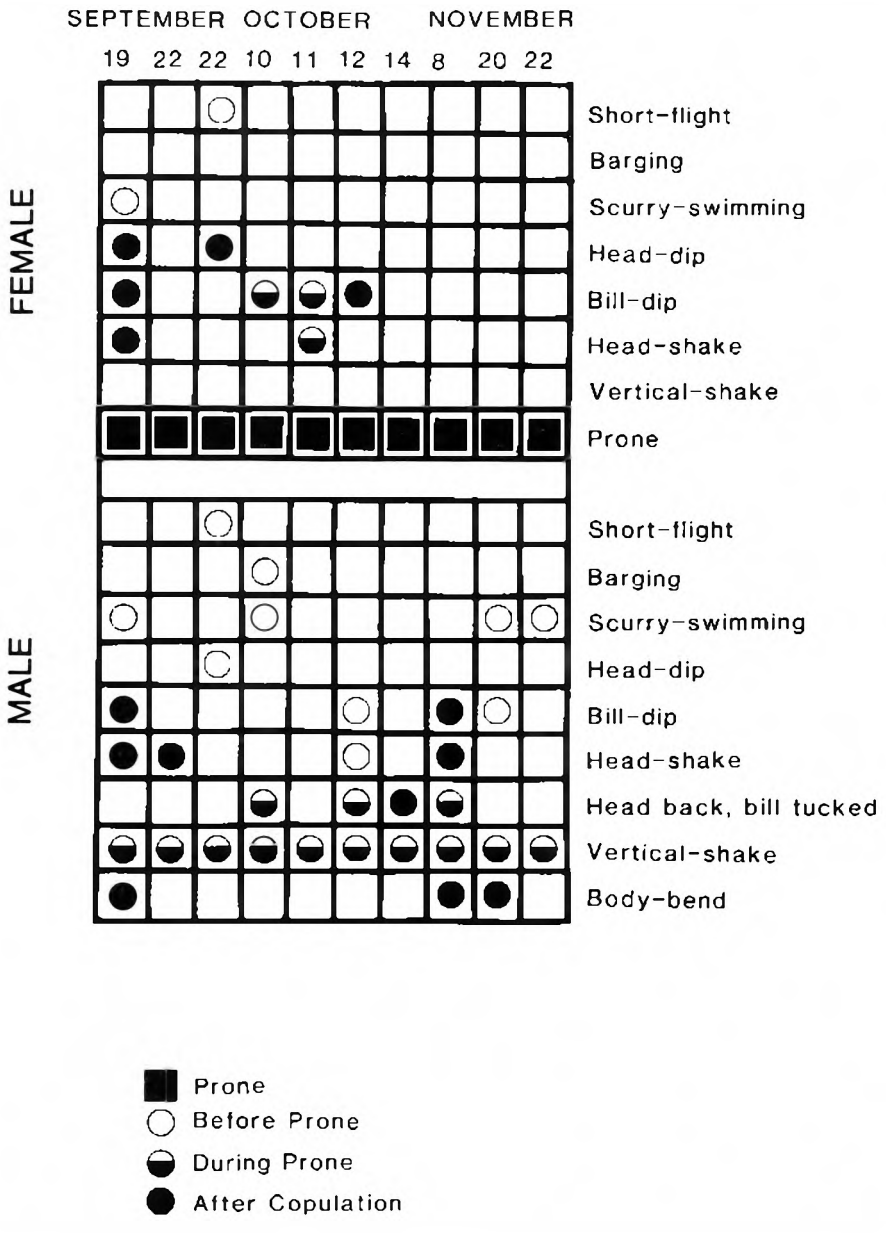

Figure 6. Interactions that resulted in copulations.

and lone males were long, intense and involved many displays, interactions with lone females were less intense, shorter and involved fewer displays (Table 2).

Both sexes had a similar display repertoire and performed displays in similar proportions (Table 3). Pair members responded differently to the intruder's sex and paired status (Table 4). When a lone male intruded, the territorial male performed most of the displays. When a lone female intruded, the territorial female performed. When a pair intruded both performed equally but the male confronted

Table 2. Aggressive interactions varied in the number of displays performed, duration, and intensity depending on the status of the intruder(s). Mean values are expressed with standard error.

Intruder type	n	Displays	Duration (min)	Intensity
Pair	2	246 ± 17	20 ± 9	3.34 ± .04
Lone male	2	168 ± 54	36 ± 18	3.5 ± .23
Lone female	2	48 ± 6	6 ± 4	2.7 ± .14

Table 3. Display type performed by territorial male and female during aggressive interactions. Expected values from the Chi-square analysis are in parenthesis. Territorial birds did not differ from expected in the types of displays they performed ($x^2=9.336$, df=4, $p>.05$).

	VS	MK	BB	WF	SS
Male	48 (44)	67 (68)	109 (118)	38 (41)	44 (35)
Female	23 (27)	44 (43)	83 (74)	29 (26)	13 (22)

the intruding male and the female confronted the intruding female (Fig. 7).

Most interactions were intense but without overt physical aggression. Even when the downriver male pursued the upriver male in an aerial chase and forced the upriver male to land, he did not attack but landed nearby and displayed. When rivals were very close in intense interaction, however, Wing-flaps were directed to strike, Mule-kicks became body blocks that knocked a rival from a rock and Body-bends bumped rivals into the water.

Table 4. Displays performed by the territorial male and female in response to intruders. Parenthesis indicate expected values from the Chi-square analysis. Display performance differed significantly from expected ($x^2=80.89$, df=2, $p<.005$).

