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ADULT BEHAVIOUR OF *XANTHOCNEMIS ZEALANDICA* McLACHLAN AND *AUSTROLESTES COLENSONIS* WHITE AT SELECTED SOUTH ISLAND (N. ZEALAND) HABITATS (ZYGOPTERA:*COENAGRIONIDAE, LESTIDAE*)

W.J. CRUMPTON

Department of Zoology, University of Canterbury,
Christchurch 1, New Zealand

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Aspects of adult behaviour of the endemic New Zealand Zygoptera *Xanthocnemis zealandica* McLachlan and *Austrolestes colensonis* White are examined. Both species commonly occur together around their aquatic breeding sites, and have similar long flight periods lasting from spring to autumn. No adults of either species were found to be active at air temperatures below 14°C, and they became most active at the highest temperatures and in sunny areas.

There was a distinct difference in oviposition sites of the two species. *X. zealandica* oviposited in aquatic and semi-aquatic plants at and just below water level, depositing one egg at a time; *A. colensonis* laid eggs in groups inside the stems of plants in or near water, about one metre above it. Mature males patrolled these oviposition areas; *X. zealandica* males tended to form swarming groups when populations became dense. However, *A. colensonis* males never swarmed; they probably regulated their numbers by territorial behaviour.

Descriptions are given of reproductive behaviour including copulation, exploration for oviposition and oviposition. They compare well with the behaviour described by other workers in related Zygoptera.

INTRODUCTION

Two endemic zygopteran species, *Austrolestes colensonis* White (*Lestidae*) and *Xanthocnemis colensonis* McLachlan (*Coenagrionidae*), are present in the South Island of New Zealand. The New Zealand Zygoptera are easily identified as adults or larvae using PENNIKET's (1966) key. The taxonomic status of the genus *Austrolestes* was discussed by WISE (1973). Both species commonly occur together in and around swamps, ditches, ponds and lakes where there is emergent vegetation suitable for endophytic oviposition. A detailed study of their larval and adult ecology was carried out at selected habitats in Canterbury and Westland from 1969 to 1972, supplemented with observations made in 1973 and 1974. In this paper, adult behaviour, particularly reproductive behaviour, is described and compared with work done outside New Zealand on related genera.

Published notes on the biology of adult New Zealand zygopterans are brief and scattered. HUDSON (1904) gave flying seasons for both species and some notes on reproductive behaviour in *X. zealandica* and later (1950) mentioned resting positions of *A. colensonis*; WOLFE (1949) included a photograph of *A. colensonis* ovipositing underwater; PENDERGRAST & COWLEY (1966) mentioned the flying season and oviposition behaviour in *X. zealandica*; and SCOTT (1963) recorded further observations on the flying season and reproductive behaviour in *X. zealandica*. Information on reproductive behaviour in both species has been obtained from ARMSTRONG (pers. comm.), and CLARK (pers. comm.).

METHODS

Observations of adults were made at the habitats shown in Figure 1 and the altitudes were estimated from New Zealand Mapping Service Series 1 topographic maps. Descriptions of some of these habitats will be given in a later paper. Coleridge Kettle Pond was described by STOUT (1969). Both species were present at all habitats except Arthur's Pass Tarn.

During the period 1969-72, counts of adults, including immatures, single males and females, and tandem pairs of each species, were made at some of the habitats listed, at different times of the day. At the same time, the following weather conditions were noted: air temperature in the sun one metre above the ground, light intensity, and wind velocity and direction.

Direct observations of reproductive activity were made, often being recorded on tape. A stopwatch was used for timing activities. Weather conditions and time of day were always noted. All times were converted to sun time in which solar noon was at 1200 hours.

The sequence of reproductive events followed by BICK & BICK (1963, 1972), and BICK & HORNUFF (1965, 1966) in their general survey of zygopteran reproductive behaviour are used in this account.

