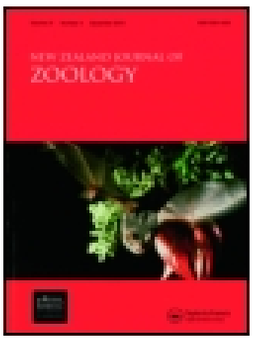

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Seasonal dissociation, habitat selection, population structure, and adult behavior in New Zealand *Lycaena* (Lepidoptera: Lycaenidae)

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The distribution, flight periods, and food plants of *Lycaena boldenarum* (White), *L. salustius* (Fabricius), and *L. feredayi* (Bates) are described, and *L. feredayi* is recorded for the first time from Central Otago. In sympatry, *L. feredayi* and *L. salustius* are seasonally dissociated in peak abundance when only one larval food plant (*Muehlenbeckia australis*) is present. In Central Otago habitat selection, correlated with larval food plants, appears to be mutually exclusive between *L. boldenarum* and the other two species, but only partially so between *L. feredayi* and *L. salustius*. Capture/recapture data show that all three species are sedentary, with adult life spans averaging 10 days in *L. salustius* and about 7 days in *L. feredayi* and *L. boldenarum*. Field sex ratios of the three species favour males. Flight, oviposition, and encounter behaviour of the three species are described. Competition in sympatry or different environmental conditions in previous allopatry might explain their ecological separation.

INTRODUCTION

Lycaena salustius (Fabricius), *L. feredayi* (Bates), and *L. boldenarum* (White) are common insects, yet little is known about their flight periods and distributions. Descriptions of the three species are given by Hudson (1928), and notes on life history and distribution can be found in Hudson (1928, 1939, 1950). The only recent work on the ecology of the three species deals with flight periods and sex ratios (Flux 1968).

L. salustius is found throughout the North and South Islands in a wide variety of habitats, including coastal cliffs and sand dunes, podocarp/broadleaf and *Nothofagus* forest, and lowland and subalpine scrub and tussock grassland. This species has been recorded from the Three Kings Islands and Coppermine Island (J. S. Dugdale, pers. comm.), and from Little Barrier Island, Kapiti Island, and Stephens Island (specimens in National Museum collection). Larval food plants are present on both Stewart Island and the Chatham Islands, but *L. salustius* has yet to be recorded from either (J. S. Dugdale, pers. comm.). *L. salustius* is known to be widely distributed, but *L. feredayi* is generally considered to be confined to forests, having been recorded from various localities in both the North and South Islands (Hudson 1928, Gibbs 1961). During December 1969, I discovered *L. feredayi* flying amongst scrub in tussock country in three localities on the eastern side of the Dunstan Mts, Central Otago, at 500–700 m a.s.l., and also amongst kanuka (*Leptospermum ericoides*) scrub on sandhills near Waikanae, Wellington. *L. boldenarum* occurs in the Wairarapa, Central Plateau, and Hawkes Bay areas of the North Island and over most of the South Island. It is abundant in river and stream beds, and also occurs in tussock grassland and above the timber line where the vegetation is low and open. Both *L. boldenarum* and *L. salustius* are found between sea level and 2000 m (Flux 1968), but the upper altitude limits of *L. feredayi* are at present unknown.

In all localities where I have observed *L. feredayi*, *L. salustius* has also been present. These two species are sympatric over a large part, if not all, of the range of *L. feredayi*; *L. salustius* and *L. boldenarum* are sympatric in certain areas of the North Island and over most of the South Island. In Central Otago all three species have been observed flying within 20 m of each other.

Simmonds (*in* Hudson 1928) considered that *L. boldenarum* resembles an ancestral *Lycaena* species that established itself in New Zealand and then speciated into *L. boldenarum* and *L. salustius*. Subsequently several varieties diverged from these two species, of which *L. feredayi* was the most stable. Klots (1936), on the other hand, in his extensive study of the genitalia of *Lycaena* species, considered that "no definite relationship of *L. boldenarum* to other Coppers can be traced with any security". Furthermore, he stated that *L. feredayi* and *L. salustius* "show no particular relationship to *boldenarum*". Morphological relationships and intraspecific variation of both adult and immature stages are being studied, and preliminary work suggests that *L. feredayi* and *L. salustius* are more closely related to each other than either is to *L. boldenarum* (Craw, in prep.). Ecological relationships of the adults of the three species are considered in this paper.