	Intruder Status		
	Lone male	Lone female	Pair
Territorial Male	154 (114)	18 (45)	134 (147)
Territorial female	31 (71)	56 (29)	105 (92)

A fight was observed on one occasion during a very intense display burst when the upriver pair intruded. All four birds were standing on a rock and the downriver female drove the upriver female off the rock with a brief flurry of wings. This interaction took a fraction of a second and it was the only physical fight observed in 248 minutes of aggressive interaction. The spurs were much more commonly used in display postures particularly by the male after performing a Mule-kick or Wing-flap or while standing in the Upright near a rival.

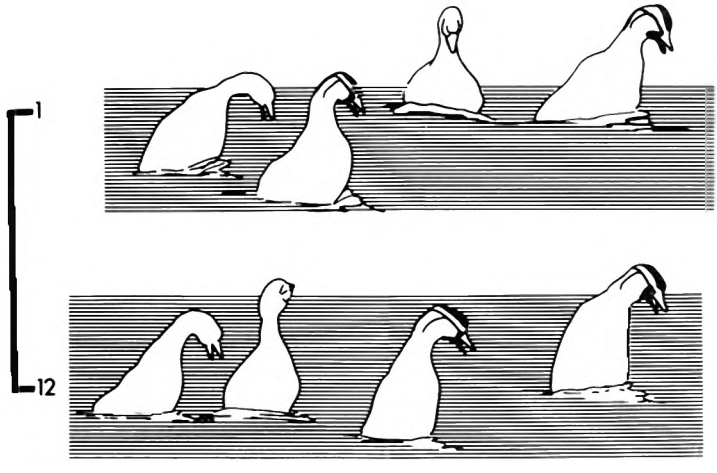

Figure 7. A filmed aggressive interaction between territorial pair and intruding pair. The interaction begins with pair mates in close proximity performing Bent-neck displays. They quickly move apart to confront rivals of the same sex. The numbered line indicates frames from a film exposed at 24 frames per second.

Laying

By October 11 the pair returned regularly to a large hole 1 m wide and 2 m deep in the face of a 20 m gravel cliff. This hole had been used by Torrent Ducks before and the female built upon the old nest. Three eggs were laid at 6- to 8-day intervals between 14 and 25 October. Egg measurements, in order, were: 57 g, 62 × 41 mm; 56 g, 64 × 41 mm; 59 g, 63 × 41.5 mm. The eggs were elongate, pointed and creamy tan with a smooth, somewhat glossy surface. Mean egg size was 16% (14–18%) and the entire clutch was 47% (43–55%) of female body weight which I estimated to be 364 g from 315–349 g reported by Neithammer (1952) and 400 g for a female I weighed on Rio Chanleufu.

During this period, the pair remained together but not as constantly as before (Fig. 1). They separated because the female visited the nest for one to two hours each day.

On three occasions during this period the pair encountered lone intruding females. The male's reaction was quite different when lone females attempted to escape without confrontation or display. He attacked the intruding female in an aerial chase, and forced her to land. Each time the male immediately lunged at the female, grasped her by the nape and flapped his wings as she attempted to dive. He did not appear to be striking the female, however, as was the case when the downriver female attacked the upriver female. His wings were held high and the intruding female was beneath him in the water in what appeared to be a forced copulation.

Incubation

Incubation began on 27 October and was performed exclusively by the female. During the first few days she left the nest irregularly several times a day but by the second week she was averaging 7 hr and 26 min on the nest during daylight hours, breaking early in the morning before 07.00 and late in the day after 15.00. The recesses were long; six afternoon breaks averaged 2 hr 21 min.

During the incubation period, the male was increasingly absent from the nest (Fig. 1). He became more secretive and mobile, occasionally venturing into the upriver territory. He returned regularly to the nest area and his returns were conspicuous and noisy; he stood on rocks near the nest entrance, called and performed several Body-bends.

Although the male spent less time around the nest, he usually accompanied the female during breaks. If he wasn't near the nest when the female left the nest cavity, she assumed a high, erect stance, craned her neck apparently searching for the male. On two occasions she performed a "ga-ga-brr" call with Bent-neck and the male responded by flying to her and performing a Body-bend.

During breaks, the female dabbled almost continuously in the shallows and the male alternately fed and watched in an alert stance near her. During the second week of incubation the female solicited the male with a Prone and a copulation followed. The female usually returned to the nest accompanied by the male. Each time they stood on rocks near the nest entrance for several minutes, interacting as they did while nest searching.

Nest destruction

The nest was destroyed by a flood during a storm that lasted from 12–16 November. The pair immediately resumed nest searching and copulations. The male once again actively followed the female and searched for her if she was out of sight. Both dabbled and dove in equal proportions while feeding and both actively participated in defending the territory. In short, they behaved as they had at the beginning of the study (Fig. 1).

Discussion

The most conspicuous aspect of the Torrent Duck's behaviour was their strong pair bond and cooperative defence of territory. Territorial conflicts were prolonged and the displays were elaborate and seemed energetically expensive. Although the wing spurs were used primarily in display, the birds probably risked serious injury if aggression became overt. The pair's sex specific reaction to intruders suggests that an intruder threatened both the territory and the pair bond. It is possible that both sexes can acquire a territory by displacing a paired territorial rival.

This possibility may explain the variety of

pair maintenance activities that I observed throughout the study including: close following, proximity to mate and searching for mates, copulations weeks before and after egg laying, and prolonged interactions between mates while nest searching. I think that mutual defence of the territory was also a form of pair bond maintenance. The pair members displayed synchronously before and after each interaction and many of the displays during the interactions were performed simultaneously.