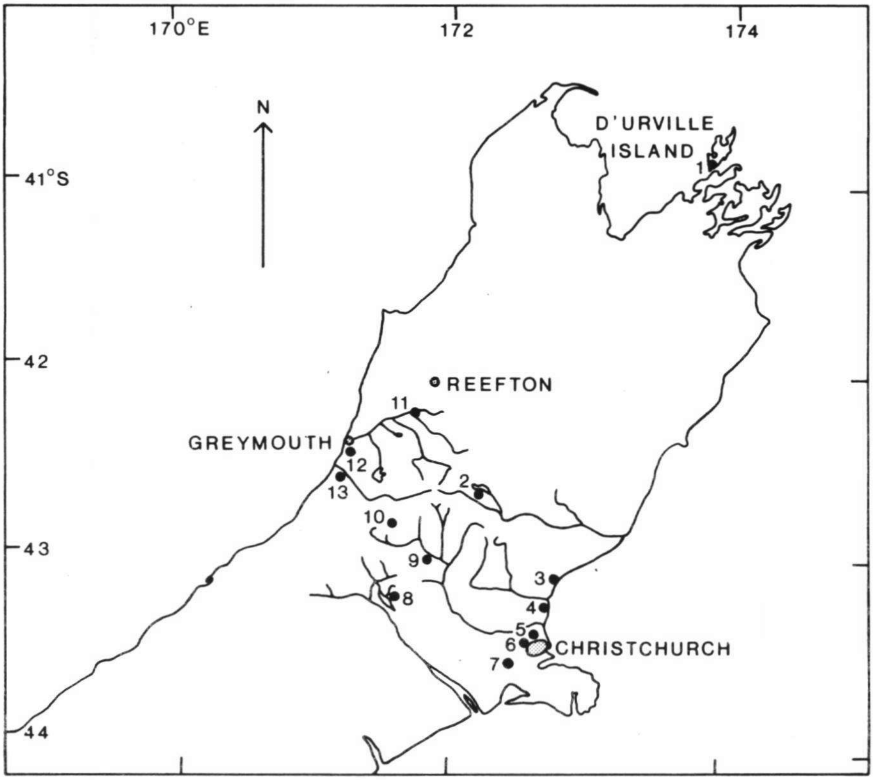

Fig. 1. Study habitats for *Xanthocnemis zealandica* and *Austrolestes colensonis*: (1) Te Puna Lagoon (0 m); – (2) Lake Katrine (550 m); – (3) Leithfield Lagoon (0 m); – (4) Woodend Pond (0 m); – (5) Groynes (15 m); – (6) Shipley's Large Pond (27 m); – (7) Lincoln Ditch (21 m); – (8) Coleridge Kettle Pond (189 m); – (9) Lake Sarah (610 m); – (10) Arthur's Pass Tarn (924 m); – (11) Hukarere Pond (113 m); – (12) Welshman's Habitats (61 m); – (13) Kumara Straight Pond (61 m).

RESULTS

FLIGHT PERIOD

Adults of both species fly throughout the spring, summer and autumn months in lowland habitats, but have shorter seasons at higher altitudes (Tab. I).

FACTORS AFFECTING FLIGHT ACTIVITY

Adult activity in Odonata is affected by time of day and weather conditions, particularly temperature and light intensity (LUTZ & PITTMAN, 1970). Adult

Table I

Adult flight periods

Species	Locality	Flight period	
		Start	*Finish*
X. zealandica	Laboratory	21 August 1971	
	Lowland	1 October 1971	28 April 1970
	High country*	15 November 1969	21 March 1969
A. colensonis	Laboratory	31 August 1971	
	Lowland	6 Octobre 1970	12 May 1969
	High country*	November	22 March 1969

* Observations from STOUT (1969).

X. zealandica and *A. colensonis* were found to be active during daylight hours. Figure 2 shows the numbers of adults and tandem pairs related to the air temperatures, including all observations made from 1969-1974, from all habitats and at different stages of the season. No adults of either species were active below 14°C, and no tandem pairs of *A. colensonis* were seen below 19°C.

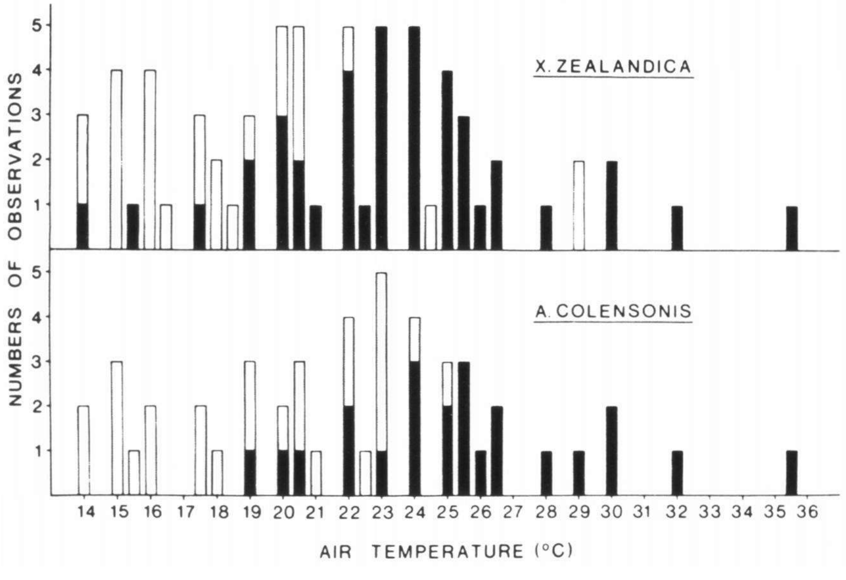

Fig. 2. Number of active adults of *Xanthocnemis zealandica* and *Austrolestes colensonis* plotted against ambient temperature. Dotted, single adults; black, tandem pairs.

To illustrate the effects of weather on adult activity selected adult counts are compared (Tab. II), together with the weather conditions at the time. Woodend Pond is sheltered from the cold southerly winds by a dense stand of *Salix caprea* but it is exposed to easterly and north-westerly winds.

During December 1970 no *A. colensonis* adults were seen at the pond. On 9 December 1970 only *X. zealandica* adults were present. Between 1429 and 1529 h the air temperature dropped 5,5°C, light intensity was halved, and the wind speed increased by almost 0.4 m/sec. By 1529 h the number of active *X. zealandica* adults had decreased, and reproductive activity stopped. At 1629 h, when the weather had become duller and windier, no adults were active in the oviposition area and at 1729 h all adult activity had ceased.

On 2 February 1971, with a light easterly wind blowing, adult activity was greatest at 1218 h when the temperature and light intensity were highest. Both species were present at the pond although there was no reproductive activity in *A. colensonis* and more *A. colensonis* adults were seen away from the oviposition area than within it.