Study Areas and Methods

At Linden (41°10′S,174°51′E), both *L. feredayi* and *L. salustius* are present, and adults and larvae have the same food plants. Flux (1968) found at Lower Hutt that the two species as adults had different times of peak abundance. During 1972–73, I measured their flight periods at Linden, where the vegetation of the study area was second-growth native bush with *Beilschmiedia tawa* and *Dysoxylum spectabile* dominant. The larval food plant *Muehlenbeckia australis* is common throughout the bush and is frequented by *L. feredayi* and *L. salustius*, especially when growing in association with *Parsonia heterophylla* and *Metrosideros perforata*, on which the adults feed. The only other flower on which the adults were seen to feed often was the introduced watercress *Rorippa nasturtium-aquaticum*. Adult butterflies were counted on average on 4 days in each 2-week period from late November 1972 to early April 1973. In order to ensure that no butterfly was counted twice on any one day, individuals were caught and marked with nail varnish before release.

Intensive observation and collection of the three species during December 1969 and January 1970, and a quantitative study of their abundance in different vegetation types at Woolshed Creek, Dunstan Mts, Central Otago in February 1974, provided data on habitat selection. Eight areas in Central Otago with different vegetation types were studied: areas A–C were at Woolshed Creek (44°56′S,169°42′E, 600–650 m a.s.l.); D–H were at Prospect Farm (44°57′S,169°43′E, 500 m a.s.l.). Areas A and B were collected in for 1 hour each day on 1–3 February, and area C for 1 hour each day on 2 and 3 February. Areas D–G were collected in either for 1 hour or until no more butterflies were seen each day on 5, 6, 9, and 11–13 February, and area H was collected in similarly on 11–13 February. Captured butterflies were placed individually in glass vials. At the end of each collection period butterflies were sexed, marked with nail varnish, and released in the area of capture.

The vegetation types of the collection areas are indicated in Table 1. Area A was separated from B by a band of *Festuca novae-zelandiae* and *Discaria toumatou* about 15 m wide. Area G was approximately 10 m east of F, separated by a stream and a 10-m-wide band of *Carex* sp. and *Festuca novae-zelandiae*. Area H was about 50 m north-west of D and about 150 m north-west of F.

TABLE 1—Vegetation types of Central Otago collecting areas for *Lycaena* spp.; selected plant species associations, excluding food-plant species (X, distributed throughout; (X), scattered plants)

	Area, and dimensions (m)							
	A 30×15	B 40×20	C 40×20	D 50×20	E 50×20	F 25×6	G 15×8	H 15×10
Raoulia australis	X					X	X	
Festuca novae-zelandiae	X		X	X	X	(X)	(X)	(X)
Discaria toumatou		X	X	X	X	X		
Carmichaelia petriei		X		X	X			
Olearia odorata		X						
Hypolepis millefolium (12167)		X						
Polystichum vestitum (12163)		X						
Rubus schmidelioides (12162)		X						
Wahlenbergia albomarginata			X					
Blechnum pennamaria			X					
Carex sp.			X	X	X	(X)	(X)	
Clematis marata (12166)					X			
Geranium sessiliflorum								X
Scleranthus uniflorus								X

In the two studies reported, over 1000 individual *Lycaena* butterflies were marked and released. A few damaged by marking were destroyed. Some butterflies were recaptured 2 weeks after marking; all those recaptured were flying normally.

During 1969–74, several populations of the three *Lycaena* species have been observed and adult behaviour noted, particularly those aspects relevant to the quantitative studies. More detailed observations were made during November and December 1973 and January 1974 at Linden. On 10 days in that period, I spent from 4 to 8 hours continuously observing the *L. feredayi* and *L. salustius* populations, noting the number, sex, and behaviour of individuals of both species in each hourly period.

Specimens were collected of all plants that could not be positively identified in the field, and some of these are deposited in the herbarium of the Botany Department, Victoria University, Wellington. These voucher specimens are indicated by a number at their first mention in the text or tables.

