APPARENT SITE AFFINITY IN *SCELIO PARVICORNIS* DODD AND *SCELIO IMPROCERUS* DODD (HYMENOPTERA: SCELIIONIDAE) IN PASTURES INFESTED WITH *PHAULACRIDIUM VITTATUM* (SJÖSTEDT) (ORTHOPTERA: ACRIDIDAE)

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Abstract
The abundance of adult *Scelio parvicornis* and *S. improcerus* in a pasture site in the Southern Tablelands of New South Wales exhibited stable spatial variation commensurate with site affinity. Both species were abundant on an uncultivated, lightly timbered granite knoll supporting native grasses and introduced broad leaved weeds but virtually absent in extensive improved pasture skirting the knoll. The cause of the site affinity is unknown but was possibly associated with biotic factors such as a seasonally stable host population and reduced competition from other parasitoids. The site affinity was also coincident with the habitat of *Phaulacridium vittatum* in climax savanna woodland pre-european settlement and may represent an anachronistic, instinctual habitat preference. Although parasitism by scelionids was secondary to that of mermithid nematodes in influencing host population trends at all sites, the supplementary parasitism by scelionids could be important in habitats less favourable for mermithid nematodes. An inverse density dependence was apparent which could result in localised host extinction, extending the duration of the recessionary phase of the host outbreak cycle so limiting the frequency of grasshopper outbreaks.

Introduction
The role of scelionid egg parasites in the population dynamics of wingless grasshopper, *Phaulacridium vittatum* (Sjöstedt), has been little studied in tableland regions: Clark (1967) found a *Scelio* sp. at levels of <20% in the Canberra-Yass district at the end of an outbreak and Baker et al. (in press) recorded *Scelio* spp. at a mean parasitism rate of 33.5% in tableland districts, also at the end of an outbreak. The relative abundance of scelionid species has been assessed by sweep net catches made during an outbreak of *P. vittatum* (Baker et al. 1985) and the generally low abundance of species parasitic on *P. vittatum* suggested a minor role in the population dynamics of this host. However they may have a more important role in the population dynamics of other acridid species in the tablelands (Baker et al. 1985, Baker and Dysart 1992, Baker and Pigott 1993). Factors such as parasitism by mermithid nematodes (Baker and Capinera 1995) and reduced oviposition under dry conditions (Baker et al. 1993) are generally considered of greater significance than scelionids in influencing the population dynamics of *P. vittatum*.

The observations reported in this paper were made during a long term study of the population dynamics of *P. vittatum* in tableland districts of New South Wales.

Methods
Sampling of fixed sites in pastures in the Southern Tablelands was undertaken...
at irregular intervals throughout the season (October-April) between 1989-90 and 1994-95 seasons. The data presented in this paper are from site #14, 10 km south of Captains Flat [36°41'S, 149°27'E] at 1050 m in the Southern Tablelands of New South Wales. The site consisted of an elevated saddle connecting the main range with a granite knoll. The knoll was covered in decomposing, exposed granite tors and lightly timbered (Figs 1-2) with unimproved vegetation (Fig 3) consisting of introduced broad leaved weeds: Lamb's tongue *Plantago lanceolata* L., sorrel *Rumex acetosella* L., Aaron's rod *Verbascum thapsus* L., native tussock grasses (*Stipa* spp.) and the naturalised grass, rat tail fescue *Vulpia bromoides* (L.) S.F. Gray. Skirting the knoll was improved pasture (Figs 1-2) following cultivation in the 1987/88 season and planted to white clover *Trifolium repens* L. and perennial rye grass *Lolium perenne* L. (Fig 4). Samples were taken by making 120 low sweeps with a 45 cm net. Acridids were scored for species and stage and then dissected to determine parasitism. Acridid density was calculated from a prior calibration of sweep net efficiency. Three sub-samples were taken: 1, in uncultivated areas associated with granite knoll, 2, mid-slope of improved pasture, 3, lower-slope of improved pasture.

