The Predatory Behaviour of a New Zealand Araneophagic Spider, *Taieria erebus*.

Presented in partial fulfilment of
the requirements for the Degree
of
Bachelor of Science with Honours
in Zoology
in the
University of Canterbury

by
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University of Canterbury
1983

DEDICATED TO GOD

CONTENTS

ABSTRACT

The predatory repertoire of *Taieria erebus* (Gnaphosidae) is unusually large and complex for an arthropod. *T. erebus* is a proficient predator of insects and spiders both on and off silk, a kleptoparasite in alien webs and a predator of the eggs of other spider species. On webs and nests of other spiders, *T. erebus* acts as an aggressive mimic. Approximately 11 distinct predatory behaviours occur, the one the predators used depending on whether the prey item was a spider or insect and whether the prey was on a web, in a nest, or away from silk. Predatory behaviour on nests and especially on webs is more complex, of longer duration than predatory behaviour in the absence of silk, and involves vibrational behaviour. Predatory behaviour that occurs in the absence of silk includes no vibration, has fewer behavioural elements than used in silk-predation and is of shorter duration. *T. erebus* is an effective invader of cribellate (amaurobiid) webs but not ecribellate (theridiid) webs. Vision has no evident role in the predatory behaviour of this spider. Apparently, prey is located by means of tactile and vibrational cues and there is preliminary evidence of the use of olfaction. Scopulate hairs on the forelegs probably assist in the retention of prey during attacks. *T. erebus* has very fast acting venom. The results of this study are supportive of a hypothesis concerning the evolution of the Salticidae. Also, similarities of the scopulate hairs of *T. erebus* to scopulate hairs of certain salticids, suggests the Salticidae and Gnaphosidae are closely related.

INTRODUCTION

Taieria erebus is a small brown spider native to New Zealand. Before now it had attracted little scientific interest. However, as a result of this study, *T. erebus* was found to have some highly unusual characteristics with biologically important implications. This spider is unusual as it is an exceptionally versatile predator that catches insects and other spiders, both on and off webs.

Although *T. erebus* does not build webs, it routinely invades the webs of other spiders and feeds kleptoparasitically by preying upon insects trapped in the webs. It also vibrates on webs, apparently mimicking the struggles of trapped insects, thus deceiving the host spider which it subsequently attacks. This is one of the few examples of aggressive mimicry (Wickler, 1968) known to occur in animals.

Scanning electron microscopy has revealed unusual morphological structures that probably assist in grasping prey during prey capture. The characteristics of *T. erebus* have significant implications concerning the current hypothesis of spider evolution.

To provide a background against which to consider the biology of *T. erebus*, a brief review of the predatory behaviour of spiders will be presented. Next a current hypothesis concerning the origins of the salticids, or jumping spiders, will be given and the potential significance of *T. erebus* to this hypothesis pointed out. Finally, a more complete introduction to *T. erebus* will be provided, before the presentation of the results of this study.

Review of the Predatory Behaviour of Spiders

The Araneae is a massive order of ca. 40000 spiders (Levi, 1982; Kaestner, 1968). Spiders have been informally divided into two groups: web-builders and hunters (non-web building spiders) (Gertsch, 1949; Main, 1976; Barnes, 1980). Webs are difficult to define strictly, but the term usually implies a silken device built by spiders that slows down or entangles prey. Using this loose definition, approximately half the known species of spiders do not build webs (Levi, 1982).

However, classification based solely on web-building ability is too restrictive, and I shall provide a different classification that allows a more complete description. Spiders are again divided into two groups - sedentary and mobile (Table 1). Sedentary spiders are those that tend to stay in one place for a prolonged period of time. The length of this period can vary appreciably depending on many variables (e.g. wind speed and rate of prey capture: Turnbull, 1973). Silk can be used in various ways by both categories of spiders. Two major uses are in the building of nests and webs. For protection during moulting, oviposition or periods of inactivity, a spider may spin a nest formed from many layers of silk. The nest is usually only slightly bigger than the spider itself (Barnes, 1980) and is not generally used in prey capture. Webs, however, are used in prey capture, and can be fixed or manipulated.

All silk is probably sticky to some minor degree (i.e. it adheres to the prey at least momentarily). However, the term 'sticky web' will be reserved for webs that have special substances added that enhance the natural stickiness of the basic structural silk foundation. All spiders possess spinnerets, but only the cribellate spiders have a cribellum which is a spinning plate in front of the spinnerets (spinning appendages). The cribellum secretes extremely thin silk strands which are combed by the calamistra (specialised rows of setae on the fourth pair of legs) onto the structural threads secreted by the spigots of the spinnerets (Fig. 1). Ecribellate spiders posses neither a cribellum nor a calamistrum. Web stickiness is not provided by a fine 'wool' of thin silk strands around the structural threads as in cribellate spiders, but by beads of

Table 1 Categories of Spiders According to Predatory Behaviour.

- I Sedentary
  - A. Web-builders
    - 1. fixed webs
      - a. non-sticky (ecribellate)
      - b. sticky i (ecribellate)
        - ii cribellate
    - 2. manipulated webs
      - a. ecribellate
      - b. cribellate
  - B. Ambushers (cursorial)
    - 1. attract prey
      - a. use silk
      - b. do not use silk
    - 2. do not attract prey
- II Mobile cursorial spiders
  - A. Non-visual
    - 1. spitters
    - 2. silk users
    - 3. seizers
  - B. Visual
- III Web invading spiders
- IV Versatile spiders

sticky fluid strung along the threads (Fig. 2) (Savory, 1928).

The best known manipulated webs occur in dinopids. These spiders hang from a non-adhesive supporting silk strand. A small web of cribellate adhesive silk is held by legs I and II. When potential prey wander by, the predator separates these legs slightly, causing the web to expand. The web is then manoeuvred over the prey, and the prey scooped up (Robinson and Robinson, 1971; Austin and Blest, 1981).

Other sedentary spiders are cursorial ambushers ('cursorial' as used in this paper refers to a spider that does not use webs in predation). Some of these, such as Neotropical *Mastophora* (Eberhard, 1979, 1981), and possibly New Zealand *Celaenia* sp. (Forster and Forster, 1973), may use chemical attractants to lure prey. Others use the habitat to conceal their presence (e.g. trap-door and crab spiders). Crab spiders (Thomisidae), for instance, often hide in flowers, which they resemble in colour, and seize insects as they land (Fales and Jennings, 1979; Barnes, 1980; Morse, 1981). Some ambushing species use silk in detecting and capturing prey. The 'bolas spider' *Mastophora*, for instance, swings a line with a glue drop on the end at the moths it lures.

Trap-door spiders from several families, including Lycosidae and Ctenizidae (Forster and Wilton, 1968; Main, 1978), construct and hide in silk-lined burrows that are closed by a lid covered with moss, soil, and other materials. The spider may build silk lines that radiate out from the burrow entrance. As prey cross the lid or trigger the silk lines, the trap-door spider detects the vibrations and rushes out and grabs the prey which is then carried back to the burrow and eaten (Buchli, 1969; Marples and Marples, 1972).

Mobile spiders move about to locate and capture prey. Most mobile spiders do not have highly developed, acute vision. The scytodids attack their prey by spitting:ejecting a mucilaginous secretion from their fangs over the

Fig. 1 Silk from amaurobiid web.

C: cribellate silk. S: spinneret silk;

Scale: 5 μ

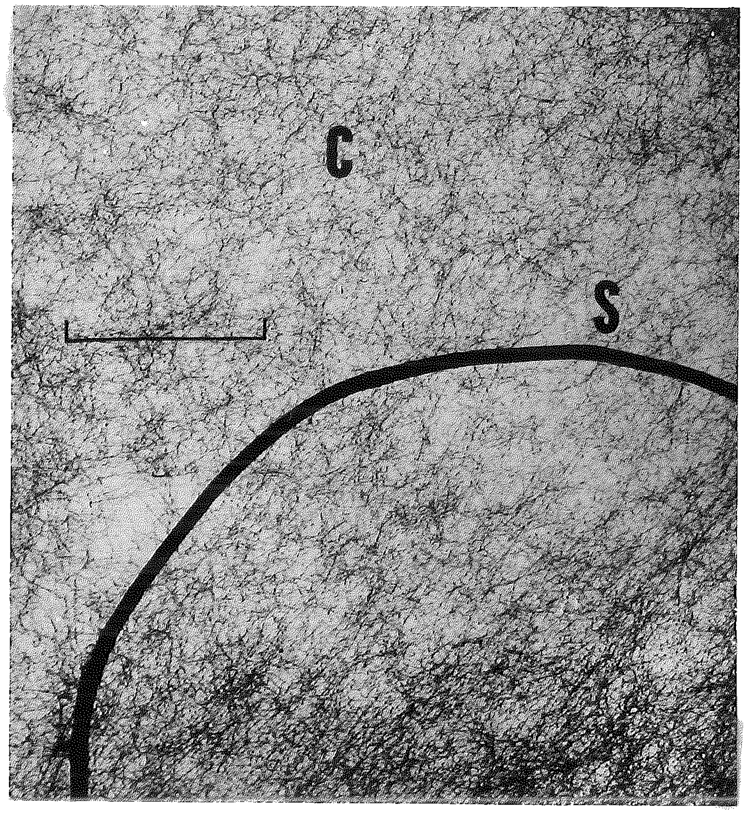
Web stickiness is provided by the cribellate silk (C) forming a fine 'wool' around the basic structural threads (S) of the web.

(S.E.M. by R.R. Jackson)

Fig. 2 Silk from araneid web.

Web stickiness is provided by droplets of glue (lower, centre) strung along the silk strands.

(S.E.M. by R.R. Jackson)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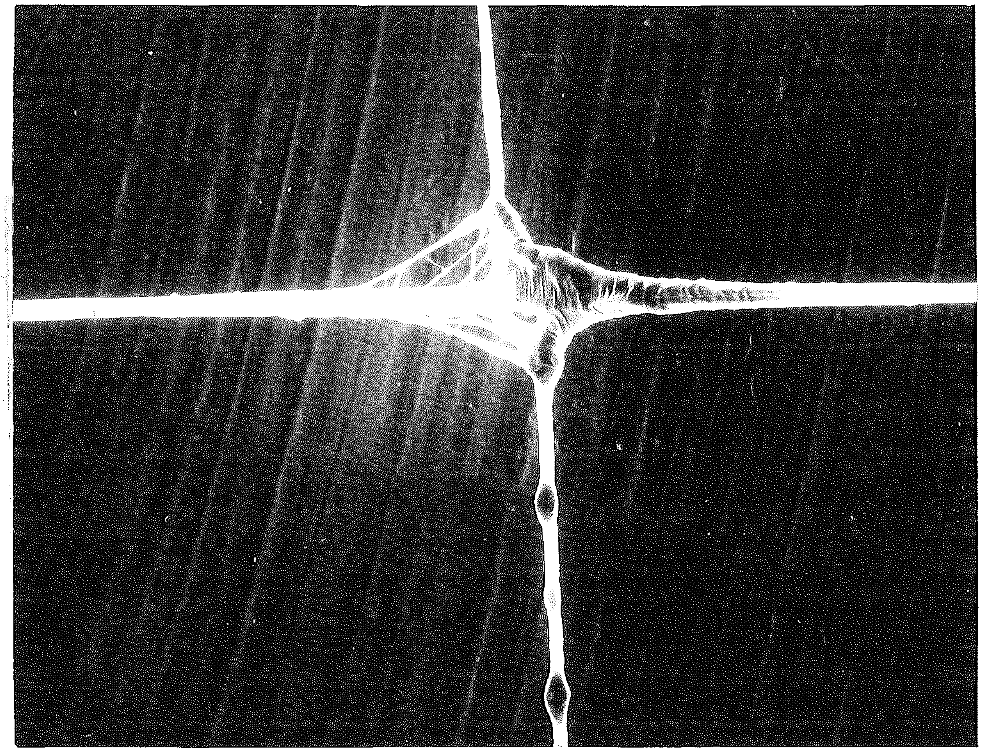

prey (McAlister, 1977). Oecobiids, hersiliids and some gnaphosids throw silk over their prey as they attack (Bristowe, 1941; Jackson, 1976), thus entangling the prey and hampering its escape. However, most mobile spiders do not use silk-or spitting-prey-capture. Little is actually known about how most non-visual, mobile spiders detect and locate prey, but the basic attack seems to be to seize the prey with the forelegs and/or chelicerae with a sudden lunge at close range (Bristowe, 1941). Salticids are visual mobile spiders. They possess one of the most complex and unique visual systems in the animal kingdom (Land, 1969a,b; Forster, 1982a; Blest, 1983), which enables them to stalk and leap on their prey.

Web-invading spiders are those that routinely live and feed in the webs of other species, rather than building their own webs. The Mimetidae, as far as is known, never build webs and never catch prey cursorially. They always live in, and feed in, alien webs they invade (Czajka, 1963). *Argyrodes* are specialised kleptoparasites that normally live and feed in webs of other species, taking insects caught in the webs (Vollrath, 1979).

Versatile spiders are spiders that fall distinctly into more than one of the previous three categories (I-III). *Portia fimbriata* is a distinctly versatile predator that will be reviewed in the next section. It is a web spider (sedentary), mobile spider, and a web-invader. *Taieria erebus*, as this study has revealed, is also a distinctly versatile spider and one of the very few members of this remarkable category.

Evolution of the Salticidae

Salticids are diurnal insect predators and often possess highly complex behaviour patterns (Forster and Forster, 1973; Forster, 1982a; Jackson and Harding, 1982; Jackson, 1982a, ,c). Their relationship to other spider families is poorly understood (Jackson and Blest, 1982; Blest, 1983). However, like *T. erebus*, the salticid *Portia fimbriata* invades webs, vibrates on webs, eats spiders and spider eggs, and is a kleptoparasite, although it prefers spiders as food and is more proficient at catching spiders than insects (Jackson, 1983).

Jackson and Blest (1982) use *Portia* to support their hypothesis concerning salticid evolution. The main proposals of their hypothesis are, firstly, that ancestral salticids were web builders with poor vision and, secondly, that vision evolved in the Salticidae in conjunction with the adoption of vibratory web invasion as a predatory specialisation.

According to this hypothesis, these ancestral salticids began to invade the webs of other spider species, gradually invading a greater range of web types. However, the webs of different species of web-building spiders differ greatly in their vibrational characteristics (Langer, 1969; Frolich and Buskirk, 1982). Hence, a web-invading predator would be faced with a complex array of vibrational patterns if it invaded diverse web types. With the development of acute vision, the salticids were freed from restrictions imposed by reliance on vibrational cues, and could be effective at invading a diverse range of webs.

Quick and accurate detection of the prey and its location in the web are of primary importance if the predator is to increase the chances of it gaining a meal, and decrease the possibility of it becoming one. An efficient visual system, providing such a means of prey detection and localisation across a range of webs, would also be useful for a mobile predator of insects. Hence, according to the Jackson and Blest hypothesis, vision arose in the context of web invasion, but became a preadaptation for visual predation on insects away from webs.

Any spiders that routinely invade alien webs to prey upon the inhabitants are of considerable importance to this hypothesis. It is widely assumed that all mimetid spiders are specialised web-invading predators of other spiders, although observations have been published for only a few species (Czajka, 1963; Lawrence, 1981). The Archaeidae are also commonly considered to be specialised web-invading predators; even less is known about this family (Legendre, 1961). *Lampona cylindrata* (Gnaphosidae) has been reported to prey on the cribellate web-building spider *Ixeuticus martius* (Forster and Forster, 1979); however, no details have been published about this spider either. *Taieria erebus* is also a gnaphosid and also, as this study revealed, one that routinely invades the webs of other spiders. According to Jackson and Blest (1982), such non-salticid web-invaders would either use well developed vision or be less proficient at invading diverse types of webs than *Portia fimbriata*. One goal of this study was to test this prediction.

Taieria erebus (Gnaphosidae)

The Gnaphosidae are one of the major non-visual mobile spider families (Gertsch, 1980). Their eyes are small and their vision is assumed to be poor (Platnick, 1971). According to Forster and Blest (1979), the genus *Taieria* is found throughout New Zealand, although it has been recorded from neither the subantarctic islands nor the Chatham Islands. These spiders are commonly found in river beds, swamps and tussock. This distribution does not appear to include sub-alpine conditions. Individuals are found throughout the year, usually inside silken nests beneath bark and stones.

Taieria erebus was chosen as the subject for this study for two major reasons: firstly, as a result of an accidental observation by Dr Robert Jackson, and secondly, due to my interest in New Zealand native fauna. In 1982, Dr Jackson was using various types of spiders and insects as prey for feeding a colony of Kenyan social spiders, *Stegodyphus mimosarum* (Eresidae). These cribellate spiders build very sticky webs that completely immobilise most insects and spiders, even if the host spiders fail to attack. A *Taieria erebus*, intended as prey, was dropped on a *S. mimosarum* web; but instead of being ensnared, it walked with apparent ease across the web.

Since *T. erebus* was obviously a New Zealand species of special interest, my initial goal was to simply find out more about its biology. After I found that *T. erebus* exhibited web-vibratory behaviour similar to *Portia* the focus of the study became the predatory versatility of *T. erebus*. The study included experiments designed to investigate what sensory modalities were important in prey detection, localisation and capture, both on and off webs, and scanning electron microscopy to examine morphological features that could be involved in prey capture (scopulate hairs). There are inconsistencies in the literature concerning the use of the term 'scopulate hairs'. Claw tufts are clusters of adhesive hairs on the extreme tip of the leg tarsi (Figs 18 and 19), and scopulate hairs are adhesive hairs on the ventro-lateral sides of the legs themselves (Figs 20 and 23). Both types of hairs have suction end feet and confusion arises because some authors refer to both types of hairs with the single term 'scopulate hairs'. I will keep the two terms distinct. Claw tufts, which web-building spiders usually do not possess, assist in locomotion, especially up smooth or steep slopes (Forster, 1967). The function of scopulate hairs, which occur on the forelegs of spiders from various families, is poorly understood. However, Rovner (1980) demonstrated that these hairs are used by lycosid spiders to hold onto large, active prey.