RESULTS

LARVAL FOOD PLANTS

The larval food plants of the three species are all Polygonaceae. Larvae of *L. salustius* were recorded as occurring on *Muehlenbeckia* by Hudson (1928), but no species were mentioned. Purdie (1882) found *L. salustius* eggs on the introduced weeds *Rumex acetosella* and *R. obtusifolius*. Despite extensive searching I have never found *L. salustius* eggs or larvae on these or any other species of introduced Polygonaceae. In the Wellington area forest populations of *L. salustius* are associated with *Muehlenbeckia australis*, whereas Wellington coastal and Central Otago tussock grassland populations are associated with *M. complexa*. On Colonial Knob, Wellington, where coastal and forest forms of *L. salustius* fly together, both *M. australis* and *M. complexa* grow. Larvae of *L. feredayi* appear to be restricted to *M. australis* (Flux 1968), though one larva of this species was found on *Rumex acetosa* (Walker 1904). *M. australis* grows in most places where I have observed *L. feredayi*, including two of the three known Central Otago localities; in the third, the hybrid *M. australis* × *M. complexa* (12165) grows next to normal *M. complexa*. *Lycaena boldenarum* larvae were recorded from a small-leaved species of *Muehlenbeckia* by Hudson (1928). This

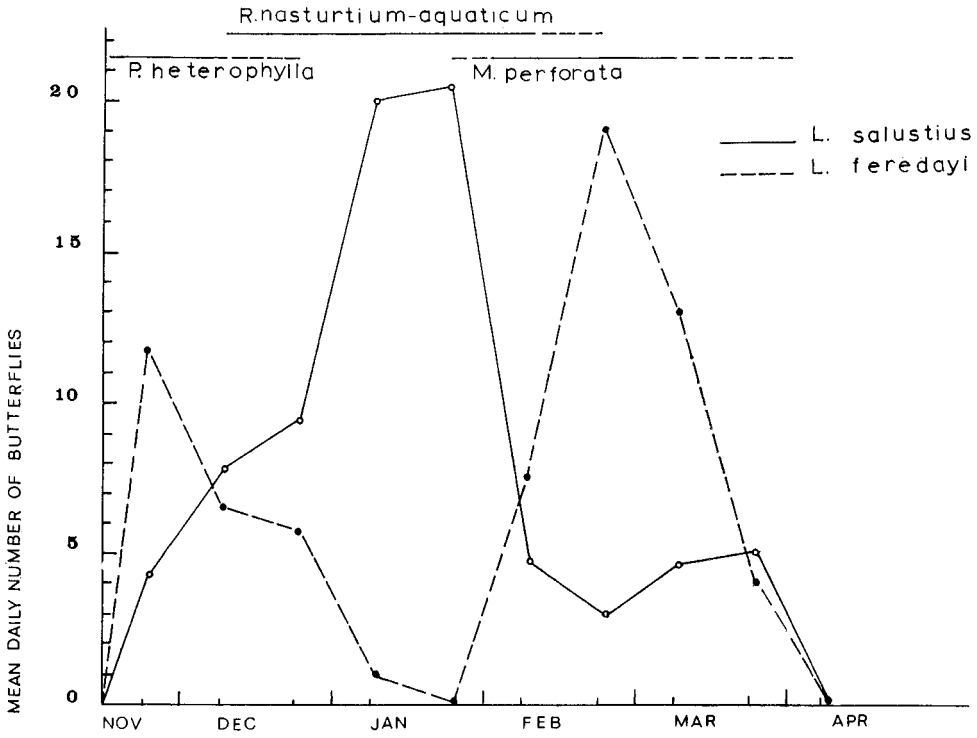

FIG. 1—Flight periods of *Lycaena feredayi* and *L. salustius* at Linden, 1972–73. Flowering periods of nectar sources at top of graph (heavy line indicates peak flowering period).

appears to be *M. axillaris*, as I have found eggs and larvae of *L. boldenarum* on this species in Central Otago and at Island Pass, Upper Wairau Valley, and on *Rumex flexuosus* in Central Otago.

In the laboratory, larvae of all three species will feed on species of *Muehlenbeckia* other than those on which they are found in the field. However, the larvae are extremely sedentary until just before pupation, and their food plant will be dictated by the adult females, which have never been observed to oviposit on food plants other than those mentioned above.

SEASONAL DISSOCIATION OF *L. feredayi* AND *L. salustius* AT LINDEN

L. feredayi had two broods, the first in late November-December and the second in February-March (Fig. 1). During early January *L. feredayi* was very scarce, the few individuals present being worn and tattered. In late January this species was absent from the study area, and during this month *L. salustius* reached peak abundance. When the second brood of *L. feredayi* was flying in peak numbers during late February, the few *L. salustius* that were present appeared old and tattered, but fresh insects appeared on the wing in early March. By late March *L. salustius* was slightly more numerous than *L. feredayi*, and all individuals were fresh, whereas those of *L. feredayi* were old and worn. Observations made in the same area in 1973–74 revealed a pattern of seasonal abundance for the two species similar to that found in 1972–73.