Territoriality has been correlated with a food resource that is economically defensible, depletable, and renewing (Brown 1964; Gill & Wolf 1977; Pyke 1979; Davies 1980). The river territory is strategically defensible because there are only two boundaries, one at each end of a territory. The invertebrate resource varies by zones in the river and is most abundant in the shallow riffles (Hynes 1970b). The resource is renewing because invertebrates have a diurnal periodicity that results in population redistribution known as invertebrate drift (Waters 1972).

The pair I observed maintained a large territory but a number of factors suggest that their foraging behaviour closely matched the food resource. The entire territory was not suitable for feeding and the birds concentrated on a few major riffles. Although they returned to feeding areas, they did not return to the same area within a single day. This suggests that the resource may be depletable and that returns coincide with daily renewal by invertebrate drift.

Several factors suggest that the food resource was limited and that the female's energy reserves were insufficient for egg laying and incubation without extensive supplemental feeding. It is not uncommon for female anatids to forage more then pair males prior to egg laying (c.f. Afton 1979) but the Torrent Duck pair seemed to partition the resource by feeding at different depths using different feeding techniques and so reduced overlap. The clutch was small but the eggs were large relative to other anatids (Lack 1967). The female fed most of the time but laid eggs at intervals of 6 to 8 days. During incubation, the female took long breaks, twice daily, during which she fed almost continuously.

While the invertebrate food resource in mountain streams may be predictable, it probably never is overly abundant (Hynes 1970b). In recent times the food resource may be limited further by several changes that have resulted in deterioration of Torrent Duck habitat. Introduced trout probably compete for the invertebrate food resource and reduce the quality of a stream for Torrent Ducks. Increased floods caused by deforestation further limit the food supply by scouring invertebrates from submerged rocks (Hynes 1970a). During this study, eight flash floods occurred on Rio Nalcus and their frequency and sediment load probably reduced available food in addition to destroying the nest.

Acknowledgements

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Summary

A Torrent Duck *Merganetta armata armata* pair during an austral spring in Chile cooperated in defending a river territory of approximately 1700 m. Although they shared a similar threat display repertoire, territorial birds primarily confronted intruders of the same sex. The pair remained strongly bonded throughout the study and pair bond maintenance activities and copulations were common weeks before and after egg laying. They nested in a large hole in a gravel bank and the female laid three eggs in an old Torrent Duck nest. After the nest was destroyed by a flood the pair prepared to renest.

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Jan L. Eldridge, Bell Museum of Natural History, 10 Church Street, S.E., Minneapolis, Minnesota 554 55, U.S.A.

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Torrent Ducks are found in pairs throughout the year and are thought to be monogamous (Scott 1954; Johnson 1963; Johnsgard 1966; Moffett 1970). They nest in a variety of locations, including trees, rocky ledges and crevices and holes in river banks (Johnson 1963; Moffett 1970). Nesting areas are used repeatedly; incubation periods arc unusually long compared to other ducks and both sexes cooperate with brood rearing (Johnson 1963; Cecil 1969; Moffett 1970). They are highly territorial and both sexes cooperate in territorial defence, with similar displays (Moffett 1970; Eldridge 1979).

Year-round territoriality and long-term pair bonds are unusual traits in Anatidae but are present in three other anatid river specialists: the African Black Duck *Anas sparsa* (Ball *et al.* 1978; McKinney *et al.* 1978), Salvadori's Duck *Anas waigiuensis* (Kear 1975), and the Blue Duck *Hymenolaimus malacorhynchos* (Kear & Steel 1971; Kear 1972; Eldridge 1985). These species are not closely related (Woolfenden 1961; Brush 1976; Bottjer 1983) and the similarities have probably evolved independently in response to the fast-water stream environment.

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Study area

Río Nalcas begins in the snow fields of Volcán Puntiagudo and drains about 27 km^2 before emptying into Lago Rupanco. My study area included the lower 2600 m of the river between a major 50-m waterfall and the lake. The pair I observed defended the lower stretch of about 1700 m and a second pair defended a small stretch of about 900 m between the downriver territory and the falls. The gradient was milder in the downriver territory and the river channel was less than one meter deep. Wide, shallow riffles with reduced current and numerous exposed rocks alternated with deep, fast, unbroken channels or pools. In several places the river branched through a network of small, stony islands covered with brush and beached logs. In most areas the stream was contained in a channel of rounded rocks and boulders but in some areas it cut into gravel banks. Much of the downriver territory was bordered by 15–20-m cliffs with pasture in the surrounding uplands. In contrast, the smaller upriver territory had a steep gradient, a strong, unbroken current, and was bordered by cliffs with dense, overhanging native vegetation, which made observation of the upriver pair almost impossible.

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variation in the black-and-white feather pattern of the head-and-neck region. Individual females could be identified by gaps in the rectrices, which are molted periodically throughout the year (Weller 1968).

Results

I watched the downriver pair from September 14 through November 26, 1975. During this time they remained strongly bonded; they nested and the female laid three eggs and incubated them until the nest was destroyed by a flood. The pair then prepared to renest. This study can be divided into four time periods based on the pair's breeding chronology: prelaying, 14 September – 13 October; laying, 14–25 October; incubation, 26 October – 16 November; and renesting, 16–26 November.

Prelaying

During the month before egg-laying began, the male and female were together almost constantly (Fig. 1). They moved throughout their 1700-m territory but they concentrated their activities on particular areas of the river (Fig. 2). Although they fed throughout the territory, they preferred the wide, shallow riffles probably because stream riffles contain greater invertebrate abundance (Hynes 1970b). For analysis, the river was divided into 68 segments, each 25 m long , but varying in width depending on the river channel. During 29 days of observation 1 recorded 102 feeding locations. They used particular riffles on a regular basis but only once did they return to the same 25-m area in one day.