**Results**

*Site affinity:* Scelionids were first collected in the 1992-93 season and were restricted to site 1. In the 1993-94 season there was a substantial increase in abundance (>15 in 120 sweeps: Fig 5) which was again largely restricted to site 1. On all four of the six sampling occasions when scelionids were recorded, they were significantly more abundant at site 1 than all other sites (*F*2,15 = 22.6, *P* < 0.001). Scelionids were virtually absent from adjacent improved pasture. In the 1994-95 season there was a sharp decline in abundance (Fig. 5).

Three species were recorded, *Scelio parvicornis* Dodd, *S. improcrerus* Dodd and *S. bipartitus* Kieffer. The former two species are parasites of *P. vittatum* and the latter of *Gastrimargus musicus* (F.). *S. improcrerus* predominated throughout the 1993-94 season (Table 1) but was equal in abundance with *S. parvicornis* in the 1992-93 and 1994-95 seasons.

*Phenology:* In the 1993-94 season the abundance of scelionids peaked rapidly in early summer (December) when the host was at the 5th instar stage, i.e. some 5-6 weeks after hatching of the host. Abundance slowly declined over mid-late summer (January-February) and rose again in early autumn (March)

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**Figs 1-4.** Grasshopper sampling site (Jerangle #14): an elevated saddle and granite knoll. 1, 1992-93 season (17.xii.1992) a season of above average spring rainfall (site 1, adjacent to knoll, site 2 in vicinity of granite slab (arrowed), site 3 in foreground). 2, 1993-94 (14.i.1994) a season of below average spring and summer rainfall. 3, native vegetation (site 1, 14.i.1994). 4, improved pasture (site 2, 17.xi.1993).
Table 1. The relative abundance of scelionids in the 1993-94 season in unimproved pasture (site 1) and improved pasture (sites 2-3) in the southern tablelands of New South Wales.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>Site*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td><em>S. parvicornis</em></td>
<td>M</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>5</td>
</tr>
<tr>
<td><em>S. improcerus</em></td>
<td>M</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>14</td>
</tr>
<tr>
<td><em>S. bipartitus</em></td>
<td>M</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>2</td>
</tr>
<tr>
<td>Total/sex</td>
<td>M</td>
<td>57</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>21</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>78</td>
</tr>
</tbody>
</table>

*Number in 12 x 120 sweep samples (2 on each of 6 sampling occasions).

Table 2. The phenology of scelionids in 1993-94 season in the southern tablelands of New South Wales.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>Month*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Nov</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10</td>
</tr>
<tr>
<td><em>S. parvicornis</em></td>
<td>M</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0</td>
</tr>
<tr>
<td><em>S. improcerus</em></td>
<td>M</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0</td>
</tr>
<tr>
<td><em>S. bipartitus</em></td>
<td>M</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>0</td>
</tr>
<tr>
<td>TOTAL</td>
<td></td>
<td>0</td>
</tr>
</tbody>
</table>

*Number swept in 6x10 sweep samples (2 at each site)
(Fig 5). Males predominated at all sampling occasions (Table 2) possibly because males searching for a mate are more vulnerable to capture than females which are possibly restricted to the litter zone in the search for host egg pods. The persistence of scelionids throughout the season was unexpected and may have been in response to a delay in the onset of oviposition by the host, a consequence of the relatively dry conditions in the 1993-94 season. The increase in early autumn was due to the emergence of the non-diapause component of the population.

**Seasonal abundance in relation to rainfall and host density:** Scelionids were first recorded in 1992-93, the second season of high rainfall and increased substantially in the 1993-94 season which received below average rainfall and declined in the 1994-95 season, also initially a season of low rainfall (Fig. 5). As their high abundance in the 1993-94 season was predetermined by conditions in the previous season, high rainfall was coincident with their initial increase in abundance but no direct causal relationship is proposed. A decline in abundance in the 1994-95 season followed dry conditions in the previous season.