Field observations and laboratory rearing of the larvae of *L. feredayi* have established that the second brood results from eggs laid in late November and December; the larvae feed during December and early January and pupate in January to produce the February

TABLE 2—Food plants of larval and adult *Lycaena* butterflies, and numbers of the three species caught, in the Central Otago collecting areas (—, nil)

	Area							
	A	B	C	D	E	F	G	H
LARVAL FOOD PLANTS								
Muehlenbeckia australis		X						
axillaris	X					X	X	
complexa		X	X	X	X			
australis × *complexa*					X			
Rumex flexuosus								X
ADULT NECTAR SOURCES								
Muehlenbeckia axillaris	X					X	X	
Circium sp.		X	X	X	X			X
Hypochoeris radicata								
NOS OF BUTTERFLIES CAUGHT								
Lycaena boldenarum	126	3	—	1	—	83	96	35
salustius	2	70	23	20	22	—	—	—
feredayi	—	8	—	—	1	—	—	—

butterflies. Two of 26 larvae reared from eggs laid by the first brood ceased feeding when quite small, and assumed a coloration similar to that described by Hudson (1950) for the larvae of this species before 'hibernation' in the autumn. These two larvae remained alive amongst withered leaves of *M. australis*, without feeding or moving, for 1 month, but eventually died from desiccation. Most of the larvae hatching from eggs laid by the first brood pupate to emerge as butterflies in the same season. Apparently some do not pupate until after the winter, along with larvae from eggs laid by the second brood, to emerge as butterflies of the first brood the following season.

Flowering periods of the three plants that the butterflies mainly feed on coincided with the peak abundance of *L. feredayi* and *L. salustius* to some extent (Fig. 1). The flowering periods of the two native plants used as nectar sources by the butterflies (*Parsonia heterophylla* and *Metrosideros perforata*) coincide with the November-December and February-March broods of *L. feredayi*. It is of interest that the only nectar source available during most of January to *L. salustius* (*R. nasturtium-aquaticum*) is an introduced plant.

HABITAT SELECTION IN CENTRAL OTAGO

The numbers of individual butterflies of all three species caught in the eight collecting areas in Central Otago during February 1974 are given in Table 2. All recaptures, except seven *L. boldernarum*, were made in the original capture areas. It is clear from the table that adults of the three species occur almost exclusively in the vegetation type containing the preferred larval food plant. During the entire study, 340 *L. boldenarum* were captured in 4 areas containing the larval food plants *M. axillaris* or *R. flexuosus*, and only 4 were caught in areas not containing these plants. Similarly, 135 *L. salustius* were caught where the larval food plant *M. complexa* grew, and only 2 elsewhere. Eight *L. feredayi* were caught in an area containing *M. australis*, and one where the hybrid *M. australis* × *M. complexa* grew.

Qualitative observations in December 1969, January 1970, and February 1974 support the above quantitative data. *L. boldenarum* is common, and in some places abundant, in the Woolshed Creek area on open ground in creek bottoms, around rocky outcrops, slips, and eroded ground, and in open tussock grassland where *M. axillaris* and *R. flexuosus* grow. *L. salustius* is found amongst scrub in creek bottoms and tussock grassland where

M. complexa grows, particularly in damp hollows and gullies. In the Woolshed Creek area, *L. feredayi* has never been observed flying more than 10 m away from *M. australis* or its hybrid with *M. complexa*.

The Central Otago Population of *L. feredayi*

L. feredayi is at present known in Central Otago from three localities within 4.8 km of each other; two of these localities are described above. The species is most abundant in the third locality, located along the banks of a small stream entering Woolshed Creek. The main vegetation along the stream is closed scrub with *Discaria toumatou*, *Carmichaelia petriei*, *Olearia odorata*, *Aristotelia fructicosa*, and *Coprosma propinqua* co-dominant. *Leptospermum ericoides* and *Coriaria sarmentosa* (12164) are common on slopes near the stream. Other common plants are *Polystichum vestitum* and *Hypolepis millefolium* in the ground layer, and the lianes *Clematis marata* and *Rubus schmiedelioides*. Both *Muehlenbeckia australis* and *M. complexa* are common along the banks of the stream.