Salticids have generally been regarded as lacking scopulate hairs, although possessing well developed claw tufts (Hill, 1977). However, recently several species of *Portia*, and some salticids from closely related genera, were found to have scopulate hairs on their forelegs (Foelix *et al.*, in press). These scopulate hairs are unusual, not only because they are on salticid legs, but also because they have raised, notched bases more typical of the tricobothria (mechanoreceptors: Barth , 1982). No other spiders are known to have scopulate hairs with this type of base. Unlike claw tuft hairs (Foelix, 1975), the salticid scopulate hairs are innervated. Apparently, histology has never been done of the bases of scopulate hairs of spiders other than the salticids, so it is not known whether ordinary scopulate hairs are innervated (Jackson, pers. comm.). The salticid scopulate hairs, like these lycosid scopulate hairs (Rovner, 1978), are erected by hydrostatic pressure (Parry, 1960) as the spider attacks, resulting in the suction end-feet being positioned so as to contact the prey (Foelix, *et al.*, in press).

The structure of the scopulate hairs of *T. erebus* (which have not been studied previously), and their function, will be considered. Some remarkable similarities to the salticid scopulate hairs were found, as well as important differences.

MATERIALS AND METHODS

Animals Used in the Study

Laboratory studies were carried out using 123 *Taieria erebus* collected at various times from Spencer Park, Christchurch city and various localities on Banks Peninsula (Fig. 3). Since the behaviour of the specimen did not vary with the locality of origin, results from all the populations will be pooled. Spiders used as prey and in the laboratory experiments were collected from the same areas at the same times. Collecting was carried out as spiders were needed. *Drosophila melanogaster* were obtained from laboratory cultures, and aphids, mites, opilionids and woodlice were collected locally as required (Table 2).

Cages and Maintenance

T. erebus and other cursorial spiders were housed individually in cages made from small plastic pottles (Fig. 4). All web-building spiders were housed communally in large transparent plastic cages (Fig. 5). Construction of these cages and maintenance procedures were essentially similar to those used in other spider studies (Jackson, 1974, 1978; Phibbs and Jackson, 1981). Dead twigs were placed inside each cage as substrate for web building, and the design of the cages was such that they could be openned with minimal damage to the webs. Spiders were fed once weekly by removing corks from the cages and adding *Drosophila melanogaster*, except when *T. erebus* was sometimes fed other spiders as well. Both modular (Fig. 6) and wooden glass-sided cages (Fig. 7) were also used to house web-building spiders. The modular cages (with glass roofs) were used in Experiments I, II, V, VI, VII and IX. The wooden cages were similar to those used by Clayton-Jones (1983) and were used in Experiment VIII.

Terminology

The terms 'selection', 'choice' and 'preference' are used throughout this paper, and refer to actions by *T. erebus*. A situation may exist where one

Fig. 3 Collection Sites for Spiders Used in this Study *

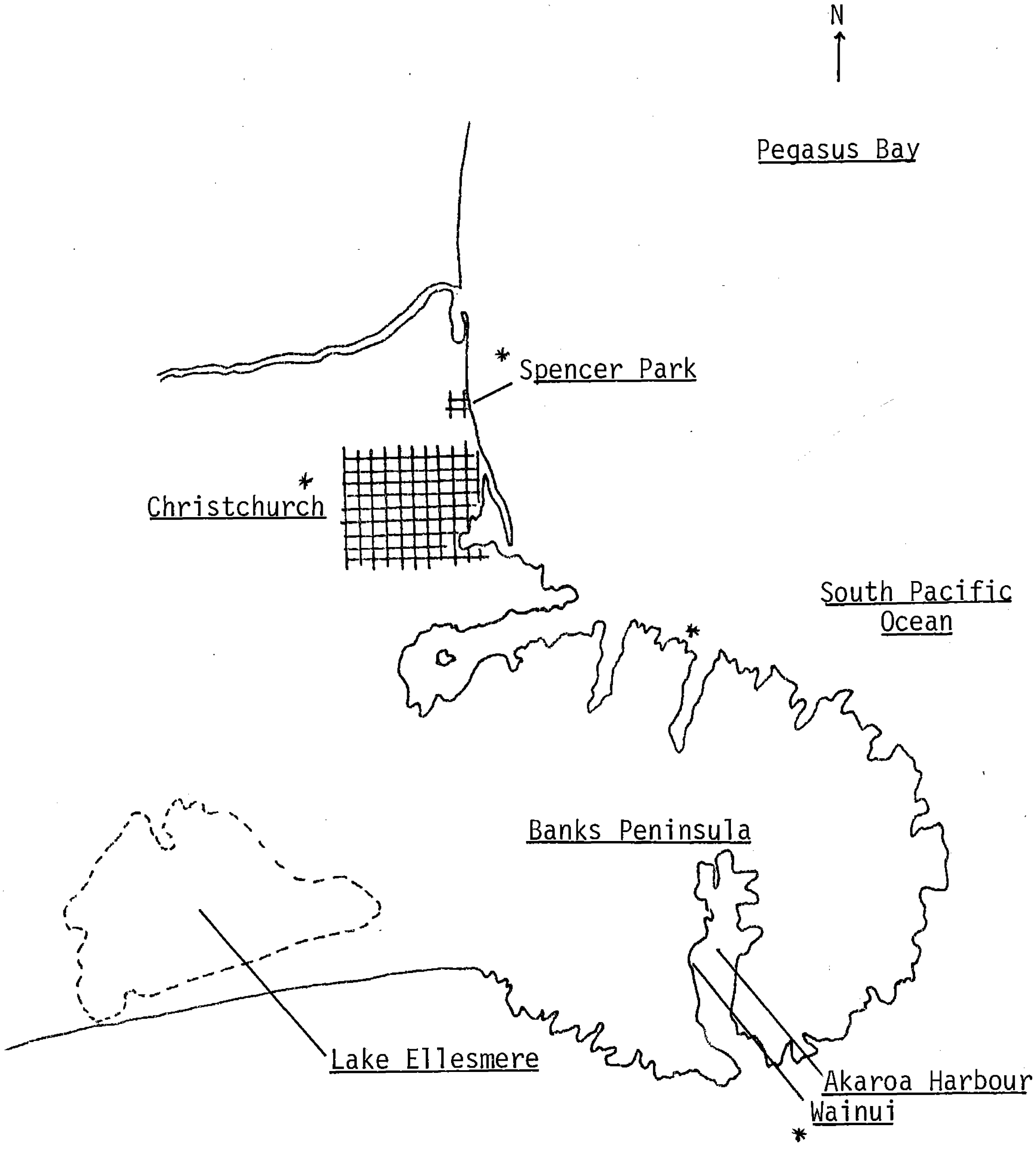

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Fig. 4 Small plastic cages used to house non-web-building spiders. Spiders were fed *Drosophila melanogaster* once weekly by putting the flies through the hole in the top of the cage (in this photograph the hole is blocked by a cork). Constant moisture was provided from lower pottle (containing water) by means of a cotton wick. Note: *Taieria erebus* in lower right of cage, only partially in view.

Fig. 5 Plastic cages used to house web-building spiders. Twigs were added as substrate. Spiders were fed once weekly by removing the cork (top of cage) and adding *Drosophila melanogaster*. Constant moisture was provided from two pottles containing water by means of cotton wicks.


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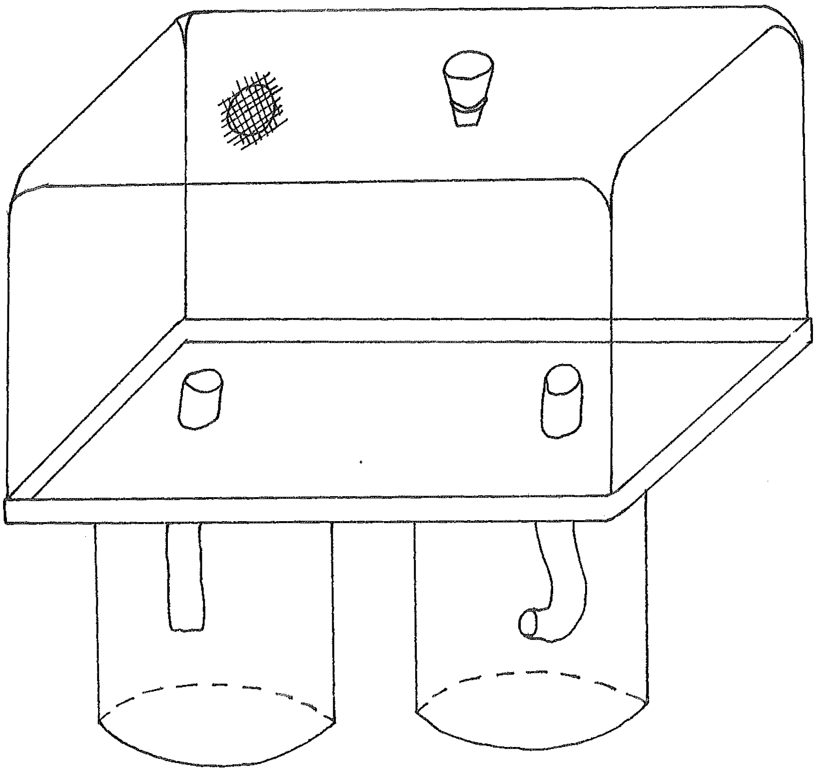
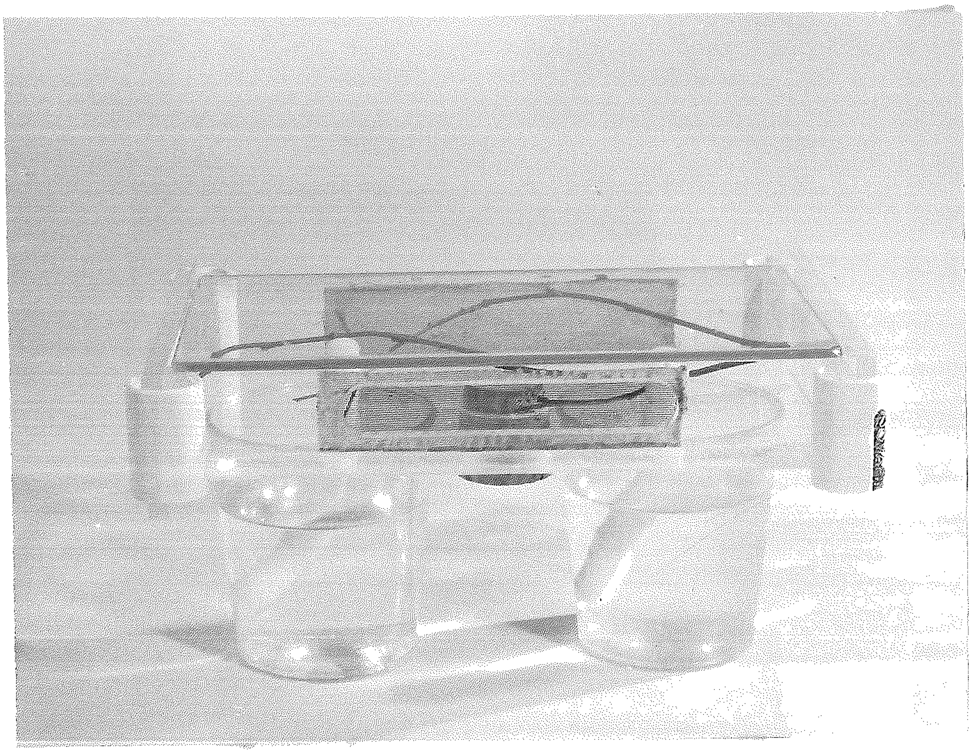
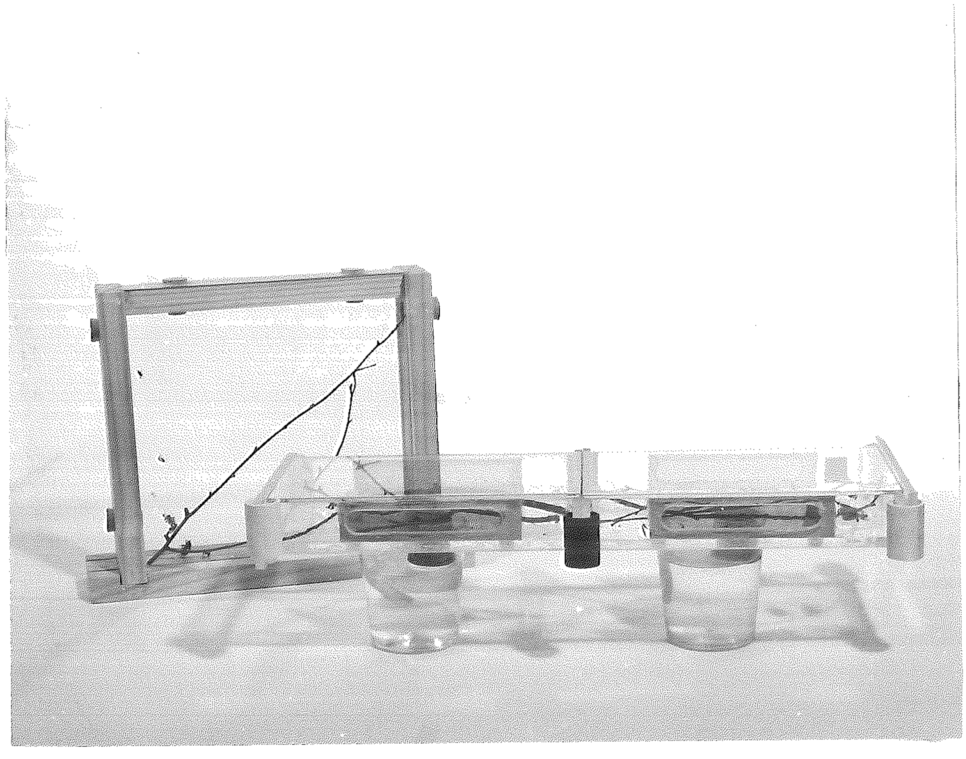


Fig. 6 Modular cage used to house web-building spiders, and used in Experiments II, IV-VII and IX. Moisture was supplied by cotton wicks set in pottles of water.

Fig. 7 Apparatus used in web discrimination and artificial vibration experiments. The two cages in the foreground were used in Experiments VI and VII (web discrimination: 24 hr; fresh and stale silk, respectively). The wooden cage in the background was used in Experiment IX (artificial web vibration).





particular prey type is attacked and eaten more frequently, or where a web type is investigated more often by the predator. The terms mentioned above may be used to describe situations such as these; they are used with a purely mechanistic viewpoint and conscious behaviour on the part of *Taieria erebus* is not implied.

Webs

Webs were obtained for Experiments I, II, V, VI, VII and IX by housing amaurobiid and theridiid spiders in modular cages. Amaurobiid spiders housed in wooden cages built webs used in Experiment VIII. Spiders were housed in these cages until well developed webs were spun (ca. 14 days). Only one species, but several individuals, were housed in a given cage. Comparable quantities of twigs were used in each cage to aid web-building. Host spiders were removed within 24 hr of testing unless stated otherwise.

Light-free Chamber

When continuous darkness was required during an experiment, a light-free chamber was used. This was a large box (765 x 590 x 530 mm), painted black on the inside and covered with a thick black serge blanket.

Randomisation

Experiments II-VI involved the use of random numbers tables (Rohlf and Sokal, 1969). In Experiment II (prey selection), the order in which potential prey items were presented was determined randomly, as was the orientation of webs inside the light-free chamber (Experiments V, VI and VII: web discrimination). Of the two vials used in Experiments III and IV (olfactory discrimination), which one was to contain the prey item was also determined randomly.

Cleaning

The apparatus in Experiments III-V was cleaned before each test was conducted. The perspex runways in Experiments III and V, glass vials in Experiments III and IV, and the modular cage and L-tubes in Experiment IV, were all cleaned by the same method. Paper tissues dipped in 70% ethanol were used to wipe the apparatus. Fresh tissues dipped in water were used to remove traces of the ethanol.

Scanning Electron Microscopy

Spiders to be examined were dissected and mounted for scanning electron microscopy. Two microscopes were used. The first was a Cambridge 600 which was replaced by a Cambridge 250 mark 2. The latter gave greatly superior micrographs.

Experiment I. Locomotion on Silk

In the laboratory, individuals of *Taieria erebus* were dropped onto well developed webs of amaurobiid, araneid and theridiid spiders, and onto nests of salticid spiders, and their locomotion observed. Species from other gnaphosid genera and of other families of spiders were also tested on amaurobiid webs. The host spider was removed before dropping any spider onto the web.

Imformal Observations of Predation

T. erebus was presented with a wide range of prey and observed for variable lengths of time. Sometimes *T. erebus* was left with the prey overnight, and checked the next morning. All potential spider prey except *Supunna picta* were eaten. Of the non-spider potential prey given, only *Drosophila* were eaten. Aphids, houseflies, mites, opilionids and woodlice were rejected (Table 2).

Procedures for Determining Prey Selection

Confusion may arise over use of the term 'selection'. *T. erebus* may not eat prey items of one or more of the kinds tested in Experiment II (prey selection) because a) the predator does not detect them, b) it detects, but cannot catch them, or c) it can catch them but does not like to eat them (distasteful). Experiment II does not enable a distinction between a, b or c, to be made. Here the term 'selection' is used, as in other studies (e.g. Freed, in press), in a broad sense, and does not specify whether a, b or c is the case.

Table 2 Arthropods Used in Study

Higher order taxon	Species	Brief description
Phylum : Arthropoda		
Class : Arachnida		
Order : Acarina		
Family Anystidae	Sp.1[2,5]	Cursorial predator
Order : Araneae[6]		
Family Agelenidae	*Neoramia* sp.1[3,4]	Cribellate. Small sticky sheet web
Amaurobiidae	*Ixeuticus martius*[4]	Cribellate. Sticky sheet web
Araneidae	*Araneus pustulosa*[4]	Ecribellate. Sticky orb-web
Clubionidae	*Clubiona cambridgei*[4]	Non-visual mobile predator
	Supunna picta[2]	Non-visual mobile predator
Gnaphosidae	*Anzacia gemmea*[1]	Non-visual mobile predator
	Hemicloae rogenhofferi[1]	Ambusher
	Lampona cylindrata[4]	Araneophagic
Lycosidae	*Lycosa* sp.1[4]	Wolf spider. Cursorial predator with moderately developed vision
Mimetidae	*Mimetus* sp.1[1,5]	Aranaeophagic. Does not spin webs
Salticidae	*Trite planiceps*[4]	Jumping spider
	Trite auricoma[4]	Jumping spider
	Holoplatys sp. 1[4,5]	Jumping spider
	sp.2[4,5]	Jumping spider
Theridiidae	*Acheranea* sp.1[4]	Ecribellate. Sticky space webs
Order : Opiliones	sp.1[2,5]	cursorial predator

Table 2 continued

Higher order taxon	Species	Brief description
Class : Insecta		
Order : Diptera	*Drosophila melanogaster*[4]	Common fruit fly
	Musca domestica[2]	Common house fly
Order : Hemiptera(Aphidae)	sp. 1[2 5]	Plant sucking insect
Class : Crustacea		
Order : Isopoda	*Porcellio scaber*[2]	Common woodlouse

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[1] studied in laboratory

[2] rejected as prey item by *Taieria erebus*

[3] eggs attacked by *T. erebus*

[4] adult attacked by *T. erebus*

[5] species that could not be identified ; given code numbers.