Reproductive activity in *A. colensonis* occurred only on 24 February 1971, a very hot day with continuous cloud cover and a gusty north-west wind (Tab. II). The numbers of *A. colensonis* seen were also high on this day, especially at midday when the temperature and light intensity were highest. The fairly high winds on this day did not inhibit the reproductive activity of either species.

On 29 March 1971 conditions in the morning were similar to those on 2 February 1971. However, later in the afternoon cloud cover and wind speed increased and reproductive activity of *X. zealandica* ceased. *A. colensonis* activity also stopped, first in the oviposition area, then elsewhere.

The overall pattern for both species is that adults become active first away from oviposition areas and later, in their oviposition areas, they become reproductively active as temperature and light intensity increase; activity declines as the light intensity and/or temperature decrease. Wind speed below 2.4 m/sec has little effect on adult activity. Initiation of reproductive activity in *A. colensonis* requires higher temperatures than for *X. zealandica.*

SITES OF REPRODUCTIVE ACTIVITY

X. zealandica

Copulation of several *X. zealandica* pairs was observed on nine occasions. In each case copulation occurred within 0.5 m of the ground or water, and less than 0.5 m from the water's edge. Most copulations took place over water and just above it.

X. zealandica was only seen ovipositing in plants in permanent standing or slowly flowing water. Both living and dead stem or leaf tissue was used and the eggs were laid below the water surface or up to about 0.2 m above it. *X.*

Table II

Selected observations from Woodend Pond

Sun time (hours)	Air temp. (°C)	Light intensity (lux)	Wind speed + direction 1 m above ground (m/sec)	*X. zealandica*						*A. colensonis*					
				Oviposition area			Outside oviposition area			Oviposition area			Outside oviposition area		
				♂	♀	tandem pairs	♂	♀	tandem pairs	♂	♀	tandem pairs	♂	♀	tandem pairs
9 December 1970															
1329	22.0	8073	0.23 S	1		2	5		1						
1429	20.5	10764	0.08	5	2	5	7	1							
1529	15.0	5382	0.46	1	1		1	2							
1629	16.0	3229	0.39				1	1							
1729	12.5	2153	0.94												
2 February 1971															
0748	15.7	1076	0.85 E										1		
1018	20.5	5382	0.97	3			3			2			7		
1218	22.0	10764	1.14	32	1	4	5	1		5			7		
1318	22.5	8073	1.14										2		
24 February 1971															
0855	25.5	3229	2.34 NW	40		4	25			2		4	6		2
1055	35.5	5382	1.67	98	2	44	3		1	5		4	12		3
29 March 1971															
1025	18.0	8073	1.30 E	25		1	4	2		1			3		
1125	20.0	10764	1.28	24		4	1	4		3			3		
1225	21.0	8073	1.43	32		6	3			3			4		
1325	19.5	5382	2.10	8			4	2					3		
1425	17.5	3229	2.43				7	1							

zealandica has been seen to oviposit in the following plants:

Juncus articulatus, J. acutiflorus, J. bulbosus, Scirpus prolifer, S. lacustris, Rorippa microphylla, Ranunculus fluitans, Potamogeton cheesemanii, Elodea canadensis, Lagarosiphon major, Myriophyllum propinquum. M. elatinoides, Nymphaea alba, Salix tortulosa (young shoots) (this paper) and *Salvinia natans* (SCOTT, 1963).

Activity of single males was concentrated in these oviposition areas, immediately above or beside the water.

A. colensonis

In *A. colensonis* oviposition and activity of single males occurred at noticeably higher levels in the vegetation than adult activity in *X. zealandica*, and extended further from the water. Copulation was observed only twice: in vegetation 1.0 and 1.3 m above ground level, and 1 and 6 m away from water respectively.

A. colensonis always oviposits in stems or leaves of emergent aquatic or terrestrial plants, in or near a permanent or semipermanent lotic habitat. Table III lists typical oviposition sites. On all occasions eggs were laid in a position

Table III

Oviposition sites of *A. colensonis*

Habitat	Date	Oviposition plant	Position *	Distance from water (m)	Height of eggs above water level (m)
Groynes	18 Nov. 1969	*Agropyron repens*	O	> 0.5	0.50
Leithfield Lagoon	25 Jan. 1970	*Typha muelleri*	W		0.30
Woodend Pond	9 Dec. 1970	*Eleocharis acuta*	S	0.5	0.20
Woodend Pond	24 Feb. 1971	*Juncus effusus*	S	2.5	0.80
Woodend Pond	29 Mar. 1971	*J. effusus*	S	7.0	0.80
Shipley's Large Pond	11 Mar. 1971	*J. articulatus*	W		0.25
Lincoln Ditch	Dec. 1973	*Dactylis glomerata*	O	> 0.5	1.20
Coleridge Kettle Pond	4 Feb. 1971	*J. distegus*	O	> 0.5	0.40
Welshman's Habitat	12 Dec. 1970	*Scirpus prolifer*	W		0.40
Kumara Straight Pond	26 Jan. 1971	*J. canadensis*	O	> 0.5	0.30
Te Puna Lagoon	13 Feb. 1974	*S. lacustris*	W		0.90

*W = roots of plant in water at time of laying
S = plant in swampy ground which is dry in summer, but under water in winter
O = plant on higher ground, overhanging water

where it was highly probable that either they would hatch directly in water, or that the prolarva would fall into the water. In positions O and S (Tab. III) eggs were laid only in the upper parts of the plants, whereas in W they were laid at water level. As in *X. zealandica, A. colensonis* eggs were not always laid in living plant material. ARMSTRONG (pers. comm.) has observed *A. colensonis* laying in dead stems around pools in dense native forest near Taupo. Underwater oviposition as reported by WOLFE (1949) in *A. colensonis* was never observed.