Botanical evidence suggests the presence of forest containing *Podocarpus halli* and *Nothofagus menziesii* in Central Otago up to about the 12th century A.D. (Wells 1972). Although *P. halli* has not been found in Woolshed Creek, stands of this species are known from the eastern side of the Dunstan Mts both north (C. Craw, pers. comm.) and south (Wells 1972) of Woolshed Creek. *M. australis* has been recorded from a stand of *N. menziesii* and *P. halli* on the Pisa Range (Wells 1972). Considering both the botanical evidence and the usual forest habitat preferences of *L. feredayi*, it is highly probable that the Central Otago population is a relict that has survived the destruction of forests in the area.

Population Structure

Movement and dispersal. The study area at Linden is surrounded by pasture, wasteland, and housing. No marked *L. feredayi* or *L. salustius* were seen in these areas during the study period, and they have rarely been seen in the areas surrounding the bush during 6 years' observation. Even within the bush individual butterflies rarely moved more than 150 m, clearly indicating that both species have a small home range. Data obtained in 1972–73 revealed that the butterflies were sedentary, and in 1974 an experiment at Linden determined that *L. salustius* has a preferential return response. On 16 and 23 January, 14 and 9 male *L. salustius* were captured over a 15×3-m plot in a clearing in the bush where they were feeding on *R. nasturtium-aquaticum*. These butterflies were marked and then released in a small gully about 100 m NW of the capture site, and separated from it by wasteland and pasture. Twelve were recaptured in the original area, and none was recaptured or seen at the release site, indicating a strong preferential return response, as in the lycaenid *Philotes sonorensis* Felder & Felder (Keller *et al.* 1966).

In Central Otago the number of butterflies did not decrease with collecting in areas A and B, but this was probably due to the large numbers present in these two areas that could not be sampled adequately by one worker. The numbers of butterflies flying in areas C–H decreased towards the end of each collecting period, evidence that they were not entering the areas from the surrounding vegetation. Similar decreases in *L. feredayi* and *L. salustius* as collecting progresses have been observed at Linden and Makara, Wellington.

The sedentary nature of *L. boldenarum* and *L. salustius* is reflected in the capture/recapture data. Over the study period in Central Otago, 38% of the *L. salustius* captured in areas D and E were recaptured at least once in the original capture area, and no marked ones were caught away from their initial capture site. On some days recapture percentages were far

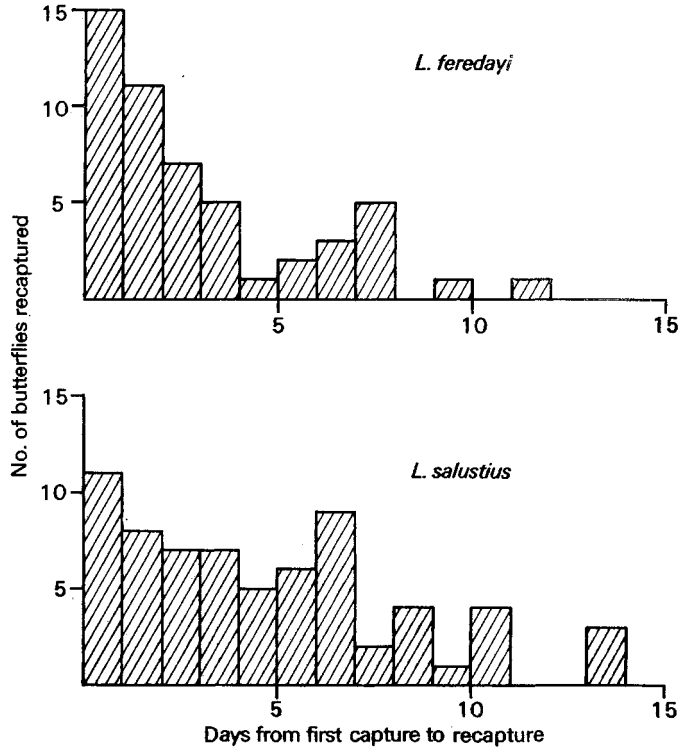

FIG. 2—Minimum life spans of marked *Lycaena* butterflies at Linden, Wellington, 1972–73, from capture/recapture data.

greater than the total recapture percentage for the study period. For example, on 5 February eight *L. salustius* (4 males, 4 females) were captured and marked in area D. The following day five of these (3 males, 2 females) were recaptured in area D. Of 214 *L. boldenarum* marked and released in areas F–H, 79 (37%) were recaptured in the original capture area, and only 7 (3.3%) elsewhere; even these had moved only 10–15 m. Clearly the 10-m-thick band of *Carex* sp. and *F. novae-zelandiae* separating areas F and G was an effective barrier to free exchange between them. There was no exchange of *L. boldenarum* individuals between areas F or G and area H in 3 days' collecting, and considering the limited exchange of individuals between areas only 10 m apart, movement between these more widely separated areas must occur very rarely. Individuals of *L. boldenarum* have the potential for such movement, because the one caught in area D presumably had flown at least 50 m, the distance to the nearest *L. boldenarum* colony in area H.