[6] Voucher specimens of all spider species have been deposited at the Otago Museum.

Experiment II. Prey Selection

As *Taieria erebus* were observed in the informal observations to be more prone to catch amaurobiids than other potential prey items, a formal observation procedure was devised with the responses to amaurobiid spiders serving as a standard. Also, feeding each *T. erebus* an amaurobiid spider prior to testing served to decrease variability in hunger levels between test sequences. This was considered potentially important as hungry spiders may accept a prey that they normally reject (Bristowe, 1941). Each prey item was 1/5 - 1/3 the predator's size and given in conditions roughly approximating those in the field (i.e., webs, twigs, etc were present).

Four potential prey types were tested: salticid and theridiid spiders, and insects (*Drosophila*) under two different conditions. The web-building Amaurobiidae and Theridiidae were exposed to *T. erebus* on their own well developed webs while the salticids were free roaming (cursorial). *Drosophila* were given either free or enmeshed (but still alive) in amaurobiid webs. *T. erebus* was never tested with more than one prey item at the same time. Thirty tests were carried out for each of the four prey-types, each test having three trials. The first and third trials were presentation of an amaurobiid spider on its web. The second trial was presentation of one of the four prey items (Salticidae, Theridiidae, trapped or free *Drosophila*).

After *T. erebus* had eaten the first trial item (amaurobiid spider) it was starved for 72 hr then placed with a test item for 24 hr. At the end of this 96 hr period the test prey item or its remains were removed and replaced by the third trial item (amaurobiid spider) which was also left for 24 hr. This occurred regardless of whether the treatment prey item had been eaten. Each test, therefore, lasted 120 hr (5 days), during which presentation of three potential food items took place.

A successful attack on the first amaurobiid spider, and starvation for 72 hr, had to occur before the second and third trials took place. Hunger was defined as eating either or both of the potential prey items given after the starvation period. If neither the second nor third prey items were eaten by the end of the 120 hr test, *T. erebus* was regarded as not hungry and ignored during any statistical analysis.

Common Methodology for Experiments III and V

Both 4 hr experiments used the same automated equipment, but slightly different methodologies. An actograph (McMurdo, England), four pairs of lights and light sensors, and a perspex runway were used. The perspex runway was made from three permanent (glued) and 11 movable parts, four of which were interchangeable. The unit was spider escape-proof. Which movable parts were used with the runway depended on the experiment (Figs 8, 10). A light-free chamber housed the runway, light and light sensors during both experiments. Since other spiders have been shown to be either completely or relatively insensitive to red light (Devoe, 1975; Yamashita and Tateda, 1976; Jackson, 1977c; Hardie and Duelli, 1978; Jackson and Harding, 1982), the light bulbs were covered with a double layer of red cellophane. The light system was arranged so that the four bulbs divided the runway into 3 equal sectors. The beam from each light bulb transected it at 90° and was detected by a sensor directly opposite. When *T. erebus* broke the light beam, the sensors were tripped, and the event was recorded by a chart recorder. Also, 5 min. intervals were marked automatically during each test for the two experiments. Intensity of the light from the bulbs was maintained at a level sufficient to sensitise the sensors to a break in the light beam, but not sufficient to raise the temperature inside the runway significantly. The automatic chart recorder and light system ran off the mains. Each experiment began when *T. erebus* was placed in the centre of the runway after removal of the glass roof plate. The roof plate was then replaced and the light-free chamber was closed immediately.

Experiment III. Olfactory Discrimination; 4 hour Trials

Taieria erebus was exposed to a possible olfactory gradient inside the runway, and its movements recorded automatically for 4 hr. The potential olfactory gradient was formed between a prey item (amaurobiid or theridiid spider) that the spider could not see, and a control (no prey item). At least half an hour was allowed for potential development of the olfactory gradient (Fig. 8).

Experiment V. Web Discrimination; 4hour Trials

Taieria erebus was tested with paired 1 day old amaurobiid and theridiid webs housed inside modular cages. Direct contact with the webs was possible. Movements were recorded for 4 hr (Fig. 10).

Experiment IV. Olfactory Discrimination; 15 minute Trials

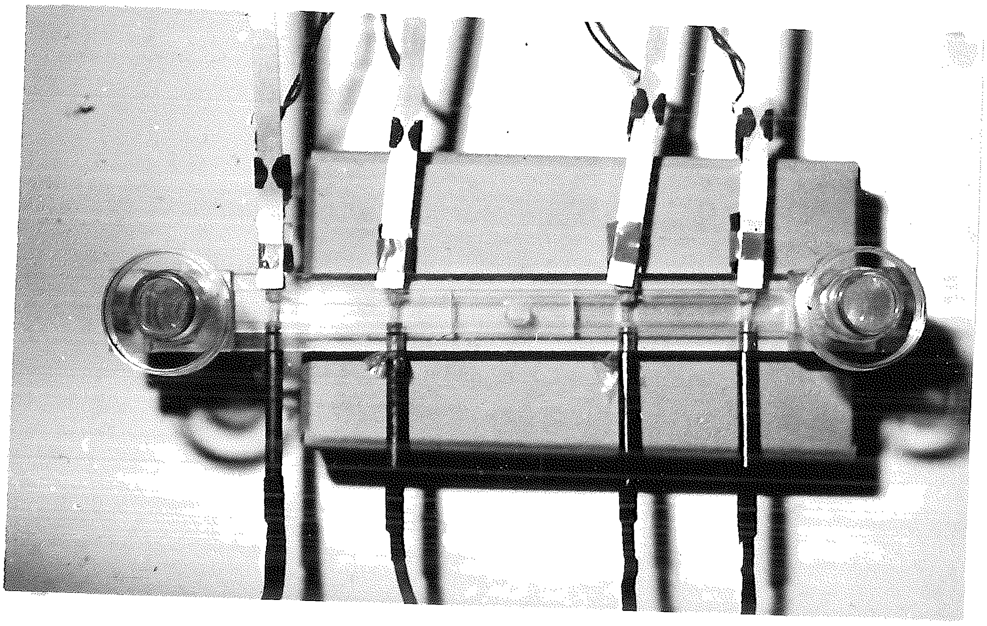
The movements of *T. erebus* in an experimental apparatus were recorded manually for 15 min. As with the 4 hr olfactory discrimination experiment, the potential olfactory gradient was formed between a prey item (amaurobiid, salticid or theridiid spider) and a control (no prey item), and *T. erebus* was placed in the olfactory chamber at least half an hour after the test spider was put in the holding vial (Fig. 9).

Experiments VI and VII. Web Discrimination; 24 hour Trials

Pairs of amaurobiid and theridiid webs in modular cages were used to test whether *T. erebus* was more attracted to either one of these web types. Both fresh (Experiment VI) and 1 month-old silk (VII) was tested. For fresh silk, the host spiders were removed 5 min. - 24 hr before the web was tested. For 1 month-old (stale) silk, host spiders were removed 30-33 days before testing. In both experiments *T. erebus* was added to the cages by lifting the glass roofs and releasing the spider on the centre-line between the two webs. The web the spider first walked on and the final position (24 hr later) were

Fig. 8 Apparatus used in Experiment III (olfactory discrimination: 4 hr trials). Prey was placed in either vial (left and right, at the end of the runway (centre). *Taieria erebus* was free to roam the runway itself. Its movements were recorded by 4 lights and light sensors that intersected the runway at 90°. Metal mesh at either end of the runway (hidden by the glass petri dish) prevented *T. erebus* from moving under the prey vial and so catching sight of the test prey item.

Fig. 9 Apparatus used in Experiment IV (olfactory discrimination: 15 min. trials). A prey item was placed in one of the two vials, and *Taieria erebus* was placed in the modular cage. The movements of *T. erebus* were recorded manually for 15 min.



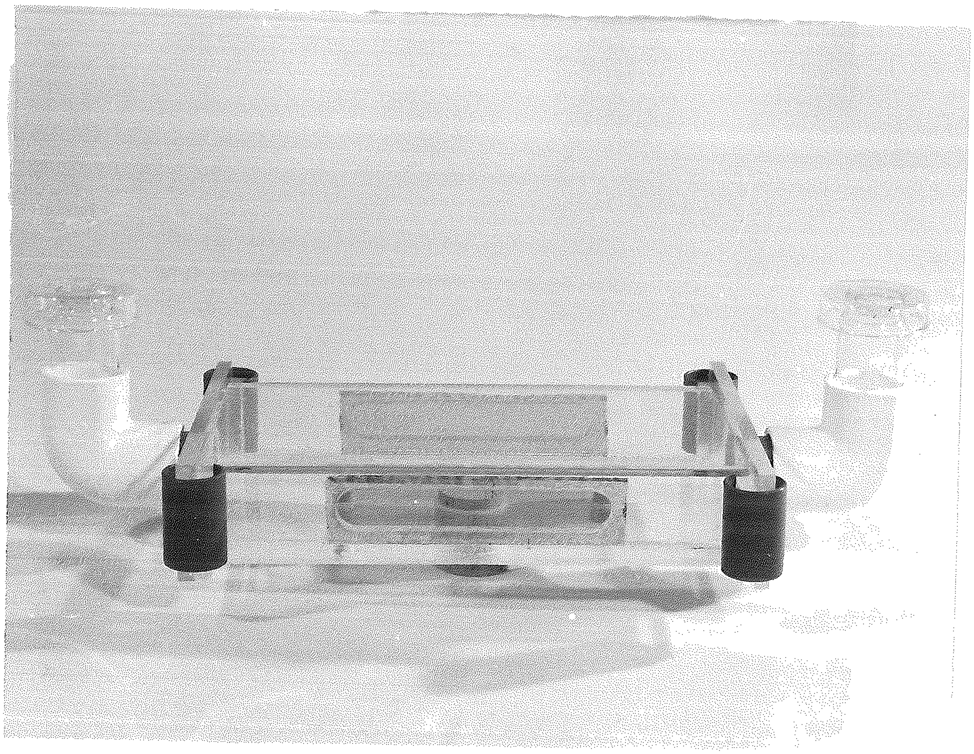
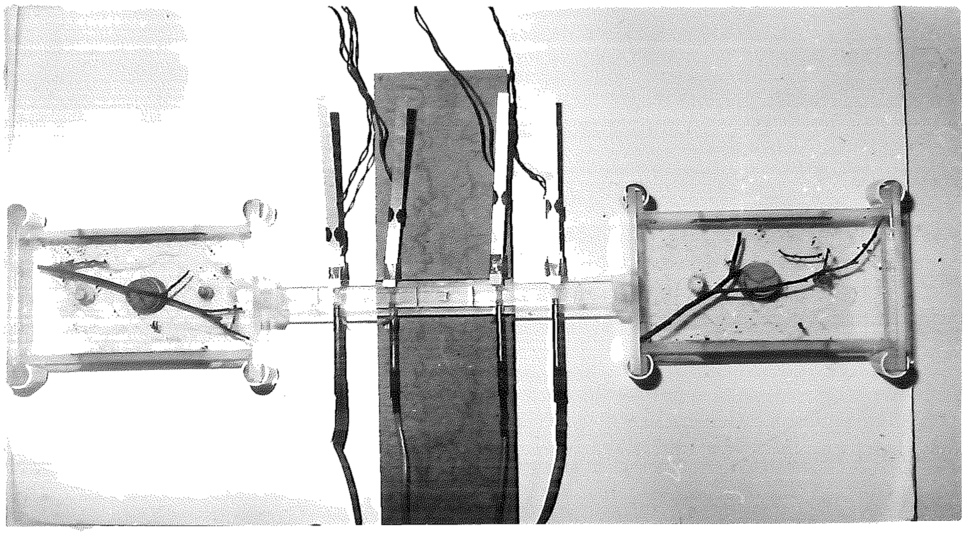
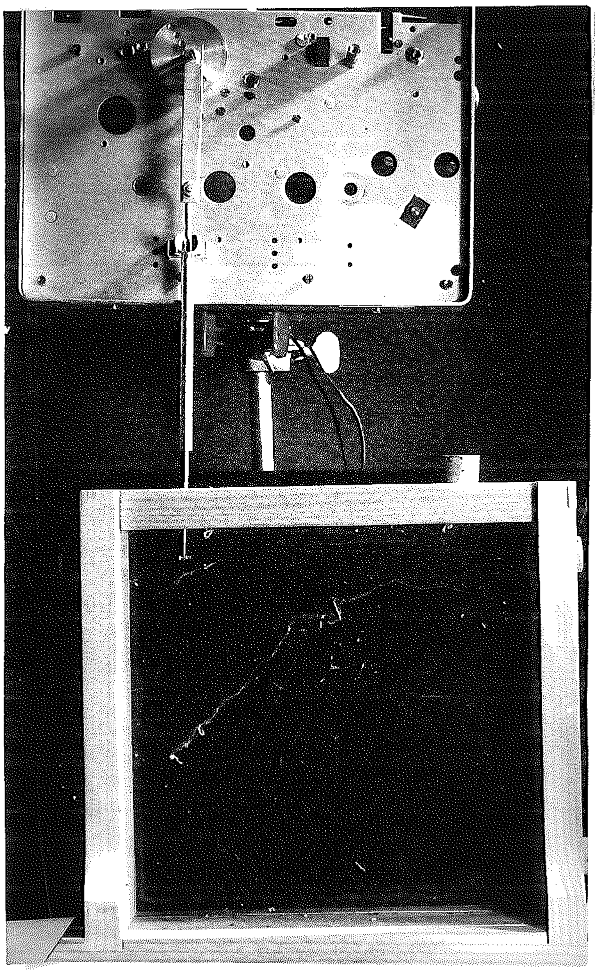


Fig. 10 Apparatus used in Experiment V (Web discrimination: 4 hr trials). Note the width of the runway (centre) compared to that of the web cages at either end. *Taieria erebus* placed in runway by lifting the centre roof plate (piece of perspex in centre of runway with a small handle on it). Four lights and sensors positioned along runway.

Fig. 11 Apparatus used in Experiment IX (Artificial web vibration). The probe (length: 9 cm) was mounted off-centre on a circular disc (diam: 5 cm). As the disc rotated, the probe moved up and down. The end of the probe was caught in the web (indistinct in this photograph) so that as the circular disc rotated the probe moved and alternately pulled and pushed the web.





recorded. The cage pairs were in complete darkness (light-free chamber) for the full 24 hr (Fig. 7).

Experiment VIII. Non-visual Predatory Behaviour of *Taieria erebus*

The eyes of *T. erebus* were covered with enamel paint (model aeroplane dope thinned 1:1 with thinner), and the predator exposed to amaurobiids and *Drosophila* as prey items in both the presence and absence of webs. To paint the spider, *T. erebus* was anaesthetised with CO_2, arranged facing upward on cotton wool and the dope spread over the entire ocular area using the tip of an insect pin. The spider was tested 2 days later. Trial-prey consisted of amaurobiid spiders on their webs, *Drosophila* trapped on well-developed amaurobiid webs, amaurobiid spiders presented without webs, or *Drosophila* without webs. All nine *T. erebus* that were painted died within 4 days of painting.

Experiment IX. Artificial Web Vibration

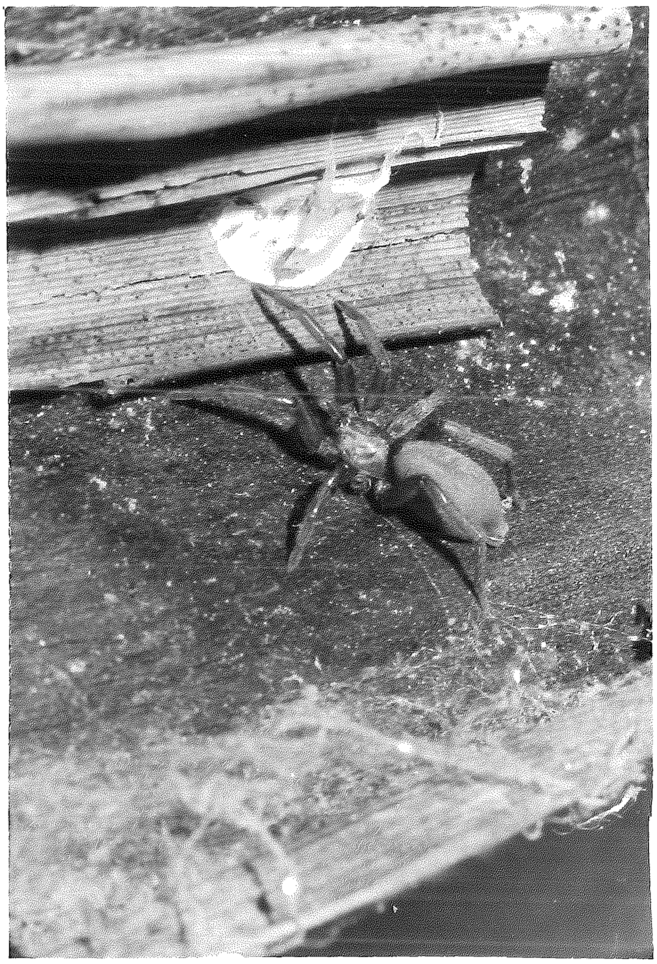
A metal probe was mounted off centre on a circular disc which was powered by an electric motor. The probe tip could be attached to an amaurobiid or theridiid web so that the probe pushed and pulled the web as the disc rotated (Fig. 11). *T. erebus* was dropped onto the web when the probe was correctly positioned and the spider's response to the artificial vibration was manually recorded for 15 min.

RESULTS

Field Observations

Taieria erebus was found in microhabitats ranging from vegetation (rolled up leaves of New Zealand flax and punga ferns) to under stones and logs on the ground. The most reliable prediction of the presence of *T. erebus* tended to be the presence of numerous other spiders, especially amaurobiids and salticids. The distinctive egg sacs of these spiders were sometimes found in amaurobiid webs (Fig. 12), usually on a solid substrate covered by the alien silk but occasionally on the silk. Egg sacs of *T. erebus* are flattened, disc-like, and formed from two thin sheets of dense silk joined along the edges. The eggs lie between the two layers of silk. Four *T. erebus* were found in webs with the amaurobiid *Ixeuticus martius*, in one case eating the host spider. Another four *T. erebus* were found in salticid nests with dead, presumably eaten, *Trite planiceps*.