The birds used two feeding methods, dabbling and diving. I did not see them up-

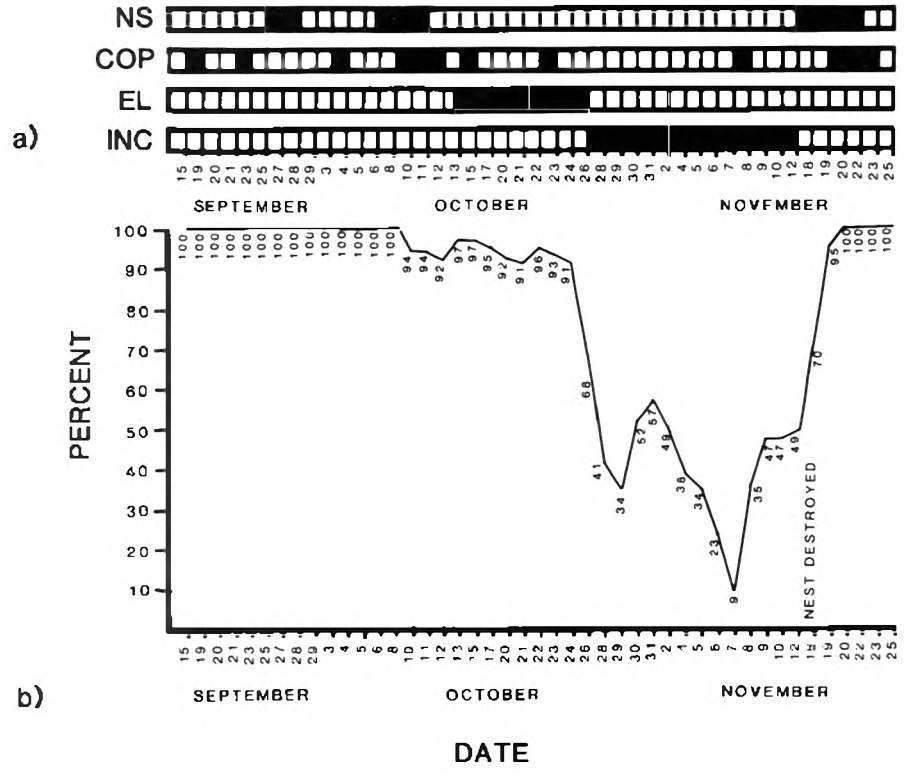

Figure 1. a) Occurrence of nest searching (INS), copulation (COP), egg laying (EL), and incubation (INC) during each day of the study. b) Time the male spent with the female as a percentage of daily observations.

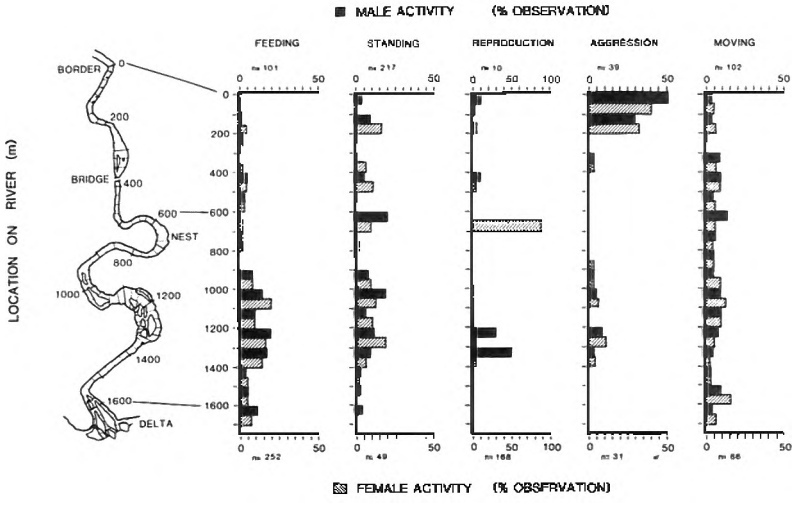

Figure 2. Location of various activities on the river, expressed in 100-meter increments as a percent of observed locations.

end, a feeding method typical of many dabbling ducks *Anas* spp. They dabbled in shallow water (0.1 to 0.2 m) along the stream edge or in wide, shallow riffles. They walked or swam in the shallows and probed around submerged rocks. Occasionally, a bird dabbled on exposed rocks in deeper water but usually feeding in the central part of the stream was accomplished by diving. Dives were clean and arched with wings held firmly to the body. Birds often dove upstream from a rock, fed along the bottom 2 to 3 m upstream and surfaced as the current carried them back to the rock. They also dove in eddies behind rocks and fed from eddy to eddy. With both types of feeding, the birds methodically probed the rocky substrate foraging for invertebrates, but on rare occasions they dashed after small fish that were 5 to 10 cm long.

Early in the study the pair dabbled and dove in equal proportions but as time passed the male spent less time feeding and dove more in the central portion of the stream while the female dabbled in the shallows along the edge (Fig. 3). While the female fed, the male followed closely and stood near her in an alert, watchful stance (Table 1). The female fed almost twice as much as the male (Fig. 4). While she fed, the female initiated most moves from one feeding area to another and if she moved out of sight the male actively called and searched for her.