Life span. The capture/recapture data for *L. feredayi* and *L. salustius* at Linden in 1972–73 permit a crude estimate of adult life span. No distinction was made during marking between fresh and worn butterflies, so the average life expectancy on emergence would be twice the observed duration (Flux 1968). For *L. feredayi* this is 7 days and for *L. salustius* 10.4 days (Fig. 2). Flux's (1968) data for smaller samples showed a similar trend, with life expectancies calculated in the same way of 6 and 8 days respectively.

Capture/recapture data for *L. boldenarum* and *L. salustius* in Central Otago do not extend over a long enough period to be analysed as above, but very few butterflies were recaptured more than 5 days after first capture. Most recaptures were made 1–3 days after original capture. This suggests that *L. boldenarum* and *L. salustius* in Central Otago have

	♂	♀	%♂
November	13	4	76
December	64	22	74
January	122	43	74
February	30	10	75
March	21	3	88
Totals	250	82	75.3

TABLE 3—Monthly sex ratios of *Lycaena salustius* at Linden, Wellington, 1972–73

similar adult life spans to *L. feredayi* at Linden, i.e., about 7 days. Short adult life spans, ranging from 2.8 to 12.1 days, have been recorded in the field for six species of North American and European butterfly (Benson & Emmel 1973).

Sex ratio. The monthly sex ratios for *L. salustius* at Linden in 1972–73 remained fairly constant from November to March, the total percentage males for the 5 months being 75.3% (Table 3). In Central Otago the percentage of males for *L. boldenarum* and *L. feredayi* was slightly above 50%, and for *L. salustius* just above 60% (Table 4). Sex ratios of *L. feredayi* at Linden, 1972–73, are not available, because it is difficult to accurately sex this species in the net without disturbing and damaging the butterflies. By placing butterflies in glass vials and examining the external genitalia, sex ratios were obtained in February 1974 for the second brood of *L. feredayi*. A sample captured and marked on 17, 20, and 22 February comprised 45 males and 33 females, i.e., 57.7% male.

ADULT BEHAVIOUR

Flight behaviour. Butterflies normally fly only in sunshine. Flight activity in all three species in Wellington and Central Otago occurs between 0730 and 1800 h, with peak flight activity from about 0900 to 1500 h. Males of all three species fly fast in a zig-zag fashion, stopping frequently to bask, feed, or court females. After feeding at an inflorescence, males often fly up to 2 m before feeding again, and feeding usually alternates with basking, courtship, and intra- and interspecific encounter behaviour. The flight of females of the three species is slower and more linear than that of the males. They spend longer feeding, and usually fly direct to the nearest inflorescence to feed further. At Linden, females of *L. feredayi* and *L. salustius* feed continuously for 5–30 min.

Both sexes of *L. boldenarum* rarely fly higher than about 30 cm, and tussock and coastal *L. salustius* seldom more than 2 m above ground level. In forest, *L. salustius* and *L. feredayi* usually fly 1–5 m above the ground. These heights are correlated with the height of the vegetation each species inhabits.

Males of *L. boldenarum* frequently fed at damp mud and sand along with males of *Argyrophenga antipodium* Doubleday and *Zizina oxleyi* (Felder) in Central Otago. *L. feredayi* and *L. salustius* have been seen to feed only at flowers.

Oviposition behaviour. Oviposition behaviour of *L. feredayi* and *L. salustius* was studied at Linden, and that of *L. boldenarum* in Central Otago. *L. feredayi* and *L. salustius* lay eggs singly on the undersides of *M. australis* leaves. The females walk along the stem of the plant and oviposit on the older leaves 5–10 cm from the young growth. *L. feredayi* females have been observed to lay only one egg per leaf, but on 8 of 31 leaves examined on which *L. feredayi* eggs were present, from 2 to 6 were found. It is not known whether a single female laid these eggs successively in one or several oviposition sequences, or several females laid these eggs singly on the same leaf. Only one egg per leaf was laid by *L. salustius* in a small sample ($n = 10$). Eggs of *L. feredayi* ($n = 54$) and *L. salustius* ($n = 10$) were

TABLE 4—Sex ratios of *Lycaena* butterflies in Central Otago, February 1974

	♂	♀	%♂
L. boldenarum			
Woolshed Creek	70	59	54.3
Prospect Farm	115	98	53.9
L. salustius			
Woolshed Creek	59	36	62.1
Prospect Farm	26	16	61.9
L. feredayi	6	5	54.5

laid 0.5–6 mm from the nearest leaf edge. Females of both species oviposit on *M. australis* plants close to the main concentrations of nectar.