Fig. 12 *Taieria erebus* in rolled flax leaf with egg case (upper). Foreground: the remnants of an *Ixeuticus martius* web destroyed when the leaf was unrolled. Note the disc-like shape of the egg case (partially distorted in this photograph due to the curvature of the leaf. Note also the size of the egg case (diam. 8 mm) in relation to *T. erebus* (length: 9 mm). Leaf cut with scissors to arrange for photography.



Elements of Behaviour of *Taieria erebus*

T. erebus performed 11 distinct behaviours in the presence or absence of prey and/or silk (Table 3). These behaviours involved the use of the legs and palps either individually, or in a variety of combinations.

Tap with palps. The two palps move simultaneously in alternate phase (one up, the other down). Each palp was raised, swung forward, and then lowered back onto the substrate. Movement of the palps was mainly femoral (i.e. mostly due to movement of the femora), with ca. 90° flexion maintained at the femur-patella joint. There was little variation from this pattern among individuals of *T. erebus*. Palp tapping occurred only when *T. erebus* was walking and each complete cycle lasted ca. 2 sec. Amplitude was ca. 2 mm.

Wave of legs. Waving involved the lifting and lowering of legs I and/or II either individually or in any combinations, as the spider walked. Generally there was a variable flexion held at the femur-patella joint, while the more distal joints were held fully extended. Movement was mainly femoral, and the amplitude was highly variable.

Both tapping with the palps and waving the legs were very common behaviours that generally occurred when the spider was active. These actions possibly had a sensory function and were probably important to the spider in predatory situations as well as in other activities. However, the following actions occurred in the presence of a potential prey item or at least the webs and nests of potential prey.

Raise legs. Commonly *T. erebus* raised legs I and/or II immediately prior to an attack or strike. This occurred only in the presence of prey, but either in the presence or absence of silk. Legs I were raised more often than legs II. As with leg waving, the tibia, metatarsus, and tarsus were held fully

Table 3 Contexts in which Behaviours Occurred (see text for details)

			On Web		On Nest	
Element of behaviour	Absence of webs, nest and potential prey	Absence of webs, nests; presence of (potential) prey	Potential prey absent	Potential prey present	Potential prey absent	Potential prey present
palp tap	√	√	√	√	√	√
leg wave	√	√	√	√	√	√
leg raise	-	√	-	√	-	√
lunge-attack	-	√	-	√	-	√
simple-attack	-	√	-	√	-	-
leg bundle	-	√	-	√	-	-
palp drum	-	-	-	√	-	√
palp tug	-	-	-	√	-	√
leg pluck	-	-	-	√	-	√
leg strike	-	-	-	-	-	√
leg drum	-	-	-	-	-	√

Fig. 13 *Taieria erebus* on web of *Ixeuticus martius* Prey (body length: 6 mm) is immediately to the left of the left hand twig (only partially in the photograph, Legs I, LII and RIII are in contact with the silk. *T. erebus* is drumming with the palps. The left palp has been moved down and is in contact with the silk; the right palp has been lifted and is off the silk.

Fig. 14 *Taieria erebus* on web of *Ixeuticus martius*. Prey (body length: 6 mm) is immediately to the left of the centre twig. *T. erebus* has rotated 100° clockwise and has continued palp drumming. Left palp of the spider (appears on the right of this photograph) is now being raised and the right palp lowered. Note that Legs I of *T. erebus* are extended toward the prey. Immediately after this photograph was taken, *T. erebus* raised legs and a successful lunge-attack occurred.

extended, and movement was mostly femoral during leg raising. There was a variable flexion held at the femur-patella joint. During leg raising, unlike leg waving, the legs were moved together (in matching phase). Once the legs were raised they were not lowered until the potential prey item moved away or *T. erebus* attacked.

Simple attack. *T. erebus* simply walked to the prey item then seized the prey with legs I and/or its chelicerae. No raising of the legs occurred and no lunge took place.

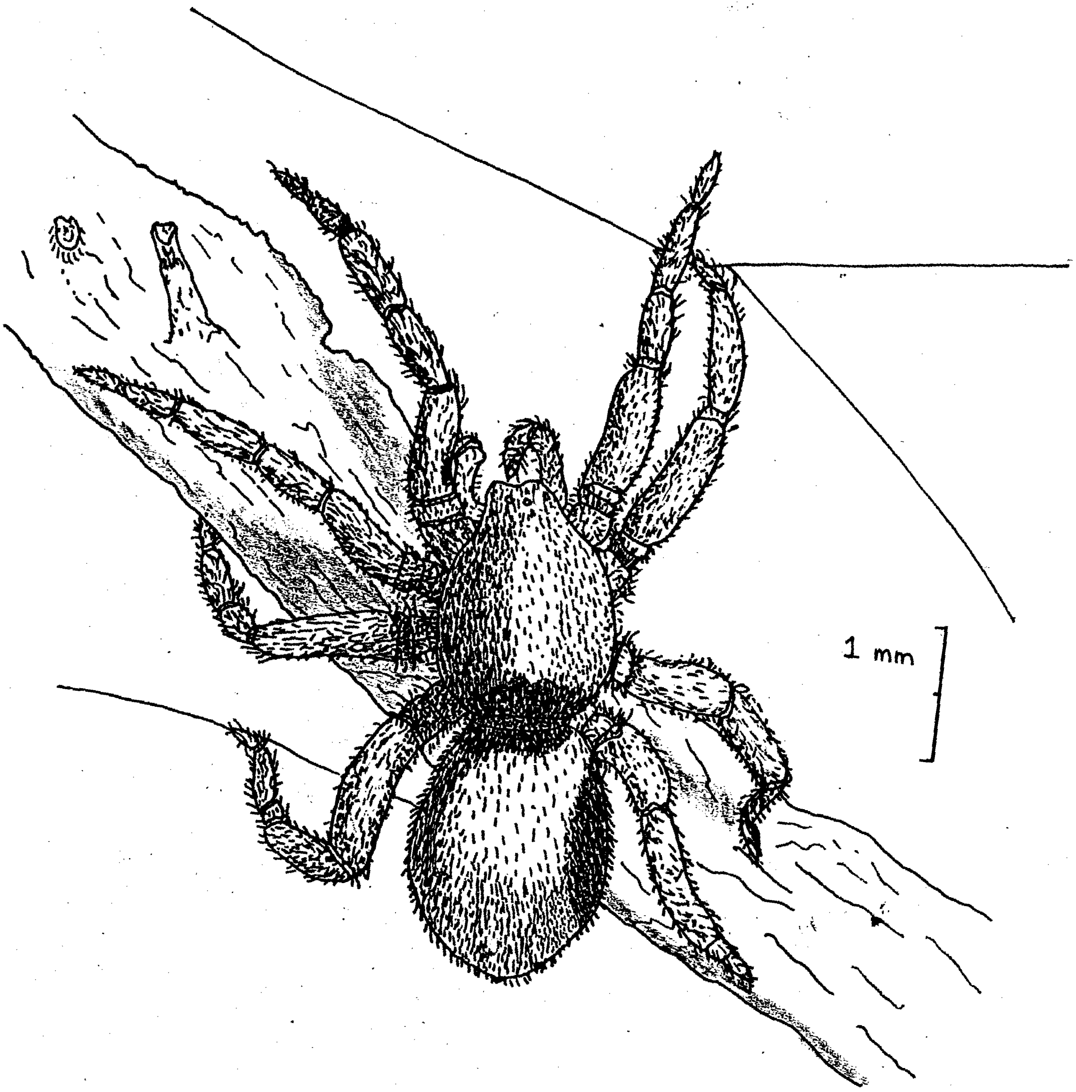
Lunge attack. *T. erebus* attacked very rapidly by lowering its raised legs as it simultaneously lunged (moved body rapidly forward as a result of extension of legs III, and especially IV). Legs I and II moved forward over the prey at the same time as the lunge, then down and back, forming a basket into which the prey was scooped. As the prey was pulled backwards, *T. erebus* moved forward and bit the prey (i.e. closed its chelicerae around the prey). Once prey was pierced by the fangs of a *T. erebus* spider, prey tended to become immobilised within 2-4 seconds, although one prey item (salticid) was still moving 1.5 min. after being bitten.

Strike with legs. To strike, *T. erebus* rapidly lowered its raised legs. Unlike the lowering of legs during lunge attacks, the striking legs did not flex but remained fully extended.

Bundle with legs. This took place after a successful attack, either in the presence or absence of silk. *T. erebus* stood over the prey, manipulating the legs of the prey so that they were tucked under the body of the prey. *T. erebus* sometimes used all eight legs to do this, but more often only the first three pairs of legs were used.

Drum with palps. Palp drumming was similar in certain basic respects to palp

Fig. 15 Sketch of *Taieria erebus* on branch plucking web with tarsus of right Leg II. Tarsus is being pulled back to the spider and will shortly release the silk strand causing a conspicuous 'jerk' to the web (refer to text for details).


1 mm

tapping. Again, it occurred when *T. erebus* was moving and the palps were moved simultaneously and in alternate phase, but there was no forward-backward swing of the palps. The palps were moved both through a greater amplitude (ca. 4 mm) and at a much faster rate (ca. 10 cycles/sec.). Unlike palp tapping, palp drumming took place only on occupied (and occasionally empty) webs and nests. It did not occur away from silk (Figs 13, 14).

Tug with palps. As during palp tapping, the palps were moved during palp tugging both up and down, and forward and backward; however, during tugging the palps were swung together (matching phase). Tugging took place only on occupied nests or webs. When the palps were moved forward, they were lowered slightly onto the silk; they were then pulled quickly back and up, tugging on the silk as they moved.

Pluck with legs. This involved the use of legs I and/or II and only took place on occupied webs, with only one leg being used at any one time. *T. erebus* remained stationary as the leg was lifted, moved forward, and the tarsus caught in the silk. The direction of movement was then quickly reversed with the tarsus releasing the silk half-way through the return journey. This resulted in the web being conspicuously 'jerked' (Fig. 15).

Leg drum. All eight legs were moved very rapidly up and down at the same time as if stepping, while the body of *T. erebus* remained in one place. This only took place when *T. erebus* was on an occupied salticid nest and occurred immediately prior to attack.

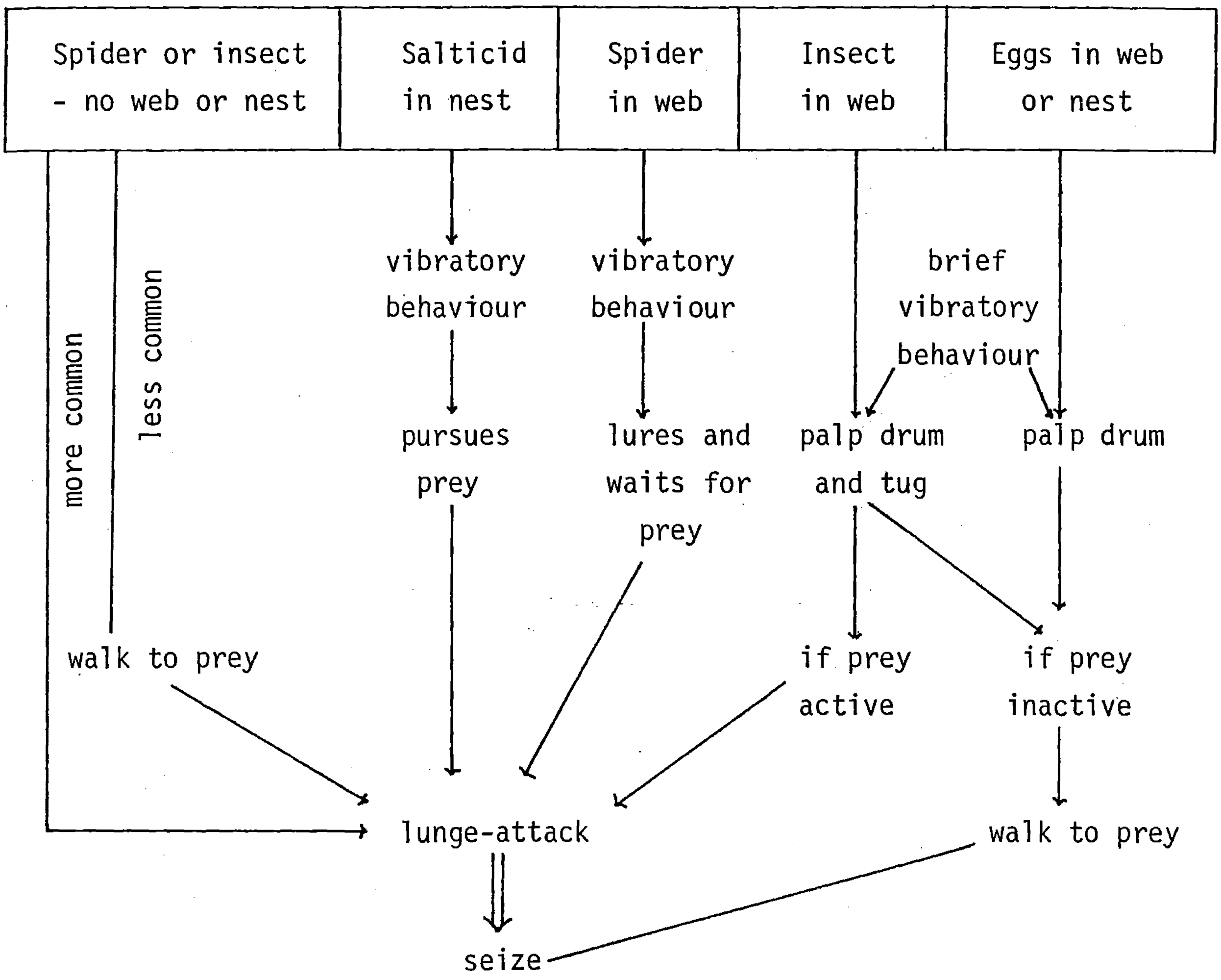
Palp drum, palp tug, leg pluck, leg strike and leg drum induced vibrations of the silk (web or nest) on which the behaviour took place. This sometimes resulted in the host spider approaching *T. erebus*. These five behaviours will be referred to collectively as vibratory behaviour.

Sequences of the Predatory Behaviour of *Taieria erebus*

Two general types of predatory behaviour occurred: cursorial predation in the absence of silk, and silk-predation in the presence of webs or nests (Table 4) Cursorial predation was generally much simpler and faster than silk-predation. The usual sequence of cursorial predation was for an inactive, standing *T. erebus* to suddenly attack a prey that passed close by (0.5 - 4.0 cm). *T. erebus* turned quickly toward, and attacked, seizing the prey, usually on the dorsal anterior abdomen. The prey sometimes, but not always, had blundered against a leg of *T. erebus* immediately prior to the attack. Usually prey were attacked from behind, but occasionally the prey were attacked from one side. In the case of flies trapped on webs, if the fly was inactive, *T. erebus* merely walked to the prey (i.e. there was no leg raising, lunging,etc), then seized it (simple attack). However, sometimes a typical lunge-attack occurred with leg raising,etc,if the fly was struggling vigorously at the time. In silk-predation, unlike in cursorial predation, *T. erebus* intermittently performed vibratory behaviour prior to the attack. *T. erebus* tended to remain inactive when the host spider was active, performing vibratory behaviour usually only when the host spider was inactive. Usually the host spider, in a web, approached the *T. erebus* that then lunged at the prey; but *T. erebus* also occasionally approached the prey.

A different pattern resulted when *T. erebus* was on an occupied nest instead of a web. Instead of remaining on one spot intermittently vibrating the silk, *T. erebus* moved over the nest frequently vibrating. Movements of *T. erebus* were faster and more energetic on nests than on webs, and striking with the legs was a common occurrence especially when *T. erebus* and the prey spider were separated only by the thin silk wall of the nest. Often in an attack on a spider inside a nest, *T. erebus* pushed its way into the silk so that it came close to the prey (5-10 mm). At this stage legs I and/or II were raised

Table 4 Typical Sequence of Behaviour of *Taieria erebus*, depending on prey type.



and a lunge attack occurred. No *T. erebus* was seen to make successful attacks when the two spiders were on opposite sides of the nest wall. Instead, successful attacks occurred when *T. erebus* was inside the nest with the potential prey, although sometimes a few silk strands still separated the two spiders. Typically potential salticid prey in nests became very agitated with the presence of *T. erebus* on the nest, sometimes performing leg-strikes similar to those of *T. erebus*.

Striking is a threat display that occurs in numerous salticid species and possibly *T. erebus* mimicked these (Jackson, 1982c). Some salticids broke halfway out of the nest as they struck at *T. erebus*. However, no prey spiders completely evacuated the nest when attacked.

During kleptoparasitic predation on insects in webs, *T. erebus* typically performed no vibratory behaviours, or else palp drummed or tugged for a shorter period than was typical during predation on spiders in nests or webs. *T. erebus* appeared almost casual in how it walked over to trapped insects. This was also true of egg eating. Palp drumming and palp tugging occurred primarily if the insect was especially active on the webs. *T. erebus* sometimes ate egg sacs it encountered in nests or webs by removing the surrounding silk casings and simply biting into the eggs. Vibratory behaviour typically did not occur, although palp drumming occurred on rare occasions.

Experiment I. Locomotion on Silk

Anzacia gemmea and *Hemicloea rogenhoferi* (Gnaphosidae) had difficulty walking on both cribellate and ecribellate webs; they also stuck to both types. (*Mimetus* sp. gave results opposite to those of *T. erebus*.) *Mimetus* sp. had difficulty walking on amaurobiid webs and stuck to these webs, but had no difficulty walking on theridiid and araneid webs. *Mimetus* sp. neither stuck to, nor slipped off, these webs. However, *T. erebus* had evident difficulty walking on araneid and theridiid webs. It tended to walk slowly and occasionally slipped and fell several centimetres down the web. When *T. erebus* contacted droplets of glue on the web it tended to adhere and extricated itself only with apparent difficulty.

In contrast, *T. erebus* walked with apparent ease on amaurobiid webs. It walked rapidly, did not slip off the web, and did not adhere to the sticky cribellate coating of the web (however, if *T. erebus* landed on its back when dropped onto a web, then it had momentary trouble freeing itself). *T. erebus* walked with comparable ease on salticid nests. In both araneid and theridiid webs, the spider soon dropped out of the web, but while in amaurobiid webs, the spider usually stayed for a more lengthy period.