They often fed by moving upriver against the current. They avoided the main force of the current by walking in the shallows along the stream edge or moving upriver in the eddies behind rocks. While following the female, many of the male's activities appeared precopulatory (Fig. 5). When the female paused on a rock, the male joined her in a hunched posture with body lowered, neck extended slightly and crest feathers depressed. When the female was in the water he approached in the hunched posture and performed repeated bill-dips

Table 1. Simultaneous observations of the male and female, with row frequencies above column frequencies for the following activities: Standing (STD), Feeding (FED), Aggression (AGG), Reproduction (REP) and Other, which included sleeping, preening and moving. Based on a total of 5485 minutes of observation.

Male activity	Female activity				
	STD	FED	AGG	REP	OTHER
STD	0.06	0.54	0	0.36	0.04
	0.38	0.51	0	0.38	0.08
FED	0.10	0.78	0	0.02	0.06
	0.33	0.37	0	0.01	0.06
AGG	0	0	0.90	0.09	0.01
	0	0	1.00	0.01	0
REP	0	0.10	0	0.85	0.05
	0	0	0	0.02	0
OTHER	0.04	0.11	0	0.49	0.36
	0.28	0.12	0	0.58	0.85

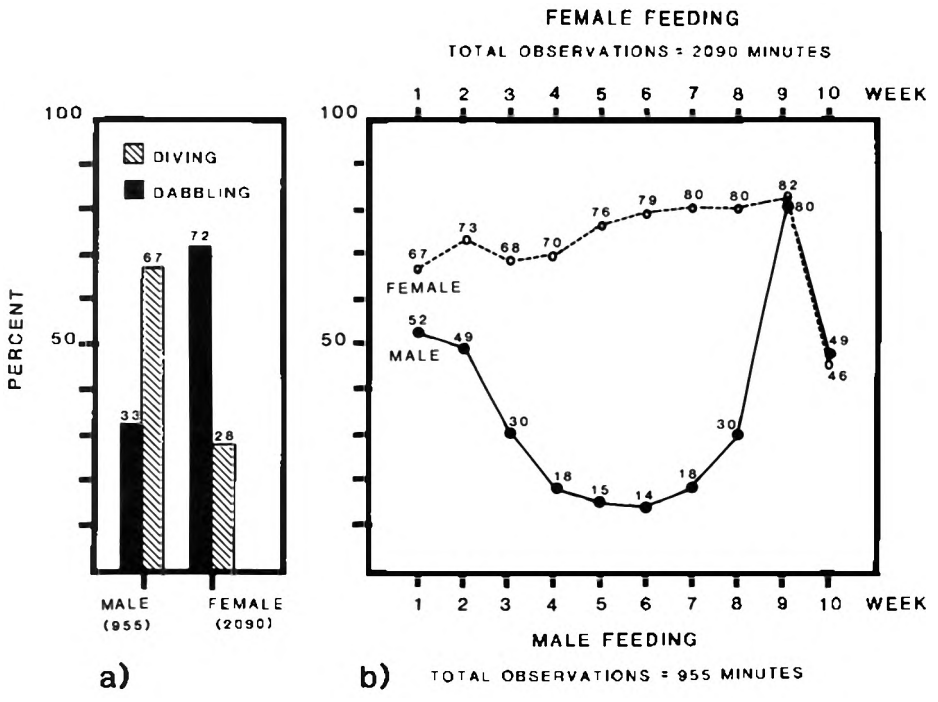

Figure 3. a) Foraging technique used by the territorial male and female, expressed as a percent of foraging time. b) Seasonal change in foraging by territorial male and female expressed as a percent of total observations each week.

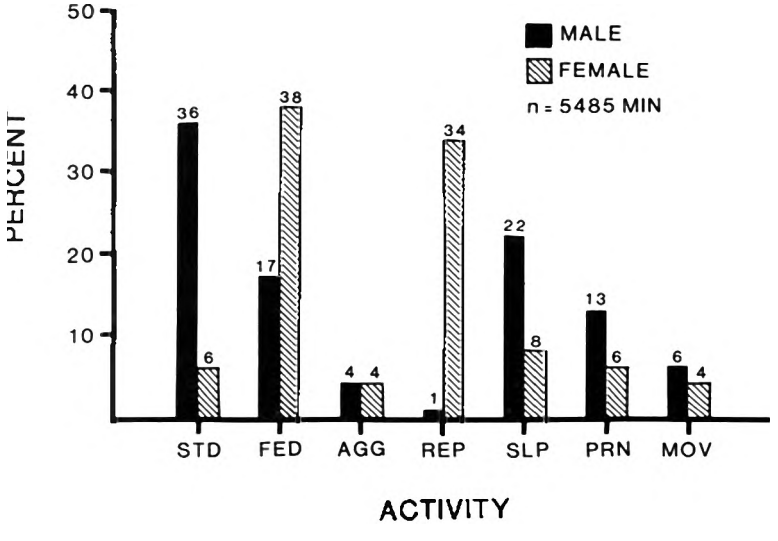

Figure 4. Time budget of the territorial pair while they were present on the river. Activities include standing (STD), feeding (FED), aggression (AGG), reproductive activities such as copulation, nest searching, and incubation (REP), sleeping (SLP), preening (PRN). and moving (MOV).