At particular oviposition sites, such as a clump of *Juncus effusus*, egg incisions were not necessarily confined to the periphery of the clump but tended to be densely concentrated on some stems. During the exploration for oviposition, females landed at suitable sites, and then appeared to select a stem already bearing oviposition incisions. For example, at Shipley's Large Pond (12 March 1974) a pair tested first a gorse (*Ulex europaeus*) stem overhanging the water, then an unused *Juncus articulatus* stem and finally laid in a *J. articulatus* stem which already contained some *A. colensonis* egg-incisions.

MALE BEHAVIOUR IN THE OVIPOSITION AREA

Two aspects of the behaviour of single males will be considered; density in the oviposition areas and behavioural interactions.

X. zealandica

Males in oviposition areas commonly rest horizontally near the ground with the wings held slightly above the body, and the abdomen slightly raised and curved (Fig. 3a). They may also perch with the body projecting at a right angle from a vertical perch.

Table IV shows the number of males counted in oviposition areas at five localities. Observations made when there were no adults present are not shown. These numbers largely reflect seasonal variations in population size, for example, at Woodend Pond from November 1970 to early January 1971, the *X. zealandica* adult population was small as few adults had emerged. In February and March, however, the population was much larger and on 12 March 1971 the highest density recorded in any habitat (162.5 males/50 m) was reached.

Swarming of large numbers of males over the oviposition areas has been mentioned previously by CORBET (1962) in some *Enallagma* species, and described by PAJUNEN (1962, 1966) as occurring in males of *Leucorrhinia dubia* (Anisoptera) and *Calopteryx virgo* (Zygoptera) when population densities become very high at the breeding site. At Woodend Pond, swarming occurred when male densities were greater than 40 per 50 m shoreline. However, at Coleridge Kettle Pond on 4 February 1971, although the density was 48.1 per 50 m, no swarming was recorded. At Shipley's Large Pond on 8 February 1971,

Table IV

Numbers of males per 50 meters of shoreline in oviposition areas

Date	Air temp. (°C)	*X. zealandica*			*A. colensonis*		
		Males	S*	Shoreline length (m)	Males	Tan.*	Shoreline length (m)
Woodend Pond							
13 Nov. 1970	15½	10.9		32			52
27 Nov. 1970	24	18.8			2.9	X	
9 Dec. 1970	20½	7.8					
2 Feb. 1971	22	50.0	X		4.8		
24 Feb. 1971	35½	153.1	X		4.8	X	
12 Mar. 1971	19	162.5	X		4.8		
29 Mar. 1971	21	50.0	X		2.9		
27 Oct. 1971	17½	7.8					
14 Dec. 1971	24	40.6	X		11.5	X	
Shipley's Large Pond							
24 Mar. 1970	15	11.2		76	7.2		76
15 Oct. 1970	24	4.6					
17 Nov. 1970	23	29.0	X		6.6		
17 Dec. 1970	16	2.0			0.7		
13 Jan. 1971	19	9.8			0.7		
8 Feb. 1971	26	31.6			1.3	X	
11 Mar. 1971	17	9.8			7.2		
21 Apr. 1971	20½	0.7			11.8	X	
Welshman's Habitats							
27 Mar. 1970	23	3.6		69	4.3		69
26 Oct. 1970	21	3.6					
13 Dec. 1970	19	7.2					
25 Jan. 1971	25	21.7			19.6	X	
Kumara Straight Pond							
26 Jan. 1971	25½	6.6		38	1.3	X	38
Coleridge Kettle Pond							
9 Feb. 1970	20	30.4		130			
26 Feb. 1970	25	3.1		130		X	
29 Nov. 1970	25	13.8		40			
4 Geb. 1971	24	48.1		130	0.4		130

* S = swarming was occurring
Tan. = tandem pairs present

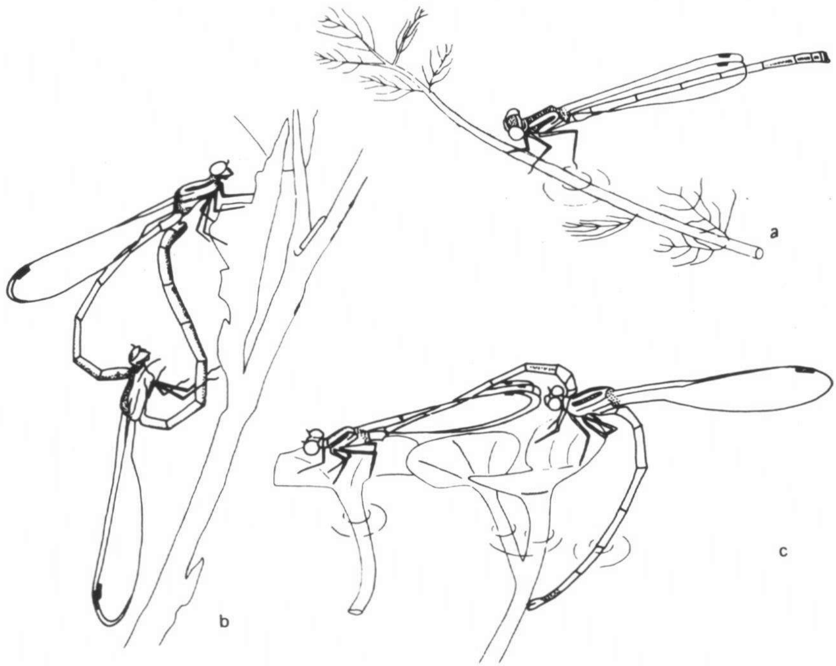

Fig. 3. *Xanthocnemis zealandica*: (a) male in oviposition area; – (b) copulation; – (c) oviposition, using watercress (*Rorippa microphylla*).