The density of *P. vittatum* was highly variable throughout the study period (Fig 5). The highest densities occurred in the 1991-92 and 1994-95 seasons, the result of high survival in prior seasons (1990-91 and 1993-94 respectively) due on both occasions to low nematode parasitism under the relatively dry conditions (Fig. 5). The decline in the abundance of *P. vittatum* between the 1991-92 and 1993-94 seasons was associated with high levels of parasitism by mermithid nematodes due to high rainfall in both the 1991-92 and 1992-93 seasons (Fig. 5). The poor survival of *P. vittatum* during the 1994-95 season is also attributed to parasitism by nematodes following high rainfall in October and January (Fig. 5). The increase in absolute abundance of scelionids over the period 1991-1994 was coincident with a nematode induced decline in host density indicating inverse host density dependence. The decline in the abundance of scelionids in the 1994-95 season corresponded with a general increase in host abundance, but perhaps significantly not at site 1 where scelionids had been most abundant in the previous season.

The level of mortality of overwintering eggs due to parasitism by scelionids was not measured in the 1993-94 season, however, nymphal survival was high (Fig 5: November-December) and, reservedly assuming an equal capture efficiency, the ratio of scelionids to *P. vittatum* nymphs at the time of peak emergence of the scelionids can be taken as the ratio of grasshopper eggs parasitised by scelionids. This provides crude estimates of parasitism at site 1 of 3.6% in the 1992-93 season (2 scelionids + 53 nymphs), 29.7% in the 1993-94 season (14 scelionids + 33 nymphs), nil parasitism at mid and lower-slopes in 1992-93 and 1.3% in the 1993-94 season (1 scelionid + 75 nymphs). These are gross underestimates of the level of parasitism as they
fail to take into account the staggered emergence of quiescent adults. The sharp increase in the estimated parasitism level in the unimproved pasture between the 1992-93 and 1993-94 seasons was coincident with a decline in host density indicating a possible inverse host density dependent relationship between parasitism level and host density. In the 1994-95 season, parasitism of overwintering eggs collected at site 1 and incubated in the laboratory was 36.36%. This parasitism may have contributed to the low abundance of P. vittatum at site 1 in the 1994-95 season relative to sites 2 and 3 where substantial increases occurred (Fig. 5).

**Discussion**

*Site affinity:* the cause of the site affinity displayed by *S. parvicornis* and *S. improcerus* is unknown but is most probably in response to physical characteristics, host population stability or an instinctive habitat preference.

There were many physical characteristics which differed between unimproved and improved pasture which may explain the disparate abundance of scelionids in the two habitats: 1, cultivation and fertiliser applications to the improved pasture site may have rendered it physically or chemically unattractive; 2, numerous bare patches in the unimproved pasture (Fig 3) possibly increased the efficiency of finding host eggs, whereas in the improved pasture potentially bare patches were colonised by *T. repens* (Fig 4); 3, unimproved pasture may contain endemic potential food sources for adult scelionids which are absent from the improved pasture where exotic vegetation predominated; 4, the leaf litter on the fringe of the timbered site may provide shelter for adult scelionids.

There are also site differences in the temporal stability of host populations which impact on the abundance of scelionids. The relative instability of *P. vittatum* populations in improved pasture is a consequence of periodic pasture rejuvenation, variable grazing pressure under the influence of stocking rates and weather conditions and high levels of parasitism by mermithid nematodes. Cultivation to regenerate pasture results in emigration from the cultivated area by *P. vittatum* and the lack of hosts could lead to localised extinction of scelionids in the area cultivated.

Also contributing to the relative stability of *P. vittatum* populations at the unimproved pasture site is the relatively reduced effectiveness of mermithid nematode parasites (*Hexamermis* sp., *Amphimermis acridiorum* Baker & Poinar and *Amphimermis mirabinda* Baker & Poinar), most apparent in the 1991-92 and 1992-93 seasons (Fig. 5), due to high run-off lowering effective rainfall (Fig. 1). At mid and lower-slope sites a seasonally variable impact by mermithid nematodes on *P. vittatum* populations results in fluctuating host densities which may also adversely affect scelionid abundance.