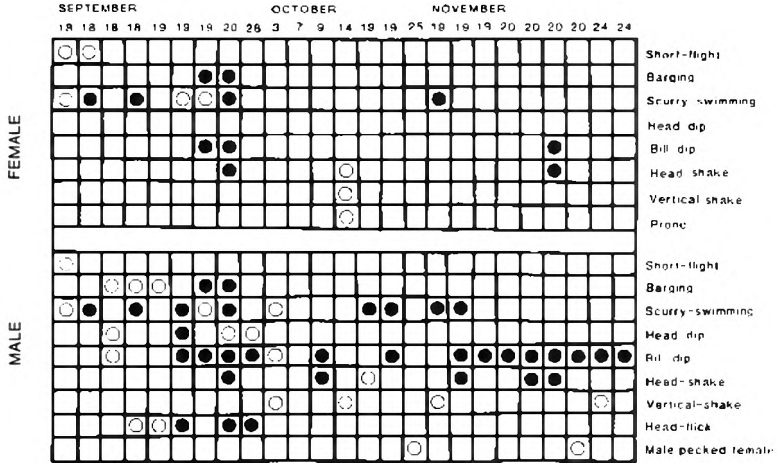

Figure 5. Chronology of laying as indicated by the dates of first egg.

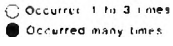

Figure 5. Interactions that appeared precopulatory during the study.

and head-shakes. At other times the male rapidly approached the female by scurrying over the surface of the water of flying a short distance, assuming the hunched position when he neared her.

Copulations usually followed when the female assumed a prone position (Fig. 6). The male responded to the female's prone with one or two vertical-shakes followed by a low barge approach with bill angled down and crest erect. He mounted and dismounted with head held back and bill tucked. He followed three copulations with a partial body-bend in the water beside the female.

The pair searched for a nest site during the month before egg-laying began. They returned repeatedly to five holes that varied from 1 to 10 m above the water in the river bank. Nest searching involved an elaborate interaction between pair members while the female, and sometimes the male, investigated a site. Throughout each 5- to 15-minute investigation the pair tail-wagged and pointed continuously and the male performed repeated body-bends with "warble" call. Often during a search they encountered other hole-nesting species such as the Chilean Cinclodes *Cinclodes patagonicus*, and the Huet-huet *Pteroptochos tarnii*. The smaller birds attacked the Torrent Ducks briefly and then left the hole to them.

Whenever the pair encountered other Torrent Ducks they aggressively confronted the intruders and both sexes performed a variety of displays described in Eldridge (1979). During the course of this study I observed 14 interactions with intruders. Most occurred at the border between the two territories (Fig. 1). Six interactions involved the upstream pair, six were with intruding lone females and two were with intruding males. Of these, I recorded displays performed in six interactions; two with intruding pairs, two with single males, and two with single females. For analysis, I considered the five most common discrete displays: Vertical-shake, Body-bend, Mule-kick, Wing-flap, and Shudder-shake. Average display intensity was determined subjectively and the displays were ranked by the apparent energy involved in their performance (Vertical-shake = 5 (most intense), Mule-kick = 4, Body-bend = 3, Wing-flap = 2, Shudder-shake = 1). In this system, adapted from Recher and Recher (1969), interaction intensity is determined by multiplying display rank by the number of times it was performed during the interaction and dividing by total displays performed. Intense interactions involved more Vertical-shakes and Mule-kicks (rank >3.0) and less-intense interactions had more Shudder-shakes and Wing-flaps (rank <3.0). In general, interactions with pairs