although the male density was high (31.6 per 50 m), swarming was not recorded. Swarming did occur on 17 November 1970 at a lower density of 29 per 50 m.

Interactions between males in the breeding area consisted of constant shifting of perching positions, threat displays, and, occasionally, chasing. The threat display was similar to that described by BICK (1966) for *Ischnura verticalis* Say in which a resting male would raise and open its wings slightly ("wing-warning") and at the same time would usually curl the tip of its abdomen down ("ventral abdomen curling").

Wing-warning, with or without ventral abdomen curling, occurred in resting males in the following situations: (1) When a swarm of *X. zealandica* flew past. (2) When another male *X. zealandica* flew nearby. (3) When a tandem pair of *X. zealandica* flew past.

If chasing followed wing-warning with ventral abdomen curling, the abdomen of the chasing male remained ventrally curled. It would sometimes fly almost into the threatening male, but on no occasion was bodily contact seen. After chasing, a male always returned to his previous perch, or to one nearby. This type of behaviour was more often seen in populations of medium density than in very dense populations.

In dense populations, when swarming was occurring, shifting and male interactions were more frequent than in sparse populations. Males were sometimes displaced by other flying insects, passing shadows and thistledown. Table V categorizes the activity of four different males during five minute observation periods on different occasions: twice in dense populations when swarming was occurring and twice when there was no swarming and the nearest perched male was 1 m away. All interactions with other Zygoptera took place in dense populations; sometimes other males were perched as close as 20 mm away.

Table V

Activity of males in oviposition areas at times when tandem pairs were present

	X. zealandica		*A. colensonis*	
	Dense populations	Sparse Populations	Dense Populations	Sparse Populations
Number of 5 min observations	2	2	5	1
Displacement by other Zygoptera	2	1	1	0
Flight toward other Zygoptera	1	0	4	0
Threat display	4	0	2	0
Spontaneous flight	1			2
Flight, reason apparent	2			1
Grooming *	3		1	

* *X. zealandica* – eye-cleaning
A. colensonis – looping abdomen tip past hind legs

A. colensonis

Figure 4a shows a male *A. colensonis* in the oviposition area resting in the position typical of members of the Lestidae (LOIBL, 1958) above ground level on a vertical stalk, with body projecting between 45 and 90° from the stalk; unlike *Lestes* spp., however, the wings are held together. Shortly after landing at a perch, *A. colensonis* showed abdominal rocking up to 10 times depending on the duration of the flight; there was no rocking following a brief shift in position, but more rocking after a long flight.

The maximum density of males in the oviposition area was 19.6/50 m shoreline at Welshman's on 25 January 1971 (Tab. IV). This is considerably lower than the maximum densities recorded for *X. zealandica*. Swarming of males was not seen in *A. colensonis*.

Wing-warning was seen, but only when reproductive activity was frequent. Resting males occasionally threatened but wing-warning usually took place

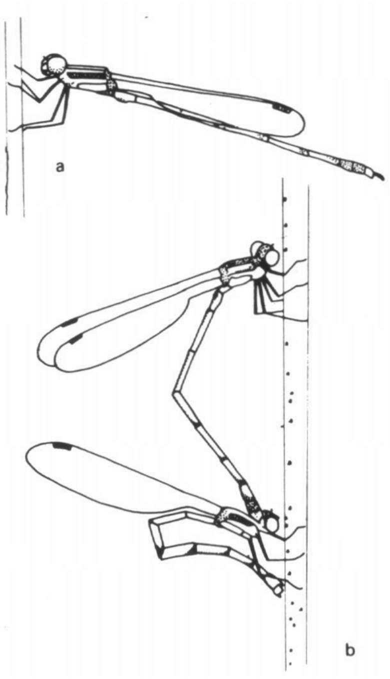

Fig. 4. *Austrolestes colensonis*: (a) male in oviposition area; – (b) oviposition.

during flight. Wing-warning was seen in reaction to the following: (1) Another male *A. colensonis*. (2) A tandem pair of *A. colensonis*. (3) *X. zealandica* adults. (4) Other flying insects.

The reaction to *X. zealandica* adults occurred only when they flew up to the same level above the ground as the *A. colensonis* male. Chasing and wing-clashing with other Zygoptera of either species also occurred, and sometimes a male *A. colensonis* would fly into a swarm of *X. zealandica*, scattering them, and chasing individuals.

Males tended to return to perch in a base area of about 1 m^2 after being disturbed or chasing. One male was disturbed 20 times in succession by waving a hand near it, but it returned to perch on the same small blackberry (*Rubus fruticosus*) bush after each disturbance.