The habitat preference may also have a behavioural basis unrelated to contemporary environmental or biotic characteristics of the habitat. Clark
Fig. 5. Seasonal changes (October-March) in the abundance of Scelio spp. at three sites in relation to host density, rainfall and parasitism by mermithid nematodes.
(1962) reported that *P. vittatum* preferentially dispersed towards tall trees and postulated that this was a survival strategy encouraging movement towards favourable habitats (= prevented dispersal into unfavourable habitats). Clark (1962) suggested that the preferred habitat of *P. vittatum* in the original climax savanna woodland of tableland regions was the short vegetation on the fringe of woodlands. This is essentially the same habitat shown in this study to be favoured by both *S. parvicornis* and *S. improcerus*. Clark (1962) further suggested that the recent creation of short improved pastures in areas previously dominated by tall native species such as *Themeda australis* (R. Br.) Stapf., had increased both the distribution and abundance of *P. vittatum*. This study has shown scelionids to be virtually absent from improved pastures and their contemporary distribution is possibly an anachronistic, instinctive habitat preference based on the former restricted distribution of their host. The failure of scelionids to adapt to the wider distribution achieved by *P. vittatum* with the replacement of native vegetation by improved pasture during post-european settlement, perhaps indicates habitat selection by a different set of environmental cues, cues unsatisfied for scelionids in the wider contemporary distribution of the host.

The relative success of mermithids under contemporary land-use patterns in the tablelands indicates that, in contrast to scelionids, they either spread simultaneously with *P. vittatum* and are co-adapted to the improved pasture environment or, subsequent to the spread by *P. vittatum*, adapted to *P. vittatum* from alternative grasshopper hosts in the *T. australis* grasslands. The later scenario is the most probable given the habitat preferences of mermithid parasites of acridids (Baker and Capinera 1995) and the former abundance of the alternative host *Gastrimargus musicus* (F.) in *T. australis* grasslands prior to the establishment of pastures and its displacement by *P. vittatum* (Key 1959).

**Seasonal abundance:** The increase in abundance of scelionids towards the end of the study period was associated with several seasons of above average rainfall and a decline in host density. Although rainfall can not be dismissed as a factor influencing the abundance of scelionids, it is here assumed the influence is indirect through its influence on host abundance. The inverse density dependent relationship between scelionid abundance and host density apparent in this study is at variance with the findings of Putnam (1953) and Farrow (1977) that the absolute abundance of scelionids is host density dependent. The relative abundance of scelionids and host nymphs in this study indicate elevated parasitism levels also associated with declining host density. Clark (1967) reports a host population increase between 1957 and 1959 coincident with a decline in the abundance of an unidentified scelionid from 20.9% to 11.3%. Although the decline is not substantial, it also indicates an inverse density dependence in parasitism level.

Although of restricted distribution, scelionids in the 1993-94 season reduced
the productivity of the host population to that of replacement only, whereas in their absence and under climatic conditions unfavourable for other biocontrol agents, there was a 10-15 fold increase in host density.

The inverse density dependence exhibited by scelionids at the unimproved pasture site does not necessarily mean they have an unimportant role in the population dynamics of *P. vittatum*; the suppression of the host when at low densities could result in a more protracted recessionary phase in the outbreak cycle than would otherwise be the case, perhaps substantially reducing the frequency of outbreaks.

Although the level of control exerted on the host population by scelionids at "hot-spots" is insufficient to prevent seasonal carry-over of *P. vittatum* populations, it may, at times, be sufficient to inhibit emigration and the development of secondary infestations. The level of control may also be sufficient to maintain host densities below the threshold density for the production of macropterous morphs so reducing the substantial contribution (Farrow *et al.* 1982) made by winged females to the initiation and spread of regional outbreaks.

**Acknowledgments**

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