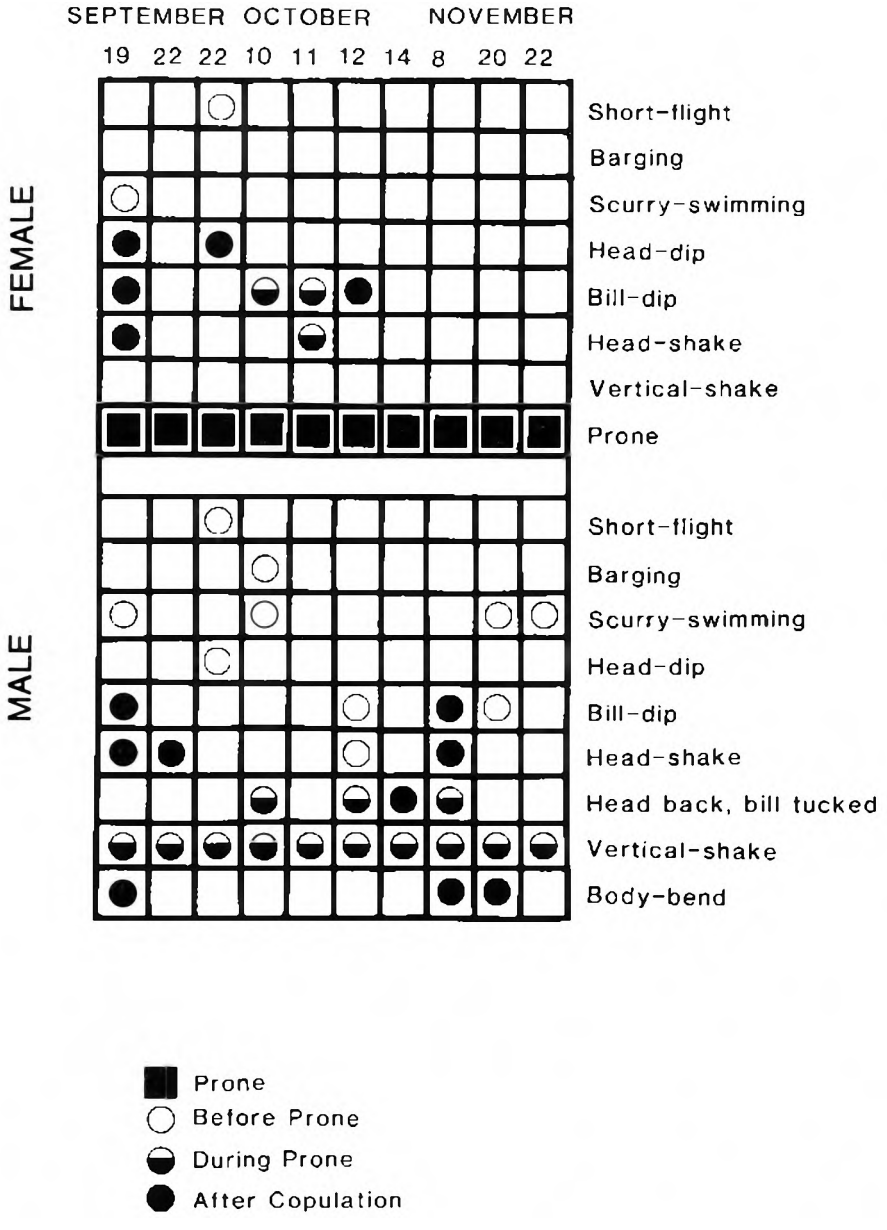

Figure 6. Interactions that resulted in copulations.

and lone males were long, intense and involved many displays; interactions with lone females were less intense, shorter and involved fewer displays (Table 2).

Both sexes had a similar display repertoire and performed displays in similar proportions (Table 3). Pair members responded differently to the intruder's sex and paired status (Table 4). When a lone male intruded, the territorial male performed most of the displays. When a lone female intruded, the territorial female performed. When a pair intruded both performed equally but the male confronted

Table 2. Aggressive interactions varied in the number of displays performed, duration, and intensity depending on the status of the intruder(s). Mean values are expressed with standard error.

Intruder type	*n*	Displays	Duration (min)	Intensity
Pair	2	246 ± 17	20 ± 9	3.34 ± 0.04
Lone male	2	168 ± 54	36 ± 18	3.5 ± 0.23
Lone female	2	48 ± 6	6 ± 4	2.7 ± 0.14

Table 3. Display type performed by territorial male and female during aggressive interactions. Expected values from the chi-square analysis are in parentheses. Territorial birds did not differ from expected in the types of displays they performed (χ^2 = 9 336, df = 4. $P > 0.05$).

	VS	MK	BB	WF	SS
Male	48 (44)	67 (68)	109 (118)	38 (41)	44 (35)
Female	23 (27)	44 (43)	83 (74)	29 (26)	13 (22)

the intruding male and the female confronted the intruding female (Fig. 7).

Most interactions were intense but without overt physical aggression. Even when the downriver male pursued the upriver male in an aerial chase and forced the upriver male to land, he did not attack but landed nearby and displayed. When rivals were very close in intense interaction, however. Wing-flaps were directed to strike. Mule-kicks became body blocks that knocked a rival from a rock and Body-bends bumped rivals into the water.

Table 4. Displays performed by the territorial male and remale in response to intruders. Parenthesis indicate expected values from the chi-square analysis Display performance differed significantly from expected (χ^2 =80;89, df = 2. $P < 0.005$).

	Intruder Status		
	Lone male	Lone female	Pair
Territorial Male	154 (114)	18 (45)	134 (147)
Territorial female	31 (71)	56 (29)	105 (92)

A fight was observed on one occasion during a very intense display burst when the upriver pair intruded. All four birds were standing on a rock and the downriver female drove the upriver female oft the rock with a brief flurry of wings. This interaction took a fraction of a second and it was the only physical fight observed in 248 minutes of aggressive interaction. The spurs were much more commonly used in display postures particularly by the male after performing a Mule-kick or Wing-flap or while standing in the Upright near a rival.

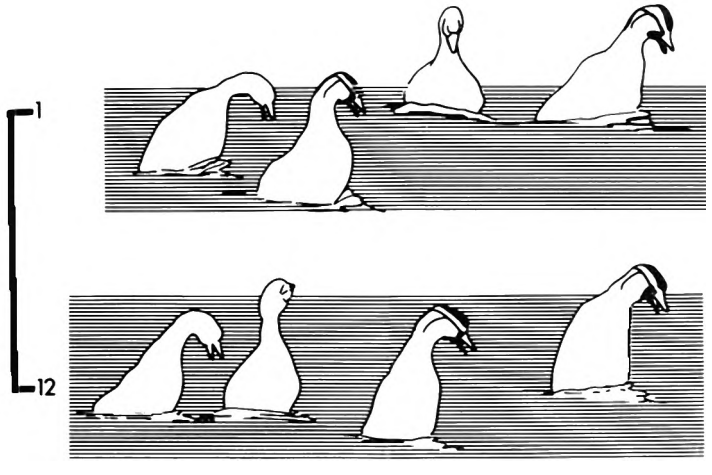

Figure 7. A filmed aggressive interaction between territorial pair and intruding pair. The interaction begins with pair mates in close proximity performing Bent-neck displays. They quickly move apart to confront rivals of the same sex. The numbered line indicates frames from a film exposed at 24 frames per second.

Laying

By October 11 the pair returned regularly to a large hole 1 m wide and 2 m deep in the face of a 20-m gravel cliff. This hole had been used by Torrent Ducks before and the female built upon the old nest. Three eggs were laid at 6- to 8-day intervals between 14 and 25 October. Egg measurements, in order, were: 57 g, 62 × 41 mm; 56 g, 64 × 41 mm; 59 g, 63 × 41.5 mm. The eggs were elongate, pointed and creamy tan with a smooth, somewhat glossy surface. Mean egg size was 16% (14–18%) and the entire clutch was 47% (43–55%) of female body weight, which I estimated to be 364 g from 315–349 g reported by Neithammer (1952) and 400 g for a female I weighed on Río Chanleufu.