Experiment II. Prey Selection

Both theridiids and cursorial *Drosophila* as prey were captured less often than amaurobiids (χ^2adj = 12.071, $p < 0.001$, and χ^2adj = 7.111, $p < 0.01$, respectively; Table 5), while salticids and trapped *Drosophila* were not. *T. erebus* ate most of the flies on webs and salticids, but only about half of the theridiids and the flies off webs were eaten. There was no evident difference between predation rates on salticids and trapped *Drosophila* and between theridiids and the flies off webs (Appendix A).

On webs, more *Drosophila* were caught than theridiids ($n = 54$, χ^2adj = 14.682, $p < 0.001$; Appendix A). In the absence of webs, more salticids were

Table 5 Results from prey selection experiments. See text for details concerning methods. Each *T. erebus* was tested sequentially with three potential prey items (first and third: amaurobiids). All *T. erebus* preyed on the amaurobiid in the first test. Predation in the second test: *T. erebus* preyed also on the second prey items. All that failed to prey on the second prey type ate amaurobiids in the third test. McNemar test for significance of changes (with Yate's Correction) was used to compare results from the first and second trials for each *T. erebus*.

	Prey Type in Second Test			
	Theridiid	Salticid	Fly on web	Fly off web
No. of test sequences	24	29	30	24
% Predation by *T. erebus* in 2nd Test	34%	93%	93%	50%
McNemar Test	$\chi^2 = 12.071$	-	-	$\chi^2 = 7.111$
	p <0.001	N.S.	N.S.	p <0.01

caught than *Drosophila* (n = 53, χ^2adj = 7.846, $p < 0.01$; Appendix A). The predation rate on salticids was more than double that on theridiids (n = 53, χ^2adj = 16.883, $p < 0.001$; Appendix A). More trapped flies were eaten than cursorial flies (n = 54, χ^2adj = 6.029, $p < 0.025$; Appendix A).

Experiment III. Olfactory Disrimination: 4 hr Trials

No significant deviation from random was recorded for *T. erebus* in either amaurobiid or theridiid olfactory gradients (Table 6). Although not significant, slightly more *T. erebus* were found close to amaurobiid spiders than close to theridiid spiders. Neither the initial distribution nor where *T. erebus* spent most of its time during the experiment affected the final distribution (Appendix A). Few *T. erebus* moved from one end of the test chamber to the other. Due to this, a different method was used to continue the study (Experiment IV).

Experiment IV. Olfactory Discrimination: 15 min. Trials

Attraction by *T. erebus* to either amaurobiids, salticids, or theridiids individually in olfactory gradients was not demonstrated (Table 7), although from the pooled ('most of time') distributions there was evidence of attraction to spiders (n = 130, χ^2adj = 4.069, $p < 0.05$; Appendix C). Attraction to spiders was shown with the pooled data but at a low significance level despite a large sample size (n = 130, $p < 0.05$). Possibly *T. erebus* was detecting the vibrations arising from activity of the prey items when trapped in the vials, but this appears unlikely as fewer than 10 spiders were active for more than half of the experiment. Most were active only 0-5 min. during the experiment.

The results may have been biased by the methodology. The initial choice by *T. erebus*, in the tests with amaurobiids and theridiids, affected its final distribution, as did where *T. erebus* spent most of its time in tests with amaurobiids and salticids (Appendix C). (Neither the initial choice of *T. erebus* caught than *Drosophila* (n = 53, χ^2adj = 7.846, p <0.01; Appendix A). The predation rate on salticids was more than double that on theridiids (n = 53, χ^2adj = 16.883, p <0.001; Appendix A). More trapped flies were eaten than cursorial flies (n = 54, χ^2adj = 6.029, p <0.025; Appendix A).

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The results may have been biased by the methodology. The initial choice by *T. erebus*, in the tests with amaurobiids and theridiids, affected its final distribution, as did where *T. erebus* spent most of its time in tests with amaurobiids and salticids (Appendix C). (Neither the initial choice of *T. erebus*

Table 6 Results of 4 hr tests for olfactory attraction by *T. erebus* to prey. Test chamber: vial at one end of the runway with a test-spider enclosed. Control: empty vial at the other end. Choice: the end of runway to which *T. erebus* was closer. Choice was recorded by three criteria: initial, final, and 'most of time'. The initial position was recorded as the first side of the chamber that *T. erebus* approached, and the final position was the side of the chamber that *T. erebus* was in at the end of the experiment. The overall ('most of time') position was calculated from which side of the chamber *T. erebus* spent most of its time in during the experiment. See text for details of methods. Binomial tests: N.S. in all cases. Null hypothesis: no tendency to choose between control and test-spider.

Test Spider	Choice Criterion	Choice Made	
		Test Spider	Control
Amaurobiid	Initial	4	4
	Final	6	2
	Most of time	5	3
Theridiid	Initial	3	5
	Final	3	5
	Most of time	4	4
All Spiders	Initial	7	9
	Final	9	7
	Most of time	9	7

Table 7 Results of 15 min. tests for olfactory discrimination by *T. erebus*. Test chamber: vial at one end of the chamber with a test-spider inside. Control: empty vial at the other end of the chamber. Choice: the side of the chamber to which *T. erebus* was closer. Choice was recorded by three criteria: initial, final and 'most of time'. Fifty *T. erebus* were tested with amaurobiids and theridiids, and 30 with salticids. All spiders: results pooled for all three types of spiders. See text for details concerning methods. χ^2 test of Goodness of Fit (with Yates' correlation): All cases N.S., except for All spiders 'most of time'. Null hypothesis: no tendency to choose between control and test-spider. * p <0.05.

Test Spider	Choice Criterion	Choice Made	
		Test Spider	Control
Amaurobiid	Initial	23	27
	Final	24	26
	Most of time	29	21
Salticid	Initial	15	15
	Final	19	11
	Most of time	20	10
Theridiid	Initial	26	24
	Final	28	22
	Most of time	28	22
All spiders	Initial	64	66
	Final	71	59
	Most of time	77	53 *

in the salticid trials, nor 'most of time' choice in the theridiid trials affected results.) However, none of these checks indicated potential biases with the pooled data (Appendix C).

Experiment V. Web Discrimination: 4 hr Trials

Taieria erebus did not consistently choose one type of web over another (Table 8). Both the initial and 'most of time' distribution affected the final choice (n = 30, χ^2adj = 6.934, p <0.01, and χ^2adj = 19.024, p <0.001, respectively; Appendix D), but orientation of the web-cages did not (Appendix D). The majority of spiders tested failed to move out of the cage initially occupied. The apparatus appeared to 'trap' the predator in either web chamber. Limitations posed by the light sensors forced the runway to be narrow, but the web chambers were much wider. It appeared that once a spider was in a web chamber, its chances of finding the single narrow exit again were small. A different method was used to continue the study (Experiments VI and VII). However, it is interesting to note that although the trend was not significant, more *T. erebus* were found in the amaurobiid webs, both at the end of the experiment ('final') and in terms of overall time ('most of time') than in the theridiid webs.

Experiment VI. Web Discrimination: 24 hr Trials (Fresh Silk)

Although the initial position of *T. erebus* did not differ from random, the final position was biased toward the amaurobiid webs (n = 41, χ^2 = 9.756, p <0.005; Table 9). Thus, evidence was obtained that indicated selection for the amaurobiid webs by *T. erebus*. Neither initial position nor orientation of the chambers affected the final choice (Appendix E).

Experiment VII Web Discrimination: 24 hr Trials (Stale Silk)

The initial position of *T. erebus* did not differ from random, but in the final position *T. erebus* tended to settle on amaurobiid webs (n = 30, χ^2 = 12.033, p <0.001; Table 10). Thus, with month-old webs, as with fresh webs, *T. erebus* selected amaurobiid webs. Neither the initial distribution of *T. erebus*

Table 8 Results of tests for 4 hr web discrimination by *T. erebus*, with two chambers, each containing different types of web joined together. Choice: web occupied by *T. erebus*. Choice was recorded by three criteria: initial, final and 'most of time' (See Table 6). Thirty *T. erebus* were tested. See text for details concerning methods. χ^2 Test of Goodness of Fit: comparison of choices; N.S. in all cases. Null hypothesis: no difference in tendency to choose between two web-types.

Criterion	Choice Made	
	Amaurobiid web	Theridiid web
initial	14	16
final	17	13
most of time	17	13

Table 9 Results of fresh web discrimination tests for *T. erebus*. Test chambers: two cages containing fresh webs, joined directly to each other. Choice: which web *T. erebus* entered. Choice recorded by two criteria: initial and final positions. 41 *T. erebus* were tested. See text for details of methods. χ^2 test for Goodness: comparison of choices. Final choice significant ($\chi^2 = 9.756$, $p < 0.005$). Null hypothesis: no difference in tendency to choose between the two web-types.

Criterion	Choice Made	
	Amaurobiid web	Theridiid web
initial	24	17
final	31	10

Table 10 Results of web attraction tests on *T. erebus* using month-old webs. Test chambers: two cages containing webs, joined directly to each other. Choice: which web *T. erebus* was on. Choice recorded by two criteria: initial and final positions. 30 *T. erebus* were tested. See text for details concerning methods. χ^2 Test of Goodness of Fit: comparison of choices. Final position significant ($\chi^2 = 12.033$, $p < 0.001$). Null hypothesis: no tendency to choose between the two web-types.

Criterion	Choice Made	
	Amaurobiid web	Theridiid web
initial	15	15
final	25	5

nor orientation of the chambers affected the final distribution (Appendix F).

Experiment VIII. Artificial Web Vibration

In basic respects, *T. erebus* responded to artificial vibrations as it responded to vibrations from arthropods on webs. When the probe moved the web, *T. erebus* responded by first jerking its legs slightly. After this, the spider typically remained in one spot and was motionless apart from vibratory movements of the palps and the first two pairs of legs. Vibrational responses by *T. erebus* were shorter, more disjointed, and less energetic than when the web vibrations were caused by an insect or another spider. Once when I was trying to free the probe when it jammed, *T. erebus* moved 10 cm up the web and touched the tip of the probe with legs I.

Experiment IX Non-visual Predation by *Taieria erebus*

Despite not being able to see, *T. erebus* used vibratory behaviour and caught prey both on and off webs (Table 11). As all spiders died within 4 days of painting, I did not feel justified in creating a larger sample size. The reasons for these deaths were not ascertained and the rapid mortality of painted *T. erebus* was surprising, since various other species of spiders are known to survive when treated similarly (Land, 1969b; Jackson and Harding, 1982; Jackson and Pollard, 1982). Anaesthetising did not appear especially stressful in itself as other *T. erebus* that were also anaesthetised by CO_2 survived. It appears that either the paint was toxic or that stresses resulting from the CO_2, handling and painting combined were severe.

Scopulate Hairs

Taieria erebus had conspicuous scopulate hairs and claw tufts, when viewed under a light microscope and especially when examined by S.E.M. (Figs 18 - 23). Scopulate hairs were leaf-like in appearance, with a stem and a flattened blade bent at an angle to the stem. On both sides of the blade there were thousands

Table 11 Responses of *Taieria erebus*, with eyes painted, to prey. See text for details. Each *T. erebus* was given amaurobiid or *Drosophila* prey in the absence of webs, or amaurobiid or *Drosophila* prey on well developed webs.

prey	on web			off web		
	eaten	not eaten	Σ	eaten	not eaten	Σ
amaurobiid	6	1	7	2	0	2
fly	1	3	4	3	1	4

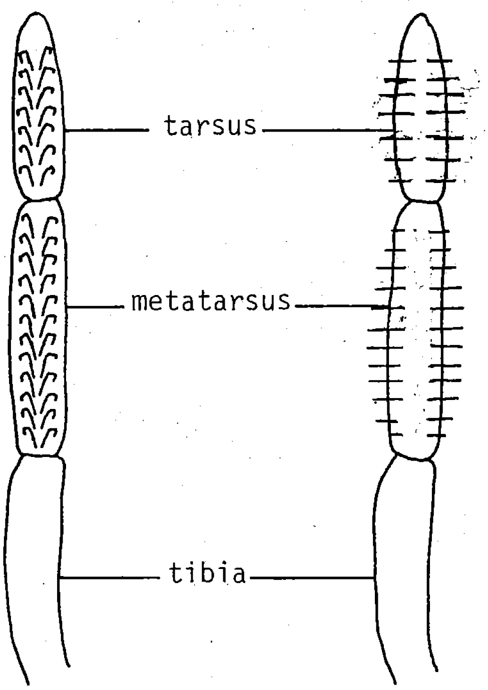
of cuticular extensions ('suction end feet') on one side of the blade. The end feet had pointed tips, while end feet on the other side had clubbed or triangular tips. The scopulate hairs were distributed along the ventro-lateral surface of each leg I and II tibia, metatarsus and tarsus; on leg III tarsi only, and not at all on legs IV. The scopulate hairs were arranged in two double rows on legs I and II, but in only a single double row on legs III.

Normally the scopulate hairs were angled toward the distal tip of the leg. The end feet were on the side of the hair facing away from the surface of the leg, and somewhat medial with respect to the long axis of the leg. However, under hydrostatic pressure (e.g. when extending the legs and lunging in an attack) or when a leg was gently squeezed between forceps (Fig. 16), the scopulate hairs became erect (perpendicular to the leg surface). When erect, the end feet faced medially, so that the two rows,on either side of the leg, faced each other (Fig. 17).

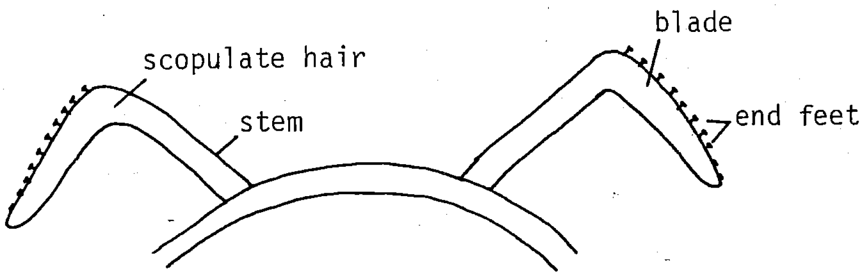
Remarkably, the scopulate hairs of *T. erebus* had raised, notched bases similar to the bases of trichobothria and similar to the bases of salticid scopulate hairs. This was such a surprising finding that the legs of some other gnaphosid species and of *Mimetus* sp. (Mimetidae) were also examined by S.E.M. The mimetid lacked scopulate hairs altogether. The three other gnaphosids examined had scopulate hairs. The scopulate hairs of *Hemicloae rogenhoferi* had simple bases, but those of *Lampona cylindrata* and *Anzacia gemmea* had scopulate hairs with raised notched bases, similar to those of *T. erebus* (Figs 24 - 27).

Fig. 16 Diagrams showing changes in orientation of two scopulate hairs of *Taieria erebus* during extension of leg. Ventral view of legs I. Hairs shown on tarsus and metatarsus only. Hairs are erected during leg extension.

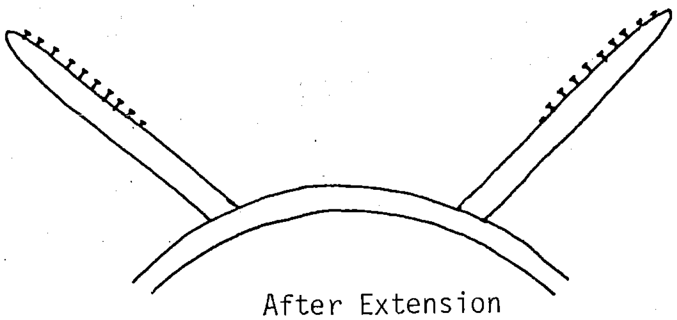
Fig. 17 Diagrams of transverse section of leg showing change in orientation of a pair of scopulate hairs of *Taieria erebus* during extension of leg. Hairs are erected during leg extension, and end feet on the two hairs face toward instead of away from each other.



Before Extension After Extension



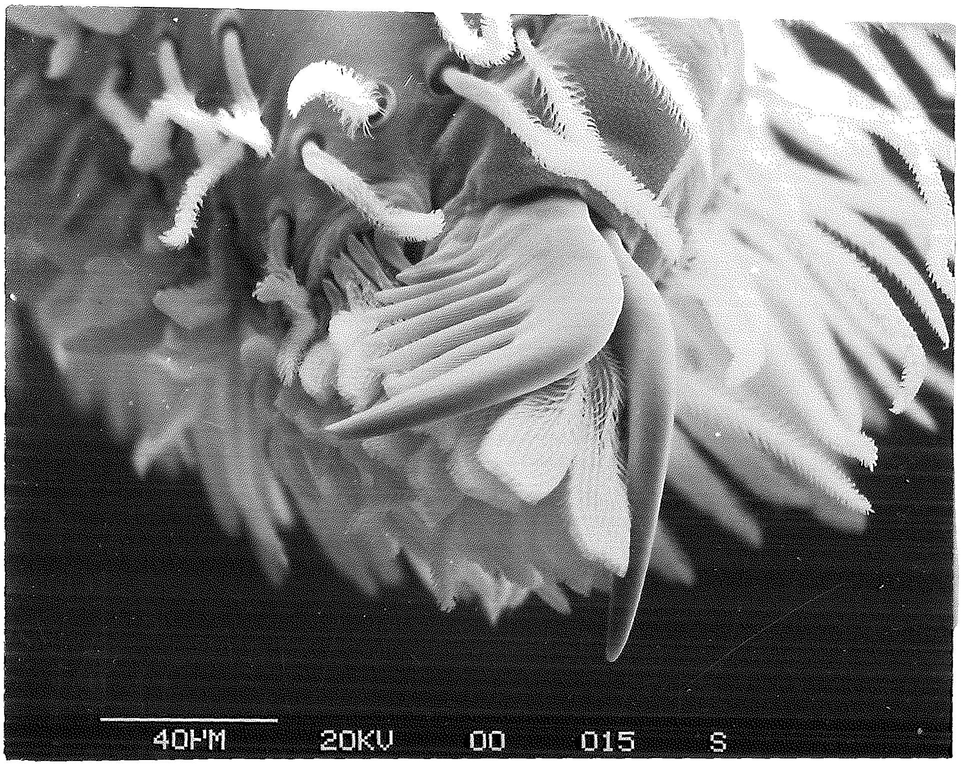
Before Extension



After Extension

Fig. 18 Pretarsus of leg I of *Taieria erebus*. Slightly dorsal view. Note claw tufts between the two claws. Scale: lower left.