L. salustius females are often observed flying low over the ground in small clearings in the bush, where males of *L. salustius* and both sexes of *L. feredayi* are never found. The significance of this behaviour is unknown, though possibly the females were searching for oviposition sites. Differential response to forest microclimate between females of *L. salustius* and *L. feredayi* is also possible. *L. salustius* females are thus more vagile and widely dispersed at Linden than males of *L. salustius* and both sexes of *L. feredayi*, and this behaviour might explain the more divergent sex ratio in this species.

Ovipositing *L. boldenarum* females crawl over the low-growing *M. axillaris* for up to 10 cm. Eggs are laid singly on the undersides of leaves as well as on the main stem of the plant. Oviposition behaviour of *L. boldenarum* on *R. flexuosus* has not been observed, but eggs have been found on the undersides of leaves up to 15 cm above ground level.

Courtship. Courtship in *L. feredayi* and *L. salustius* occurs between 1000 and 1700 h, and in *L. boldenarum* between 0900 and 1700 h. Detailed observations on courtship are not possible, because successful courtship sequences leading to mating have yet to be seen in *L. feredayi* and *L. salustius*. As would be expected, courtship differences serve as an effective isolating mechanism between *L. feredayi* and *L. salustius*. When the two species occur in the same vegetation type, males of one species have been seen to approach only briefly females of the other species. I have no records of interspecific courtship beyond the earliest phase, nor of mating in these two species. *L. boldenarum* is kept out of contact with the other species in Central Otago by habitat selection. However, a female *L. salustius* artificially introduced into an area containing *L. boldenarum* was courted for 5 min by several males, and copulation was attempted.

Inter- and intraspecific encounter behaviour. Encounters between males of the same species of *Lycaena*, and between males of *L. feredayi* and *L. salustius*, occur frequently and may serve to distribute males evenly over favourable habitat, as suggested by Sharp & Parks (1973) for the lycaenid *Plebejus saepiolus* Boisduval. Three encounters between males of *L. boldenarum* and *L. salustius* were observed in Central Otago. Apart from the two *L. salustius* captured in area A (Table 3), three male *L. salustius* were observed in this area during 1–3 February. All entered area A from the direction of area B, and were immediately chased by several male *L. boldenarum* to the edge of area A, but no further. Interspecific encounters in these two species may thus act as a mechanism in maintaining habitat selection.

DISCUSSION

A central concept of current evolutionary and ecological theory is the competitive exclusion principle, viz., "two species cannot indefinitely coexist in the same locality if they have

identical ecological requirements" (Mayr 1970). Ecological segregation has been established in a number of sympatric, closely related, and ecolocgially similar butterfly species (Owen 1959, 1971). In butterflies, this usually takes the form of differences in habitat, larval or adult food sources, or seasonal abundance of adults. However, ecological differences between related sympatric species are not necessarily due to interspecific competition, since they could have arisen in response to different selective regimes in allopatry (preceding sympatry). Clench (1967) has argued that temporal dissociations (i.e., seasonal displacement in peak abundance) arose as an adaptation to reduce competition for adult food. He discovered that sympatric hesperid butterflies rarely showed an overlap in their flight periods of more than a week. Competition for nectar was claimed to be responsible for the elimination of the overlap in the flight periods of the different species.

L. feredayi and *L. salustius* were found to be seasonally dissociated in peak abundance at Linden. However, because of the considerable overlap in their flight periods and the lack of any definite evidence that competition for food occurs between adults, this is not claimed to be an example of competitive exclusion.