As in *X. zealandica*, males of *A. colensonis* were more active and more easily disturbed when populations were dense. Of the six occasions when a single male was observed (Tab. V), five were when adult activity was high. All interactions with other Zygoptera occurred at times of high activity and spontaneous shifts in position were very frequent.

REPRODUCTIVE BEHAVIOUR

X. zealandica

Direct seizure of a female by a male was seen on one occasion. This occurred soon after the female had separated from its previous male partner following underwater oviposition. On two occasions, in the late afternoon, a mature, pruinescent female was seen being pursued by a male away from the oviposition area. At both times, the female's abdomen tip was curled ventrally in a threat position and it was not seized by the male.

Sperm translocation to the accessory genitalia of the male, followed by copulation, was seen twice in tandem pairs. During copulation the partners were either in a hanging (Fig. 3b), or a horizontal position. The male would initiate copulation by raising his abdomen to enable the female to curve her body round to his accessory genitalia. For the first minute or so of copulation there were usually several breaks in male-female contact. Later, during continuous contact, there was intermittent pumping of the male accessory genitalia against the female. One male cleaned his eyes with his forelegs during copulation, but usually the legs of both partners were not moved, and the female's legs were folded under her body. The wings were either spread slightly apart or more commonly in the female, folded. If interrupted a copulating pair would sometimes move to a nearby perch. The duration of copulation (continuous contact only) at different sites (and air temperatures) were as follows:

Woodend Pond	16 Feb. 1972	(26°C)	7½ min.
Te Puna Lagoon	13 Feb. 1974	(26°C)	17½ min.
Welshman's habitats	3 Mar. 1974	(22°C)	7½ min.

The lowest air temperature at which copulation was observed was 20°C. In the two pairs which were observed continuously, exploration for oviposition began as soon as copulation was completed.

During exploration and oviposition, the male and female remained in tandem. When they landed on a prospective oviposition site, the female's abdomen was always held straight at first, and then, if there was no disturbance, she would initiate laying movements by testing plant tissues with the tip of her abdomen. Laying began when a suitable site was reached. One egg was deposited in each incision. It was usual for the male to have support for his legs during oviposition (Fig. 3c) but occasionally a pair were seen where the male was entirely supported by the female in the position typical of most coenagriid genera (CORBET, LONGFIELD & MOORE, 1960). The wings of both partners were held together, or slightly apart.

Time spent ovipositing at any one site above water was not more than three minutes on any of five occasions of continuous observation of individual tandem pairs. One pair spent 10 minutes under water while the female oviposited in a *Potamogeton* stem. They descended to a depth of 70 mm below the surface and remained in tandem throughout.

During these timed observations, threat display towards other *X. zealandica* was seen four times, and displacement of a pair by other *X. zealandica* occurred three times. Threat displays by a perching tandem pair towards a single male or another pair of *X. zealandica* included the following:

(1) Wing-warning by male of pair only } while testing or ovipositing
(2) Wing-warning by both male and female }
(3) Ventral abdomen curling by female when abdomen is straight.

These threat displays occurred sometimes, but not always, when a single male or pair of *X. zealandica* settled close to the threatening pair; sometimes pairs oviposited within 20 mm of each other or of single males.

Displacement of tandem pairs by single males occurred more often when there was swarming, the tandem pairs then often joined the swarm.

Termination of the tandem position was observed twice; on one occasion the female remained in the oviposition area and was seized by another male almost immediately, and on the other the female flew directly away from the oviposition area with its abdomen curled ventrally.

A. colensonis

No observations were made of seizure or sperm translocation. Copulation was seen only twice, when air temperatures were 26°C and 35°C. Copulation was only observed for two minutes – the pair being in a hanging position, with the female clasping the male with her legs.

Exploration and oviposition were more distinct behavioural phases in *A. colensonis* than in *X. zealandica* because *A. colensonis*, after selecting an oviposition site, settled there for a long period, laying eggs in groups of one to 12 in each successive incision down the leaf or stem. The male and female remained in tandem throughout oviposition, although on one occasion, when the adult population consisted of three *A. colensonis* within 50 m of the shoreline at Te Puna Lagoon, the only female present oviposited alone for about three hours. In this instance, only three of the 69 eggs laid proved to be fertile. Figure 4b shows a pair of *A. colensonis* laying in *Juncus effusus* stems.

When a pair are in the exploration phase, they are easily disturbed. The female usually rocks her abdomen, then settles with the abdomen straight for a few seconds before testing for oviposition sites.

Concentrated oviposition tended to follow exploration only on days when the weather remained warm and settled. Usually several tandem pairs oviposited together at a single site. For example, five pairs were ovipositing in rushes within 0.3 m of each other at Woodend Pond on 2 February 1974. The longest period of concentrated oviposition observed for any one pair was 50 minutes. During this time the pair were not easily disturbed: when a fly crawled down over them, and another *A. colensonis* pair settled on top of them briefly, the only reaction shown was wing-warning by the male when the female of the disturbing pair touched his head. After 50 minutes, the pair flew off and began exploratory movements nearby.

Timed observations of exploration and oviposition were made on nine occasions. The following interactions with other Zygoptera, except for the wing-warning incident mentioned above, all occurred during the exploratory phase:

	No. times seen
(1) Wing-warning to single *A. colensonis* male	1
Wing-warning to two *A. colensonis* males	1
(2) Displacement by other *A. colensonis*, either single or in tandem	3
(3) Displacement by male *X. zealandica*	1

Termination was observed once, beside an oviposition site, when a tandem pair flew up, separated, and flew in different directions.