Fig. 19 Pretarsus of leg I of *Taieria erebus*. Ventral view. Note the ventral sides of the claw tuft blades are covered in tiny (adhesive) end feet, especially on two claw tuft hairs at bottom of figure. Scale: lower left.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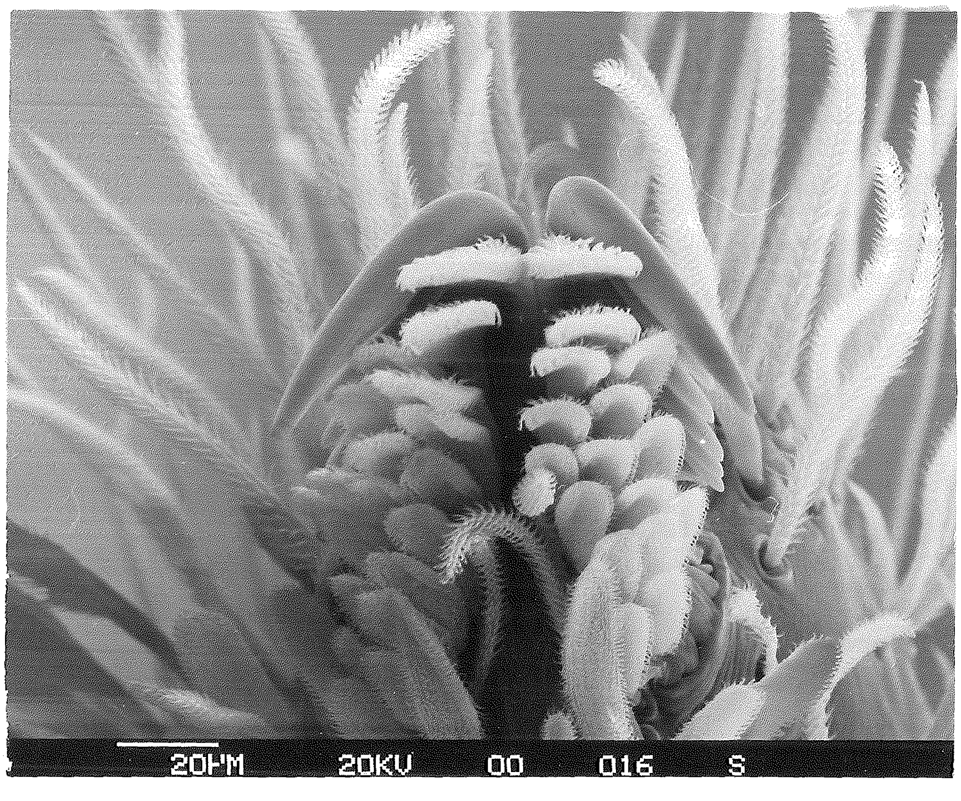
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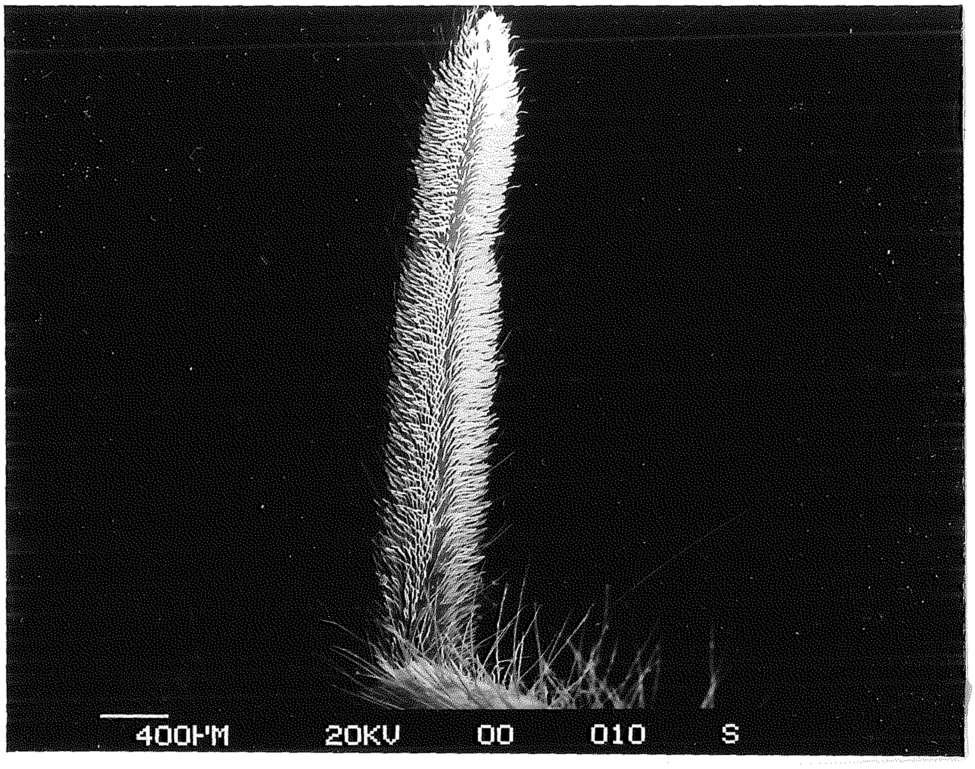
Fig. 20 Ventral view of tarsus and metatarsus of leg I of *Taieria erebus*. Scopulate hairs densely arranged in rows along two sides of leg midline. Scale: lower left.

Fig. 21 Ventral tarsus of leg I of *Taieria erebus*. Note rows of scopulate hairs. Each scopulate hair bent sharply to side. Clubbed end-feet on dorsal-medial surfaces. Also, note chemosensory hairs along midline of leg, between rows of scopulate hairs. Scale: lower left.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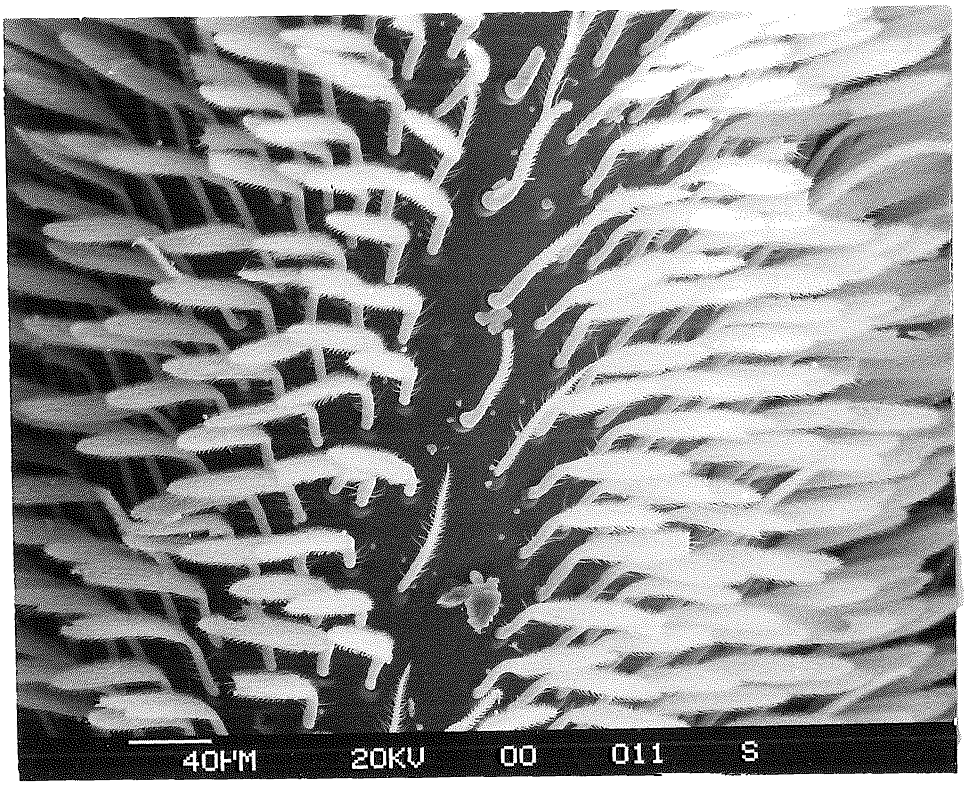
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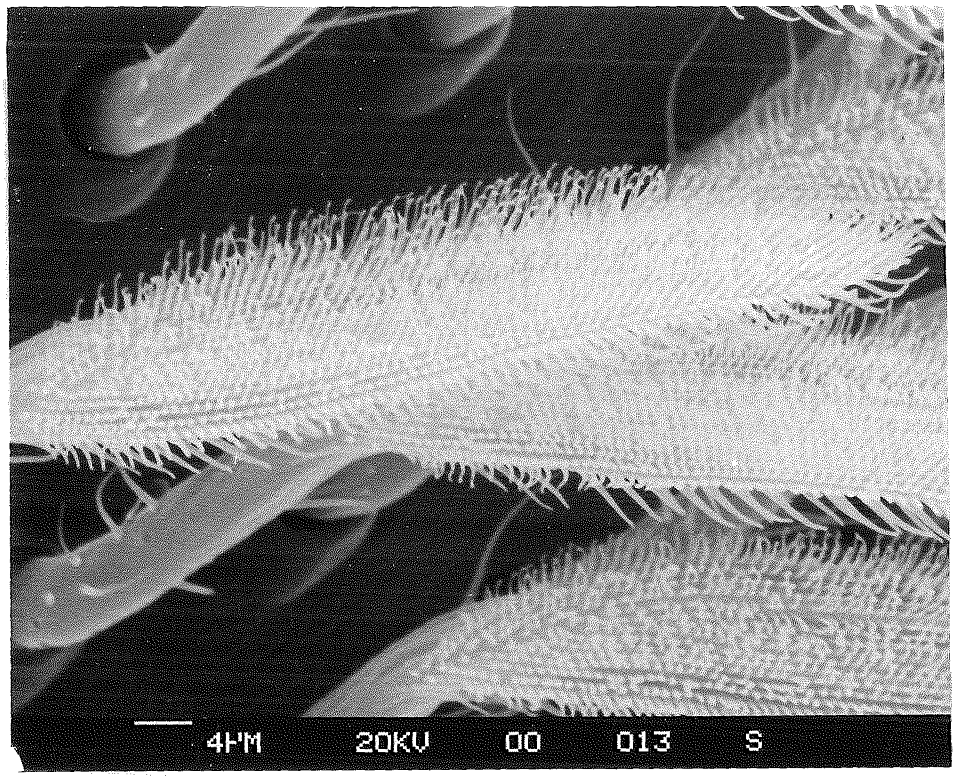
Fig. 22 Scopulate hairs on tarsus of leg I of *Taieria erebus*. Note numerous end-feet. Scale: lower left.

Fig. 23 End-feet on scopulate hair of *Taieria erebus*. Tarsus of leg I. Note: end-feet are triangular (clubbed) in shape. Scale: lower left.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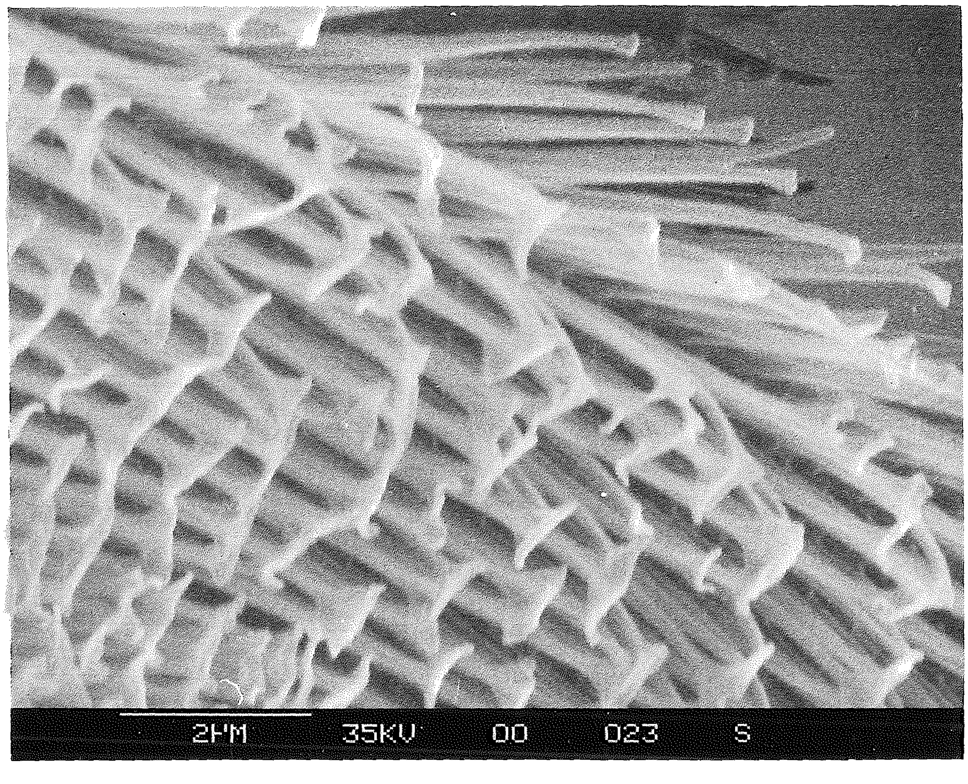
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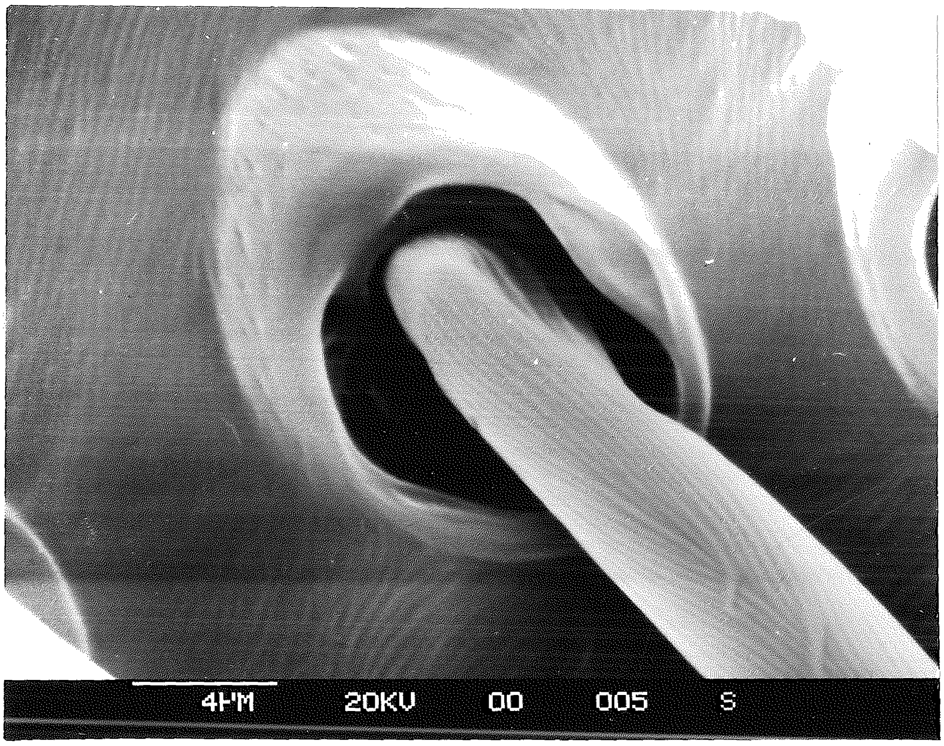
Fig. 24 Base of scopulate hair of *Taieria erebus*. Leg I tarsus. Base is raised, with notch (upper right). Stem of hair extends towards lower right of figure. Scale: lower left.