Scott (1973), in a study of convergence in the population biology of two unrelated species of butterfly, suggested that competition may be uncommon in temperate habitats. It is difficult to accept that competition for nectar might occur amongst butterflies in New Zealand when the paucity of species (four at Linden, five in Central Otago) feeding at nectar sources is compared with the abundance of these sources. Similarly, it is highly improbable that larval competition for food occurs, because of its abundance. Moreover, *Muehlenbeckia australis* at Linden supports two species of moth larvae which feed on the same types of leaves as *Lycaena* larvae. On the other hand, the limited evidence on the flight periods of *L. feredayi* and *L. salustius* in the presence of two larval food plants is suggestive. At Linden and Lower Hutt (Flux 1968), where *L. feredayi* and *L. salustius* are sympatric in the presence of one larval food plant, they are seasonally dissociated in peak abundance. This may not hold in other parts of their range. The two species are sympatric in the presence of two larval food plants at Peka Peka, near Waikanae, and at Woolshed Creek, Dunstan Mts. Fresh and worn individuals of *L. feredayi* were found at the first locality during early and late January and at the latter locality in early February. In both localities *L. salustius* was common. Young larvae of *L. feredayi*, which presumably hatched from eggs laid around the middle of January, were found at Woolshed Creek on 1 February 1974.

In Central Otago, adult habitat preferences appear to be correlated with larval food plant preferences. It appears that captive larvae will readily accept species of *Muehlenbeckia* other than those on which they are found in the wild. Observations in Central Otago revealed that females of *L. feredayi* oviposited on *M. australis* and those of *L. salustius* on *M. complexa* when the two species occurred in the same vegetation type. Furthermore, only one *Lycaena* species occurred in a particular vegetation type with one larval food plant, but with two larval food plants two *Lycaena* species occurred in the same vegetation type. Despite the apparent superabundance of larval food mentioned above, the evidence from the habitat selection study supports the argument that competition for larval food is prevented by spatial dissociation of the three species. However, without further work, particularly on larval food plants and the flight period of *L. feredayi*, the possible role of environmental factors in previous allopatry as an explanation for the ecological differences between the three species cannot be ignored.

Previous reports of the flight periods of the three species are summarised in Table 5. Flux (1968) suggested that the wide variation in the recorded flight periods of *L. feredayi* and *L. salustius* was possibly due to the fact that they were studied in different localities.

TABLE 5—Previous reports of the flight periods of *Lycaena* spp. in New Zealand (..., not applicable)

Reference	Locality	*L. salustius*	*L. feredayi*	*L. boldenarum*
Fereday 1878	Canterbury	Dec.–Mar.	Dec.–Mar.	Dec.–Feb.
Philpott 1900	Southland	Nov.–Feb.	...	...
,, 1917	Otago	Nov.–Feb.	...	Nov.–Mar.
Lindsay 1927	Canterbury	Jan.–Mar.	Jan.–Mar.	...
Hudson 1928	Unspecified	Nov.–Apr.	Nov.–Feb.	Nov.–Mar.
Patterson 1930	Whangarei	Nov.–Dec.	...	...
Dick 1940	Cass	Nov.–Apr.	...	Nov.–Mar.
Flux 1968	Lower Hutt	Nov.–Apr.	Nov.–Apr.	...
,, ,,	St. Arnaud	Nov.–Apr.	...	Oct.–Apr.

Fereday (1878) and Lindsay (1927) both observed the two species in areas of bush near Christchurch, yet Fereday gives December to March as the flight period of both species while Lindsay states that they fly from January to March. *L. salustius* flies in April at Cass, St. Arnaud, and (in some years) Lower Hutt, but usually not at Linden, although I have one record of a fresh male *L. salustius* flying there on 9 May 1974. Simmonds (1907) has recorded fresh *L. salustius* females at Titahi Bay, only a few miles from Linden, in the middle of winter. The absence of butterflies at Linden in April is most probably due to lack of nectar sources. While physical environmental factors may account for some of the differences between localities in the flight periods of the two species, the suggestion (Clench 1967) that the availability of adult food regulates butterfly populations is worthy of consideration.

The sex ratio of *L. salustius* did not show the seasonal decline in the percentage of males reported by Flux (1968) at Normandale. Instead, the sex ratio at Linden was approximately 3 males : 1 female over most of the flight period of this species. Marked disparities in the sex ratio of a butterfly species are usually attributed to behavioural differences between the sexes (e.g., Sharp & Parks 1973), and this appears to be the most probable explanation for the sex ratio of *L. salustius* at Linden. Scali & Masetti (1973), however, have shown for the satyrid *Maniola jurtina* that females are more numerous than males up to the fourth larval instar, after which differential elimination of the females results in an excess of adult males. Whether *L. salustius* has a normal or abnormal sex ratio can best be answered by rearing larvae from eggs laid by a single female.

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