OTHER ASPECTS OF ADULT BEHAVIOUR

Newly emerged individuals of both species were easily recognizable by their pale cuticles and pterostigmata. In *X. zealandica*, these tenerals showed a tendency to flutter vertically upwards, and over the oviposition area when disturbed. On many occasions, they were seen being chased by two or three mature males. At these times the immature individuals curled their abdomens ventrally.

Single mature females of either species were seen more commonly outside the oviposition areas than inside them (Tab. II). They perched in similar positions, and showed similar threat display to single males; for example, two *A. colensonis* females were seen chasing and wing-clashing a short distance away from the oviposition area at the Groynes.

Feeding of *X. zealandica* adults was observed on three occasions. Twice a single male in the oviposition area caught a small dipteran on the wing, and then perched to eat it. A female away from the oviposition area was observed eating a small beetle. After five minutes, the beetle had been eaten, and the female cleaned its mouthparts, eyes, abdomen and wings before moving from the perch.

Preening, particularly eye-cleaning, as described by CORBET (9162), was often seen in resting *X. zealandica*, and in a tandem pair during copulation. The only form of preening behaviour observed in *A. colensonis* was the abdominal movement already described in a single male (Tab. V).

At night and during bad weather, adults of both species could be found amongst vegetation near the oviposition areas, hanging parallel to leaves or stems.

DISCUSSION

Adult *X. zealandica* and *A. colensonis* have long flight periods, as indicated by earlier authors, but I have found that these may begin earlier in the spring than has been recorded previously. When temperatures are lower throughout the year, as in the Canterbury high country (Tab. I), the flight period for both species is shorter than when temperatures are warmer, as in lowland areas. In the North Island at Auckland, SCOTT (1963) found that *X. zealandica* had an even longer flight period, lasting until 18 July. The temperature threshold for both *X. zealandica* and *A. colensonis* was 14°C, similar to that found in Anisoptera studied by MOORE (1953).

Both *X. zealandica* and *A. colensonis* resemble the majority of Zygoptera in being active throughout the day (CORBET, 1962). BICK & BICK (1961) mentioned that many species of Lestes are shade-dwellers, and they found *L. disjunctus australis* was most active in the late afternoon. By contrast, *A. colensonis* is neither shade-loving, nor does it tend to be more active in the afternoon than the morning. Reproductive activity, as in *X. zealandica* (SCOTT, 1963), was seen only in sunny areas of a habitat where there was shade. Although further observations would be needed to determine whether there are minor differences in the diurnal activity patterns of *X. zealandica* and *A. colensonis*, it does seem that *A. colensonis* needs higher temperatures and greater light intensities than *X. zealandica* before reproductive activity begins.

Although *X. zealandica* and *A. colensonis* adults had similar diurnal and seasonal flying periods, they differed in their spatial location at and around oviposition areas. All activity of mature *X. zealandica* occurred near the ground but in *A. colensonis* most activity occurred at least 1 m above ground. The fact that teneral *X. zealandica* tend to fly upwards and away from this zone may be a specialized type of behaviour which reduces molestation of tenerals by matures.

Territoriality has often been found among Odonata (KORMONDY, 1961), particularly where there is sexual dimorphism (JOHNSON, 1962) as in both *X. zealandica* and *A. colensonis*. Within the oviposition areas the examination of male behaviour was made considering the possibility that males of each species could maintain a territory defended against intruding Zygoptera. It was found that single males of *X. zealandica* tended to reach greater densities in the oviposition areas than did *A. colensonis* males, and observations on both species showed that there was a tendency for males to return to a specific perching area over a period of time, indicating that some degree of territoriality may be operating. This suggests that male densities here may be controlled, to some extent at least, intrinsically by the animal's behaviour, and within the range of visibility of each species (MOORE, 1953). Disturbance of settled individuals by waving a hand rapidly past a perched adult showed that *X. zealandica* could be disturbed by a movement up to 0.3 m away, and *A. colensonis* by a movement

1 m away. This substantiates the idea that the larger species, *A. colensonis*, may have the greater distance vision for movement perception, but it is not an accurate measurement of perception.

Aggressive reactions such as threat displays and chasing, which restrict the range of flight or displace other Zygoptera (PAJUNEN, 1966) could control density by limiting numbers, particularly of males, within an oviposition area.

At the highest densities of male *A. colensonis*, other males were seen spaced on perches outside oviposition areas and within these areas they also occurred at well-spaced intervals. There was a strong tendency for males to avoid one another, with aggression being confined to occasional wing-warning or a chase and clash. Density of *A. colensonis* males in oviposition areas may thus be controlled to some extent by mutual avoidance and occasional aggression, but more evidence would be needed to confirm this suggestion.

PAJUNEN (1966) found that when population numbers of *Calopteryx virgo* males at an oviposition site were very high, some males tended to be non-territorial. They showed fewer threat displays, were displaced more easily than territorial males, and sometimes flew in swarms. KLÖTZLI (1971) found that males of this species showed lowest territorial activity at high population densities. A similar situation may exist among males of *X. zealandica* where observations of males in populations of medium density indicate that males are territorial, and swarming occurs at high density. In *X. zealandica*, territoriality amongst males does not prevent population numbers from becoming high at the oviposition sites, but when they do the tendency to swarm may be advantageous in lessening the possibility of predation by birds, which could be very high in a dense population of settled insects.