Fig. 25 Leg I metatarsus of *Hemicloae rogenhoferi* (Gnaphosidae). Lower right: scopulate hair. Note simple base. Stem extends to upper right of figure. Scale: 5000 X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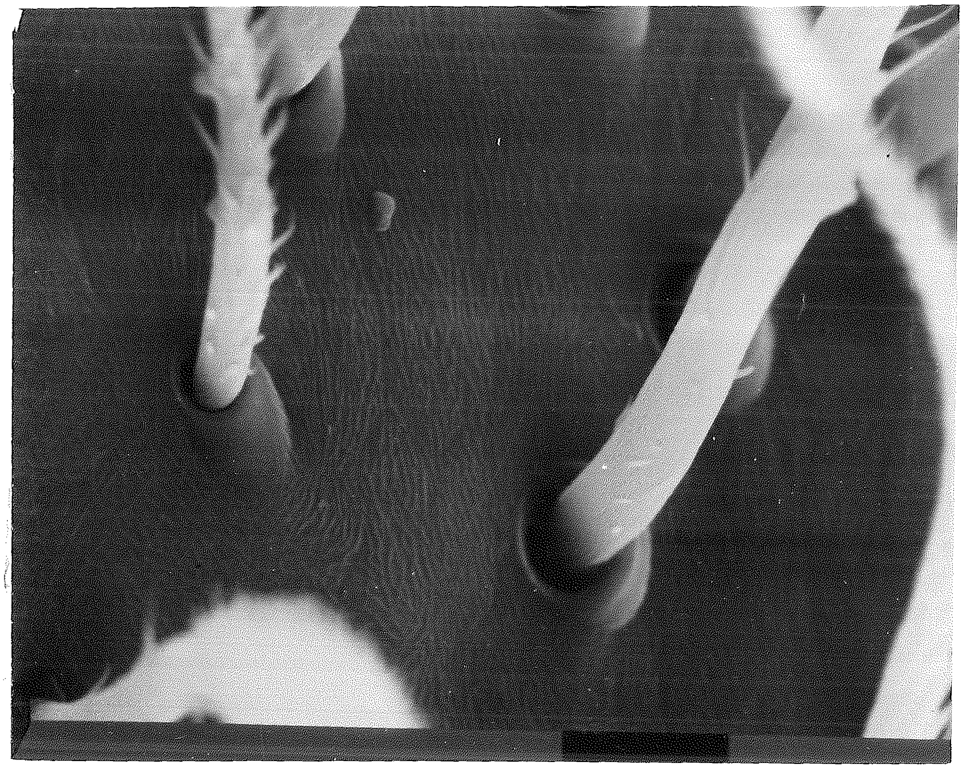
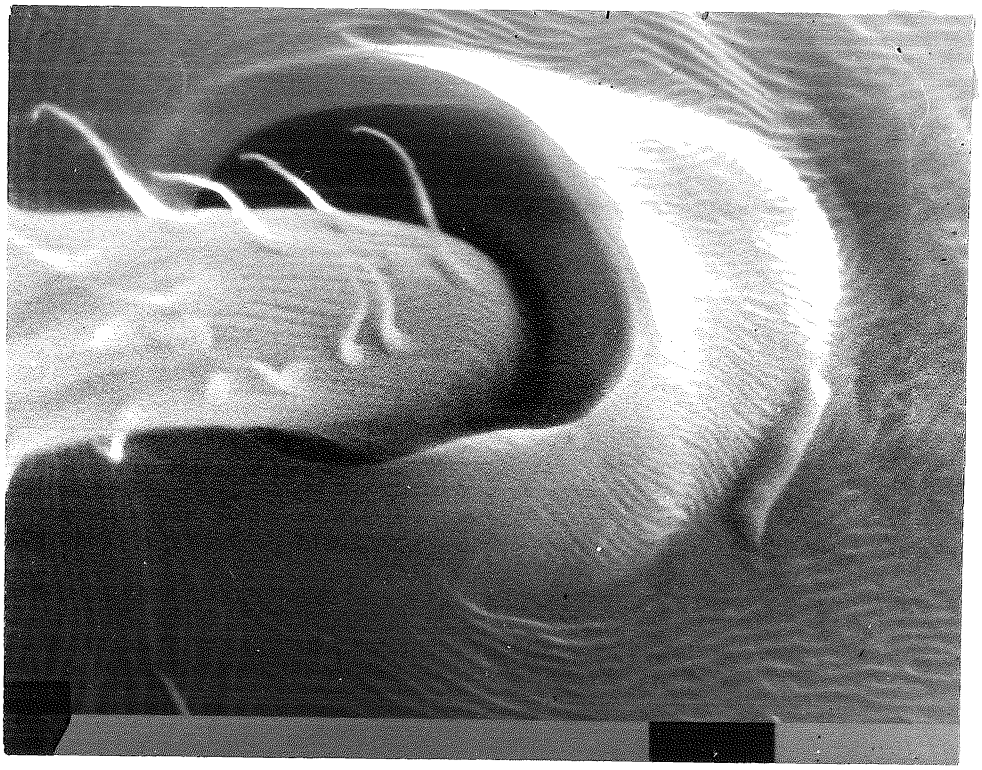
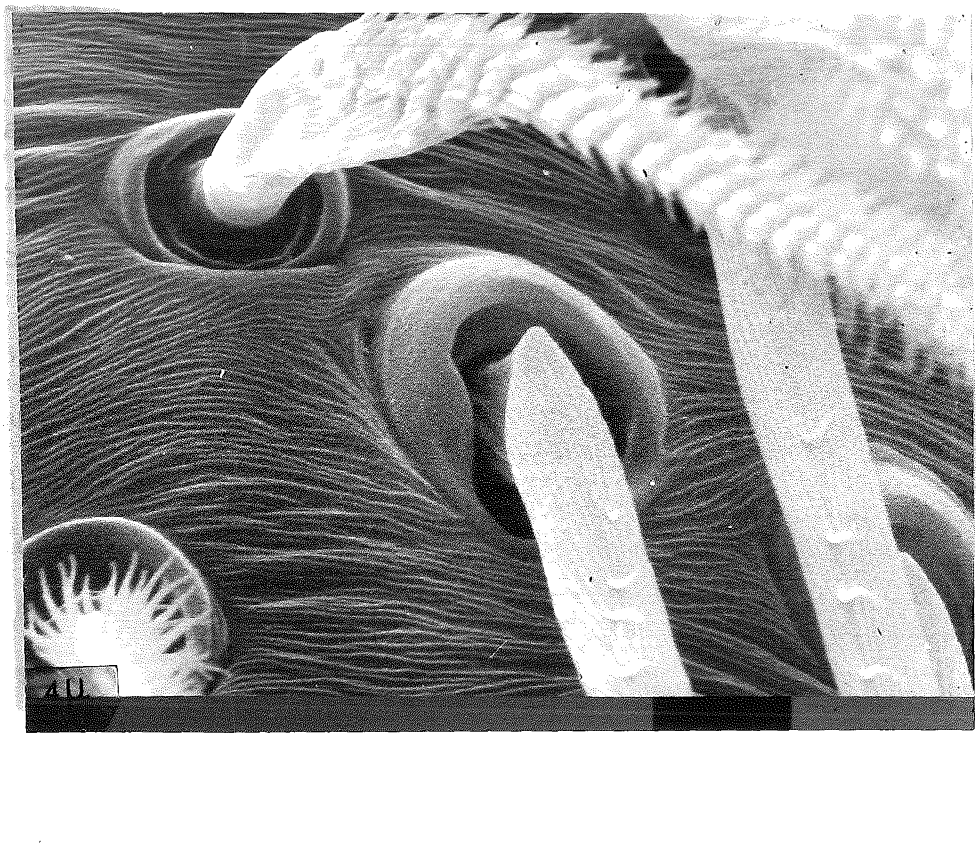


Fig. 26 Scopulate hair of *Anzacia gemmea* (Gnaphosidae). Leg I metatarsus. Base is raised, with notch (lower). Stem of hair extends to left in figure. Scale: 10000 X.

Fig. 27 Leg I tarsus of *Lampona cylindrata* (Gnaphosidae). Centre: scopulate hair. Note raised base, with distinct notch (lower left). Stem extends downward in figure. Scale: 6000 X.

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DISCUSSION

Prey Preference and Locomotion on Silk

Both informal observations and experimental results (Experiment II) indicate that *T. erebus* is more adept at catching some prey items than others (Table 7). *T. erebus* appears more proficient at preying upon salticids, amaurobiids and flies on webs, than preying on flies off webs and theridiids in webs. When dropped onto amaurobiid and theridiid webs in the laboratory, *T. erebus* walked rapidly and with apparent ease on the amaurobiid webs, but slowly on the theridiid webs, occasionally slipping and falling.

T. erebus tended to adhere to the sticky droplets on theridiid webs and extricated itself (apparently) only with difficulty, but did not seem to adhere to the 'wooly' cribellate silk of the amaurobiid webs. Hence the spider appears able to move less hampered on cribellate silk than ecribellate silk. It is not known how *T. erebus* avoids sticking to the cribellate silk while tending to adhere to ecribellate silk. It is also not known as yet, how spiders that build sticky webs avoid sticking to their own webs (Foelix, 1975). Cribellate and ecribellate webs differ not only in structure, but in layout; ecribellate web-building spiders (theridiids) always build spaced out webs that have large gaps between the threads, while cribellate web-building spiders may build webs that are much more closely knit and intermeshed. For example, *Ixeuticus martius* produces cribellate webs that are more or less closely woven.

Possibly *T. erebus* is adapted to walking on, locating and catching spiders (and insects) on webs with the basic physical design of *Ixeuticus*, but not theridiids. Also, *T. erebus* has unknown adaptations that enable it to avoid sticking to cribellate glue but do not protect it from ecribellate glue. If *T. erebus* has not become adapted to locomotion on webs with the basic design of theridiid spiders, then it is not surprising that *T. erebus* has not acquired mechanisms to avoid sticking to the ecribellate glue.

Prey Discrimination

Vision

Unlike salticids, vision is not an important modality to *T. erebus* in prey capture: blinded *T. erebus* caught both spider and insect prey, both in the presence and absence of webs. It appears that vibratory information is of more importance to *T. erebus* than vision. Vibratory behaviour, similar to that of unpainted *T. erebus*, was observed during predation on webs by painted spiders, and, as with unpainted *T. erebus*, vibratory behaviour during attack sequences was more complex and of longer duration when the web occupant was a spider and not an insect.

Somehow, *T. erebus* must be able to distinguish between the vibrations of a spider and those induced by a struggling insect. It is interesting to note here that when a trapped insect was struggling vigorously, *T. erebus* tended to perform vibratory behaviour (palp drum and palp tug) and made lunge attacks; but if the insect was relatively quiescent, *T. erebus* only briefly, if at all, vibrated (palp drum) then walked to the prey and seized it with no lunge occurring. Hence, a struggling fly induced a predatory response similar to that given to a spider, while a non-struggling insect elicited very little vibratory behaviour and no lunge attacks.

Vibrations by potential spider prey in webs were spaced out at irregular intervals, occurred in short bursts and did not often visibly disturb the web. Vibrations produced by struggling insects were also irregular, but tended to occur for long periods of time and visibly disturbed that section of the web to which the insect was attached.

T. erebus may be able to distinguish between 'fine' disruptions to the web caused by a spider, and the 'coarse' disruptions produced by a trapped insect. Possibly the magnitude of the web vibrations is the cue by which *T. erebus* could make these discriminations on a theridiid web.

Web discrimination

For a predator with prey specific behaviour, the ability to discriminate between types of prey is of obvious importance. *T. erebus* is a web-invading spider with a preference for cribellate spiders. The ability to discriminate between web types would provide a specialised web invader with an efficient mechanism of prey discrimination. Due to the presenceof the host spider, a web may possess chemical stimuli or kairomones (Brown *et al.*, 1970) that alert the predator. The chemical nature of semiochemicals (Wilson, 1975) is such that they would probably dissipate over time, if not constantly replenished by the activity of the host spider. As a result, fresh and stale silk was tested on the assumption that fresh webs might have silk-associated kairomones, while the stale silk would not (Experiments VI and VII). If *T. erebus* had chosen between the fresh (cribellate and ecribellate) but not the stale (cribellate and ecribellate) silk, then the use of kairomones in web discrimination would have been implicated. However, since *T. erebus* consistently chose cribellate webs regardless of silk age, discrimination appeared to be on the basis of structure instead of volatile kairomones. If chemical cues are important, they must be tightly bound to the silk. Structural cues seem more likely.

The two kinds of webs are structurally very different, especially as a result of one having a cribellate 'wool' that covers the structural lines and the others having fluid glue droplets strung along the lines.

The use of both chemical and structural cues in web discrimination has been demonstrated in other spiders. Social dictynid spiders (cribellate) are chemically attracted to the silk of conspecifics and chemically repelled from silk of other dictynids, and they are repelled by structural cues from araneid silk (ecribellate, sticky) (Jackson, 1982b).

Prey Localisation

A complete answer cannot yet be given as to how *T. erebus* locates its prey but some partial and preliminary answers are possible.

Cursorial predation

Contact between *T. erebus* and the potential prey often seemed important; sometimes *T. erebus* may be more of an ambusher than a mobile spider. However, *T. erebus* sometimes detected the presence of prey before contacting it, and moved towards it. Vision is not necessary. Possibly vibrations through the substrate, sound, or olfaction are used to detect and locate the prey.

Predation on nests and webs

The silk of spiders appears to be an important stimulus for initiating the vibratory behaviour of *T. erebus*. The vibratory behaviour of *T. erebus* elicits responses from the host spiders, thus informing *T. erebus* that the web is occupied. *T. erebus* can attract the prey spider to within attack distance by use of its vibratory behaviour. However, *T. erebus* can also move to the spider, apparently using vibrational stimuli transmitted through the silk from the prey.

Part of how *T. erebus* locates spiders on webs is to first locate webs and then vibrate on them, eliciting movements by the prey-spider in response. The prey-spider is deceived by the vibratory behaviour of *T. erebus* and responds in a way appropriate to its own insect prey rather than to a potential predator (i.e. *T. erebus*). Salticids respond in a way that is perhaps normally appropriate for a conspecific competitor or a potential mate on their nests, since numerous species have nest-associated vibratory communication (Jackson, 1982a); and nests are more or less opaque, and usually located under stones, in rolled leaves, and other such places with low intensity, ambient light (Jackson, 1978).

Preliminary results (Experiment IV), suggesting that *T. erebus* can follow olfactory gradients to locate spiders over distances of several centimetres, are particularly interesting. Various mammals, snakes, insects and other animals, are known to locate prey by olfaction (Curio, 1976; Wood, 1982; Burhardt, 1970), but this has not been demonstrated before in spiders. It needs to be emphasized that the conclusion that *T. erebus* locates prey olfactorily is preliminary. There was no evidence that *T. erebus* discriminated olfactorily between types of spiders and experiments have not yet been attempted to test whether *T. erebus* is olfactorily attracted to insects and other animals. It seems unlikely that substrate vibration or sound (airborne vibrations) were attracting *T. erebus*, since movements of the test spiders were not very common during the trials.

The null hypothesis of equal tendency to move to the test spider or control was rejected at only the 5% level, and 130 trials (results for all test spiders pooled) was necessary for this. Additional research is needed on this important question of olfactory prey location. *T. erebus* was placed in the test chamber by lifting the roof; this action, however, might disrupt an olfactory gradient if present. A better method might be to drill a hole in the roof of the chamber and seal this with a cork. A plastic transfer-tube containing *T. erebus* could then be placed against the hole (cork removed) and *T. erebus* gently coerced with a paint brush, inserted through the opposite hole in the tube, to move out of the tube into the chamber. Little disruption of the potential olfactory gradient should occur using this method. Use of anaesthetised or recently dead spiders in the test chambers would eliminate the extraneous variable of potential vibrational cues. Preliminary attempts at this were unsuccessful, possibly because the method used to obtain dead spiders (rapid freezing) was unsuitable. Perhaps a better alternative method would be to use chemical extracts from the test spiders.

Aggressive Mimicry

Examples of aggressive or Peckhamian mimicry are uncommon (Wickler, 1968; Curio, 1976). Fireflies and bolas spiders are perhaps the best known arthropod examples. Fireflies (Lampyridae) use flashes of bioluminescent light for sexual communication. Female fireflies of the genus *Photuris* are carnivorous and attract males of the genus *Photinus* by mimicking the flash response of *Photinus* females. *Photuris* males have carried this one step further by mimicking the signals of male *Photinus*, the prey of female *Photuris*, thus seducing hungry conspecific females (Lloyd, 1965, 1980, 1981).

Bolas spiders (Araneidae) practise aggressive chemical mimicry. These spiders are descended from orb-weavers, but their webs has become reduced to a sticky ball suspended on the end of a short thread attached to a single horizontal line. Mature female bolas spiders (*Mastophora* sp.) produce a volatile substance that apparently mimics the sex attractant pheromone of virgin females of the fall army worm *Spodoptera fugiperda* (Lepidoptera) and attracts male moths which are struck by the twirling ball of glue held on the end of the short thread (Eberhard, 1977, 1980).

T. erebus is another example of aggressive mimicry. Like the fireflies and bolas spiders, *T. erebus* mimics something for which it is normally to the prey's advantage to approach. The fireflies and bolas spiders mimic the sexual signals of the prey's conspecific females. *T. erebus* mimics, instead, the prey of its own predatory prey by vibrating webs, apparently mimicking the struggles of trapped insects. These 'false' struggles deceive the host spider, causing it to approach the predator. In this way *T. erebus* is an aggressive mimic more like the angler fish which mimics the prey of smaller predatory fish (Wickler, 1968). *T. erebus* is even more similar in the practice of aggressive mimicry to some other araneophagic web-invading spiders. *Portia fimbriata* (Jackson and Blest, 1982) some closely related salticids (Jackson, in press) and at least one species of mimetid (Czajka, 1963) have been reported to similarly deceive web-building spiders by vibrating on their webs.

If *T. erebus* is such an effective mimic as it appears to be, then it would seem advantageous for the prey to change its behaviour in such a way as to not fall victim to the aggressive mimic. However, the mimic in this case is mimicking something for which it is normally important for the prey to approach. As long as the aggressive mimic is not too abundant, then the victim (prey) may not be under strong enough selection to significantly reduce its tendency to respond positively to the signal or to distinguish the imitation from the real signal. *T. erebus*, like the web-invading salticids and mimetids, in nature probablypreys on several or many species; and perhaps it is not a major predator of any one of them.

For a hungry *Ixeuticus martius*, for instance, it might be on the whole better to take a relatively minor risk of becoming a meal than to risk losing a meal when its web is vibrated. Thorough field studies, including determination of the relative densities of *T. erebus* and its prey, would be useful.

Venom of *Taieria erebus*

Both insect and spider prey were usually immobilised 2-4 sec. after being bitten by *T. erebus*. Mimetids and the araneophagic salticids are also known to have very fast acting venom (Jackson, in press), and possibly these venoms of araneophagic spiders have biochemical specialisations that make them especially effective. Precise information is not available on many spider species, but usually ca. 20 sec. is required before spiders attacked by *Portia fimbriata* are paralysed (Jackson, and Blest, 1982). *T. erebus* venom acts more quickly than this and is probably one of the fastest acting spider venoms known. The insect prey of *Lactrodectus katipo*, for example, are not subdued usually until 3-5 min. after being bitten (Franklin, 1983). *T. erebus* would seem to be an especially attractive spider for physiological and chemical studies.

Predatory Versatility

Predators are often thought of as tending to be on a continuum between specialist and generalists. The specialist is monophagic, or stenophagic, and has a set of behavioural responses that enable it to effectively capture the single (or narrow range of) type(s) of prey in its diet. The generalist is polyphagic, or euryphagic, and has a set of generalised predatory behaviours that enable it to be reasonably effective at catching a variety of prey types. Versatile predators do not fit so conveniently within this classification system.

It is characteristic of versatile species that each individual has a set of prey-specific predatory behaviours. A different, specialised response occurs depending on the prey type. The versatile predator is polyphagic and has several specialised predatory behaviours specific to different prey. Thus the versatile predator is neither strictly a generalist nor strictly a specialist. Examples of this are not common in the animal kingdom (Curio, 1976). Excluding humans, the salticid spider *Portia fimbriata* may be the most extreme example so far recorded.

Recently,other distinctive examples, although not as extreme as *Portia fimbriata*, have been recorded for several additional species of *Portia* and related species of salticids (Jackson, in press)and a New Zealand dragonfly nymph *Hemianax papuensis* (Rowe, pers. comm.). Hence, *T. erebus* is of particular interest because it is another species with distinctive predatory versatility (Table 12).

Cursorial predation

In cursorial predation the predatory behaviour of *T. erebus* appeared simple and consistent with the common picture of the typical predatory behaviour of cursorial, mobile spiders that do not spit or use silk (see Introduction).