During this period, the pair remained together but not as constantly as before (Fig. 1). They separated because the female visited the nest for one to two hours each day.

On three occasions during this period the pair encountered lone intruding females. The male's reaction was quite different when lone females attempted to escape without confrontation or display. He attacked the intruding female in an aerial chase, and forced her to land. Each tune the male immediately lunged at the female, grasped her by the nape and flapped his wings as she attempted to dive. He did not appear to be striking the female, however, as was the casc when the downriver female attacked the upriver female. His wings were held high and the intruding female was beneath him in the water in what appeared to be a forced copulation.

Incubation

Incubation began on 27 October and was performed exclusively by the female. During the first few days she left the nest irregularly several times a day but by the second week she was averaging 7 h and 26 min on the nest during daylight hours, breaking early in the morning before 07.00 and late in the day after 15.00. The recesses were long; six afternoon breaks averaged 2 h 21 min.

During the incubation period, the male was increasingly absent from the nest (Fig. 1). He became more secretive and mobile, occasionally venturing into the upriver territory. He returned regularly to the nest area and his returns were conspicuous and noisy; he stood on rocks near the nest entrance, called and performed several Body-bends.

Although the male spent less time around the nest, he usually accompanied the female during breaks. If he wasn't near the nest when the female left the nest cavity, she assumed a high, erect stance, craned her neck apparently searching for the male. On two occasions she performed a "ga-ga-brr" call with Bent-neck and the male responded by flying to her and performing a Body-bend.

During breaks, the female dabbled almost continuously in the shallows and the male alternately fed and watched in an alert stance near her. During the second week of incubation the female solicited the male with a Prone and a copulation followed. The female usually returned to the nest accompanied by the male. Each time they stood on rocks near the nest entrance for several minutes, interacting as they did while nest searching.

Nest destruction

The nest was destroyed by a flood during a storm that lasted from 12–16 November. The pair immediately resumed nest searching and copulations. The male once again actively followed the female and searched for her if she was out of sight. Both dabbled and dove in equal proportions while feeding and both actively participated in defending the territory. In short, they behaved as they had at the beginning of the study (Fig. 1).

Discussion

The most conspicuous aspect of the Torrent Duck's behavior was their strong pair bond and cooperative defense of territory. Territorial conflicts were prolonged and the displays were elaborate and seemed energetically expensive. Although the wing spurs were used primarily in display, the birds probably risked serious injury if aggression became overt. The pair's sex-specific reaction to intruders suggests that an intruder threatened both the territory and the pair bond. It is possible that both sexes can acquire a territory by displacing a paired territorial rival.

This possibility may explain the variety of

pair maintenance activities that I observed throughout the study including, close following, proximity to mate and searching for mates, copulations weeks before and after egg laying, and prolonged interactions between mates while nest searching. I think that mutual defense of the territory was also a form of pair–bond maintenance. The pair members displayed synchronously before and after each interaction and many of the displays during the interactions were performed simultaneously.

Territoriality has been correlated with a food resource that is economically defensible, depletable, and renewing (Brown 1964; Gill & Wolf 1977; Pyke 1979; Davies 1980). The river territory is strategically defensible because there are only two boundaries, one at each end of a territory. The invertebrate resource varies by zones in the river and is most abundant in the shallow riffles (Hynes 1970b). The resource is renewing because invertebrates have a diurnal periodicity that results in population redistribution known as invertebrate drift (Waters 1972).

The pair I observed maintained a large territory but a number of factors suggest that their foraging behavior closely matched the food resource. The entire territory was not suitable for feeding and the birds concentrated on a few major riffles. Although they returned to feeding areas, they did not return to the same area within a single day. This suggests that the resource may be depletable and that returns coincide with daily renewal by invertebrate drift.

Several factors suggest that the food resource was limited and that the female's energy reserves were insufficient for egg laying and incubation without extensive supplemental feeding. It is not uncommon for female anatids to forage more than pair males prior to egg laying (*cf.* Afton 1979) but the Torrent Duck pair seemed to partition the resource by feeding at different depths using different feeding techniques and so reduced overlap. The clutch was small but the eggs were large relative to other anatids (Lack 1967). The female fed most of the time but laid eggs at intervals of 6 to 8 days. During incubation, the female took long breaks, twice daily, during which she fed almost continuously.

While the invertebrate food resource in mountain streams may be predictable, it probably never is overly abundant (Hynes 1970b). ln recent times the food resource may be limited further by several changes that have resulted in deterioration of Torrent Duck habitat. Introduced trout probably compete for the invertebrate food resource and reduce the quality of a stream for Torrent Ducks. Increased floods caused by deforestation further limit the food supply by scouring invertebrates from submerged rocks (Hynes 1970a). During this study, eight flash floods occurred on Río Nalcas and their frequency and sediment load probably reduced available food in addition to destroying the nest.

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Summary

A Torrent Duck *Merganetta armata armata* pair during an austral spring in Chile cooperated in defending a river territory of approximately 1700 m. Although they shared a similar threat–display repertoire, territorial birds primarily confronted intruders of the same sex. The pair remained strongly bonded throughout the study and pair–bond maintenance activities and copulations were common weeks before and after egg laying. They nested in a large hole in a gravel bank and the female laid three eggs in an old Torrent Duck nest. After the nest was destroyed by a flood the pair prepared to renest.

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Jan L. Eldridge, Bell Museum of Natural History, 10 Church Street, S.E., Minneapolis, Minnesota 55455, USA.