Intraspecific sexual recognition is probably aided by sexual dimorphism (HUDSON, 1904) which is evident in both *X. zealandica* and *A. colensonis*. Flight patterns could also be significant in sexual recognition in either species, as in other Odonata (PAJUNEN, 1964), although there is no evidence for this.

In *X. zealandica* seizure appears to be spontaneous. There is no evident courtship. Threat display inhibits seizure of non-receptive females.

It is probable that seizure in *A. colensonis* is also spontaneous. No special courtship behaviour by males has been noticed. It is not known whether females or males would show aggressive behaviour if seizure was attempted. A female abdomen-raising movement similar to that described by BICK & BICK (1963) for males of *Enallagma civile* as "abdominal bobbing" was seen twice in single *A. colensonis* females near oviposition sites. This could have been a type of soliciting behaviour, although as JOHNSON (1962) suggests, it cannot definitely be interpreted as such without further investigation. The movement was unlikely to have been wing-cleaning, as the wings were slightly separated so that the abdomen did not touch them.

Sperm translocation in *X. zealandica* was seen in tandem pairs, just before copulation. BICK & BICK (1965) observed this in some North American Zygoptera, and later (BICK & BICK, 1972) mentioned that this is probably a general feature of all Zygoptera.

The copulations observed in this study were of similar duration to those observed by HUDSON (1904). They lie within the long duration range characteristic of odonate species which copulate while perching (CORBET, 1962). The only record of copulation time available for *A. colensonis* is that on one occasion it took more than two minutes. This is within the medium range given by CORBET (1962). The scarcity of observations of copulation in *A. colensonis* may be because copulation usually occurs at some distance from the oviposition areas.

Both *X. zealandica* and *A. colensonis* were seen to oviposit in a range of plant species, although *X. zealandica* was apparently more liable to lay in a greater number of different plants, as long as these were in water. *A. colensonis* showed selection of oviposition sites similar to most *Lestes* species (WALKER, 1953; LOIBL, 1958). The fact that certain stems were selected repeatedly for laying in by *A. colensonis* may be advantageous to the species (contrary to what CORBET suggested, 1962) since frequent perforating would kill the stem, making it more probable that it would later fall into the water and so enable the eggs to hatch. Hatching experiments, which will be reported in a later paper, showed that eggs do not need live plant materials in which to develop.

X. zealandica appeared to be very versatile in its behaviour during oviposition, as well as in its selection of oviposition sites. SCOTT (1963) mentions three "methods" of oviposition; tandem above water, single female above water, and underwater oviposition by a tandem pair, which he saw on only one occasion. HUDSON (1904), and PENDERGAST and COWLEY (1966) also mention laying in tandem above and below water; HUDSON timed a lone female laying under water for 30 minutes. Observations made in my study confirm that laying usually occurs in tandem above water. The longest time spent by *X. zealandica* pairs in concentrated oviposition at a single site was when oviposition was under water, perhaps because of the absence of interactions with other individuals when under water.

In a comparison of *Enallagma* species BICK & HORNUFF (1966) found that all species were very "plastic" in their oviposition behaviour, but that when different species occurred together in a habitat, they adopted separate laying sites and types of oviposition behaviour. Similarly BICK & BICK (1972) found that two species of *Argia* occurring together had spatially separated laying sites. It would be interesting to examine the oviposition behaviour of *X. zealandica* at North Island habitats where the Australian migrant *Ischnura aurora* Br. occurs as well, to see whether spatial separation of oviposition sites occurs.

In contrast to *X. zealandica*, *A. colensonis* pairs settled for a long period of oviposition at one site. This can be partly accounted for by the fact that it would not take *X. zealandica* females as long to insert single eggs into each incision as it would take *A. colensonis* females to place a group of eggs into each incision. *A. colensonis* pairs, however, were very difficult to disturb during oviposition, whereas *X. zealandica* pairs interacted periodically with other adults during oviposition. *A. colensonis* also tolerated other conspecific pairs laying nearby, but single males would not tolerate other individuals as close. Thus *A. colensonis* would tolerate communal laying, with very little mutual interaction once concentrated laying had begun.

Aggression, both in single males and tandem pairs, was seen more often in the oviposition area in *X. zealandica* than in *A. colensonis*. As shown in Table V, aggression occurred five times in the two observations of single male *X. zealandica* which were made in dense populations, and six times during the five observations of single male *A. colensonis* made in dense populations, when interactions were most likely to occur. Therefore, when related to the number of observations, *A. colensonis* showed less aggression than *X. zealandica*. Similarly, during oviposition, aggression occurred four times during 39 minutes of observation of *X. zealandica*, and only twice during the longer period of 3 hours 28 minutes of observation of *A. colensonis*. This higher incidence of aggression in *X. zealandica* could be caused by competition for females and for oviposition sites, which would be greater in the denser adult populations of this species.

It has been shown that although adults of *X. zealandica* and *A. colensonis* are often present together at a habitat in similar periods both seasonally and diurnally, they are separated spatially by their choice of oviposition sites. They also show differences in aggressiveness and oviposition behaviour. In many aspects, both species resemble overseas genera from the same families.

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