Table 12	*Taieria erebus*	*Portia fimbriata*	Other *Portia*	Related Salticids
Effective Predation	Both Insects and Spiders	Salticids: Yes Insects: No	Salticids: No Insects: Moderate	Salticids: No Insects: Yes
Web invaders araneophagic vibration	cribellate webs	all webs	all webs	all webs
Kleptoparasitism and egg predation	Yes	Yes	Yes	Yes
Nest invasion Salticid	Yes	Yes	No	No
Salticid egg predation	Yes	Yes	Yes	Yes

T. erebus has predatory versatility in a pronounced form. *P. fimbriata* has specialised salticid stalking and the ability to invade more web types than *T. erebus*. *T. erebus*, however, is an effective cursorial insect predator unlike *Portia*. Other versatile salticids are more like *T. erebus* in this respect.

In *T. erebus* there were no differences between cursorial predation on insects, web-building spiders presented away from webs, and salticids presented away from webs.

Kleptoparasitism on webs

Insects were taken from amaurobiid webs with behaviours similar to those used in cursorial predation except simple attacks, rather than lunge attacks, usually occurred. In the laboratory *T. erebus* was more efficient at catching insects kleptoparasitically than cursorially.

Araneophagic predation on nests and webs

Predatory behavioural sequences on nests were more complex than in either cursorial predation or kleptoparasitism. The leg-strike of *T. erebus* was unique to on-nest predation, but palp tug and palp drum also occurred on webs. The most complex predatory sequences of *T. erebus* occurred on webs occupied by other spiders. All of the described elements of specialised predatory behaviour of *T. erebus*, except for two (leg strike and leg drum), were used in this situation. The order and duration of use of each element varied greatly. Typically, however, slightly more palp drumming occurred than either palp tugging or plucking. Plucking of the silk with legs I and/or II was unique to predatory sequences on webs.

From observations in the laboratory, a trend appeared to be that the more complicated attack sequences took place on silk, and that the more complicated they were the longer they took. Hence, silk appears to be a cue to use the more complex predatory behaviours; but it is not the only one, as one notable exception to this trend occurred: *Drosophila* trapped in webs elicited 'cursorial' predation, despite the presence of silk.

T. erebus exhibited different predatory behaviours on different forms of silk (webs or nests). Also, different predatory behaviours occurred depending on whether a spider or an insect was the occupant of the web invaded. *P. fimbriata*, unlike *T. erebus*, is an effective predator on all web types - *T. erebus* is only proficient on cribellate silk. However, *T. erebus* catches both insects and spiders cursorially and in webs, while *P. fimbriata* is ineffective at catching insects cursorially. Both spiders prey on salticid eggs in salticid nests. Hence, *T. erebus*, like *P. fimbriata*, is also an extreme example of predatory versatility.

Although the predatory versatility of *T. erebus* is not so pronounced as that of *P. fimbriata*, it is nevertheless one of the more distinctive cases described for animals in general. There are both important similarities and differences between the predatory versatility of *T. erebus* and *P. fimbriata*. One of the most interesting differences is the wide range of webs that *P. fimbriata* is effective at invading, compared to the narrower range of *T. erebus*.

Scopulate Hairs

There are both similarities and differences in the distribution and form of the scopulate hairs of *T. erebus* and *P. fimbriata*. There were many more scopulate hairs on the legs of *T. erebus* than on the legs of *P. fimbriata* In *T. erebus*, the triangular end feet lie on the side of the hair blade away from the leg surface, while in *P. fimbriata* they are arranged on the side of the hair blade closest to the leg; and in *T. erebus* the scopulate hairs lie angled toward the distal tip of the leg, while in *P. fimbriata* they point away from the distal tip.

As in *P. fimbriata*, the scopulate hairs are erectile, and greatly increase the surface area of the leg when raised. All of these spiders are able to catch oversize prey (larger than themselves).

The function proposed by Rovner (1978) and Foelix *et al.* (in press) for lycosid and salticid scopulate hairs (gripping large prey) seems likely for the scopulate hairs of *T. erebus* also: these hairs are used in grasping large active prey.

In all of the species investigated, including *T. erebus*, the end feet of the scopulate hairs,when erected, were appropriately positioned to contact the prey (Figs 16,17) although this is accomplished in different ways by the different species.

The raised notched bases of the scopulate hairs of *T. erebus* are remarkably similar to those of the salticids. A purely functional explanation for this resemblance is difficult to defend. The notch may allow the hairs to lock into the erected position, perhaps increasing the effectiveness of the hairs in gripping prey; but it is still uncertain as to how this unusual type of scopulate hair has come to be shared by these particular spiders.

T. erebus and *P. fimbriata* have behavioural similarities. Both are versatile predators that invade webs, eat spiders, eat salticids, feed as kleptoparasites and vibrate in webs. It is difficult to propose why any of these behaviours might explain the same unusual basal structures. This is a problem especially because yet other salticids and gnaphosids have such scopulate hair bases.

All of the studied salticids with this type of scopulate hairs, except one, are now known to be versatile predators, more or less like *P. fimbriata*, but the exception (*Phaecius* sp.) is an ambushing insect predator (Jackson, in press).

Of the gnaphosids with these peculiar types of scopulate hairs, *Lampona cylindrata* is a web invader (Forster and Blest, 1979) but *Anzacia gemmea* is a mobile insect predator (Jackson, pers. comm.). Whatever the functional significance of this special basal structure, the common occurrence of this trait in the group of salticids studied, all of which have been considered primitive (Jackson, in press) and in certain gnaphosids including *T. erebus*, possibly suggests that these two groups of spiders are closely related. The Gnaphosidae has not previously been suggested as a sister group of the Salticidae (Jackson, pers. comm.), although the Clubionidae which are generally considered to be closely related to the gnaphosids (Forster and Forster, 1973) has been suggested as a sister group (Platnick, 1971).

It would be premature to speculate futher on the complex questions that these results and suggestions raise. This is certainly an area needing much more research and also demanding a greater and broader knowledge of spiders than I have at present.

The Evolution of the Salticidae

T. erebus is, like *P. fimbriata* and some related salticids, a versatile predator that catches prey both cursorially and by web-invasion. Unlike the Salticidae, *T. erebus* has poorly developed vision. Jackson and Blest (1982) proposed vision was crucial in enabling the ancestors of modern salticids to be effective at invading many different types of webs. If *T. erebus* had been found to be comparable to *P. fimbriata* and its relatives at araneophagic invasion of many types of webs, then the hypothesised link between vision and invasion of many web types would have seemed invalid. However, *T. erebus* was found to be restricted compared to *P. fimbriata* in the variety of web types on which it is an effective predator. *T. erebus* had difficulty walking on ecribellate theridiid webs, and stuck to ecribellate glue. Amaurobiids were preferred as prey. *T. erebus* walked on amaurobiid webs with ease, and it did not tend to stick to cribellate glue. *P. fimbriata* has no difficulty as a predator with either of these types of webs. Thus, the study has failed to refute a basic component of the evolutionary hypothesis of Jackson and Blest (1982). However, it needs to be emphasised that more work is needed. For instance, more information is needed about the sense organs of *T. erebus*. Also, it needs to be emphasised that the results of this study seem to suggest the hypothesis that vision is needed for a spider to effectively invade many types of webs as a predator. This is not the same as proving that vision evolved in the way Jackson and Blest proposed. An ordinary salticid with well developed vision might have been preadapted to become a web invading spider. The information obtained in this study of *T. erebus* is, therefore, relevant to the hypothesis about salticid evolution but cannot prove it correct. It could have to come close, at least, to proving it incorrect, but it did not.

The surprising discovery of scopulate hairs on *T. erebus* with important similarities to scopulate hairs of *P. fimbriata* and related salticids, suggests that *T. erebus* may in fact be a close relative of the salticids and more relevant to the study of salticid evolution than originally expected.

CONCLUSION

Many New Zealand species possess features that are regarded as unusual or primitive. The kiwi, tuatara and kakapo are all well known examples. *T. erebus* is a small brown spider native to New Zealand that has, until now, attracted little scientific interest. However, like the kiwi, tuatara and kakapo, *T. erebus* has now been shown to possess unusual and exciting features.

T. erebus is unusual as it is an exceptionally versatile predator that catches insects and other spiders, both on and off webs. Although *T. erebus* does not build webs, it routinely invades the webs of other spiders and feeds kleptoparasitically by preying upon insects trapped in the webs. It also vibrates on webs, apparently mimicking the struggles of trapped insects, thus deceiving the host which it subsequently attacks. This is one of the few examples of aggressive mimicry known to occur in animals.

There are few examples of pronounced predatory versatility that have been described in the animal kingdom, and in spiders the major example is the salticid *Portia fimbriata*. *P. fimbriata* relies heavily on vision in prey localisation and preys on spiders in diverse types of webs. *P. fimbriata* also spins webs, eats spider eggs, feeds kleptoparasitically and captures cursorial salticids, both in and away from the latter's nests.

T. erebus differs from *P. fimbriata* in a number of ways, but especially by not using vision in locating prey and by being effective at invading fewer types of webs than *P. fimbriata*. *T. erebus* is especially effective as a predator on cribellate amaurobiid webs, but not ecribellate theridiid webs, and prefers amaurobiids to theridiids as prey.

The findings of this study are consistent with the hypothesis of Jackson and Blest (1982) that the origins of acute vision, predatory invasion of diverse web types, and the evolution of the Salticidae are linked, although these findings cannot be taken as having proven this hypothesis. *T. erebus* has specialized hairs on its forelegs (scopulate hairs) that probably assist in prey retention. *P. fimbriata* and some related salticids, but not most salticids, have scopulate hairs also. Remarkably, the scopulate hairs of the salticids resemble those of *T. erebus*, having a similar and unusual basal structure, suggesting a close relationship between the salticids and gnaphosids, especially the araneophagic spiders of these two families.

T. erebus seems to use tactile and vibrational cues in detecting and locating its prey. There is, also, preliminary evidence that olfaction is used to locate spiders. This is potentially important as olfactory prey localisation has not been experimentally demonstrated before in spiders.

Numerous questions are raised by the unusual biology of *T. erebus* including the question of why does pronounced predatory versatility occur in this spider. The occurrence of numerous other spider species in the same microhabitats as, or in similar microhabitats to, those of *T. erebus* suggest that simply considering adaptation and natural selection will be inadequate. It has been suggested that phylogenetic considerations, as well as adaptations, are crucual for explaining predatory versatility in *P. fimbriata* and related salticids (Jackson, in press).

Portia fimbriata is, for example, both a web-building and a cursorial predator. Part of the explanation for this particular behavioural repertoire in this spider, according to Jackson and Blest (1982), is the web-building ancestry of the salticids from which *Portia* have not greatly diverged. This invites similar considerations for *T. erebus*. Perhaps the Gnaphosidae had cribellate web-building ancestors and, if so, this would partially explain the ability of this non-web building spider to act as a specialised predator on cribellate webs. Perhaps there are web-building gnaphosids still waiting to be discovered?

ACKNOWLEDGEMENTS

I would like to thank Mr Tas Carryer and Mr Dave Greenwood for help with building and setting up the experimental apparatus used in this study, and for helpful suggestions about how to improve the design of some of the equipment. Mr Terry Williams' assistance with the photography is gratefully acknowledged. I thank Mr Richard Rowe and Dr Colin McLay for helpful discussions concerning statistical analyses.

Mr John Black provided valuable advice concerning the preparation of illustrations. Ms Mary Whitehouse provided helpful comments on the manuscript. Mr Simon Pollard is gratefully acknowledged for help with collecting spiders, and I thank Mrs K.A. Card for help with the scanning electron microscopy.

I especially thank Ms Susan Hallas for her comments on the manuscript, and for assistance with such things as collecting spiders and finding and setting up equipment and for valuable discussions about spiders, all of which she supplied cheerfully. And last, but definitely not least, I would like to thank Dr Robert Jackson for his unfailing support and guidance as a supervisor.

A SPECIAL THANK YOU

My love and gratitude go to the 4th Year Class of '83, for the care and compassion that you have in abundance: wherever you go my thoughts will follow. May God protect and guide you all.

My love, Liz Jarman

REFERENCES

AUSTIN, A.D. & BLEST, A.D. 1978. The biology of two Australian species of dinopid spiders. *J. Zool. Lond.* 189: 145-156.

BARNES, R.D. 1980. *Invertebrate Zoology.* 4th edition. Saunders: Philadelphia.

BARTH, F.G. 1982. Spiders and vibratory signals. In: Witt, P.N. & Rovner, J.S. (Eds), *Spider Communication: Mechanisms and Ecological Significance,* pp. 67-122. Princeton University Press: Princeton, N.J.

BLEST, A.D. 1983. Ultrastructure of secondary retinae of primitive and advanced jumping spiders (Araneae, Salticidae). *Zoomorphol.* 102: 125-141.

BRISTOWE, W.S. 1941. *The Comity of Spiders.* Volume II. Roy. Society: London.

BROWN, W.L., EISNER, T. & WHITTAKER, R.H. 1970. Allomones and Kairomones: transpecific chemical messages. *Bioscience* 20: 21-22.

BURGHARDT, G.M. 1970. Chemical perception in reptiles. In: Johnston, J.W., Moulton, D.G. & Turk, A. (Eds). *Advances in Chemoreception,* Volume I. Communication by Chemical Signals, pp 241-308.

BUCHLI, H.H.R. 1969. Hunting behavior in the Ctenizidae. *Am. Zool.* 9: 175-193.

CLAYTON-JONES, P. 1983. Social and predatory behaviour of two species of Australian social spider *Badumna candida* (Amaurobiidae and *Philopenella congregabilis* (Uloboridae). Unpublished B.Sc. (Hons.) Thesis, University of Canterbury, Christchurch.

CURIO, E. 1976. *Ethology of Predation.* Springer Verlag: Berlin.

CZAJKA, M. 1963. Unknown facts of the biology of the spider *Ero furcata* (Villers). *Polski Pismo. Ent.* 33: 229-231.

DE VOE, R.D. 1975. Ultra violet and green receptors in principal eyes of jumping spiders. *J. Gen. Physiol.* 66: 193-208.

EBERHARD, W.G. 1977. Aggressive chemical mimicry by a bolas spider. *Science* 198: 1173-1175.

FALES, J.H. & JENNINGS, D.T. 1979. Butterflies as prey for crab spiders (Thomisidae). *J. Lepidopt. Soc.* 31: 280-282.

FOELIX, R.F. & CHU-WANG, I.W. 1975. The structure of scopula hairs in spiders. *Proc. 6th Int. Arach. Cong., 1974,* 156-157.

FOELIX, R., JACKSON, R., HENKSMEYER, A., & HALLAS, S. In press. Tarsal hairs specialised for capture of prey in the salticid *Portia.*

FORSTER, L. 1974. Visual mechanisms of hunting behaviour in *Trite planiceps,* a jumping spider. *N.Z. J. Zool.* 6: 74-93.

FORSTER, L. 1982a. Vision, prey catching strategies in jumping spiders. *Am. Sci.* 70: 165-175.

FORSTER, L. 1982b. Visual communication in jumping spiders. In: Witt, R.N. & Rovner, J.S. (Eds), *Spider Communication: Mechanisms and Ecological Significance.* Princeton University Press: Princeton, N.J.

FORSTER, L.M. & FORSTER, R.R. 1973. *New Zealand Spiders - An Introduction.* Collins: Auckland.

FORSTER, R.R. 1967. The Spiders of New Zealand Part I. *Otago Mus. Bull. 1:*

FORSTER, R.R. & BLEST, A.D. 1979. The Spiders of New Zealand Part V. *Otago Mus. Bull. 5:* 1-173.

FORSTER, R.R. & WILTON, C.L. 1968. The Spiders of New Zealand Part II. Ctenizidae Dipluridae. *Otago Mus. Bull. 2:* 1-180.

FRANKLIN, C.E. 1983. The venom biologies of *Lactodectus katipo* and *Ixeuticus martius*. Unpublished B.Sc. (Hons.) Thesis, University of Canterbury, Christchurch.

FREED, A.N. In press. Even spiders choose. *J. Zool. Lond.*

FROLICH, C. & BUSKIRK, R.E. 1982. Transmission and attenuation of vibration in orb spider webs. *J. Theoret. Biol.* 95: 13-23.

GERTSCH, W.J. 1949. *American Spiders*. Nostrand: New York.

GERTSCH, W.J. 1980. *American Spiders*. 2nd edition. Van Nostrand: New York.

HILL, D.E. 1977. The pretarsus of salticid spiders. *Zool. J. Linn. Soc.* 60: 319-338.

HARDIE, R.C. & DUELLI, P. 1978. Properties of single cells in posterior lateral eyes of jumping spiders. *Z. Naturforsch.* 33: 156-158.

JACKSON, R.R. 1974. Rearing methods for spiders. *J. Arach.* 2: 53-56.

JACKSON, R.R. 1976. Predation as a selection factor in the mating strategy of the jumping spider *Phidippus johnsoni* (Salticidae: Araneae). *Psyche* 83: 243-255.

JACKSON, R.R. 1977. Courtship versatility in the jumping spider, *Phidippus johnsoni* (Araneae: Salticidae). *Anim. Behav.* 25: 953-957.

JACKSON, R.R. 1978. Comparative studies of *Dictyna* and *Mallos* (Araneae, Dictynidae). I. Social organisation and web characteristics. *Rev. Arach.* 1: 133-164.

JACKSON, R.R. 1982a The biology of ant-like jumping spiders: intraspecific interactions of *Myrmarachne lupata* (Araneae, Salticidae). *Zool. J. Linn. Soc.* 76: 293-319.

JACKSON, R.R. 1982b Comparative studies of *Dictyna* and *Mallos* (Araneae: Dictynidae). IV Silk mediated interactions. *Insectes Sociaux* 29: 15-24.

JACKSON, R.R. 1982c The behaviour of communicating in jumping spiders (Salticidae). In: Witt, R.N. & Rovner, J.S. (Eds), *Spider Communication: Mechanisms and Ecological Significance.* Princeton University Press: Princeton, N.J.

JACKSON, R.R. & BLEST, A.D. 1982. The biology of *Portia fimbriata*, a web-building jumping spider (Araneae, Salticidae) from Queensland: utilisation of webs and predatory versatility. *J. Zool. Lond.*, 196: 255-293.

JACKSON, R.R. & HARDING, D.P. 1982. Intraspecific interactions of *Holoplatys* sp. indet. a New Zealand jumping spider (Araneae: Salticidae). *N.Z. J. Zool.* 9: 487-510.

JACKSON, R.R. 1983. Web-building, predatory versatility, and the evolution of the salticidae. In: W.A. Shear (Ed.), *The Evolution of Spider Webs.* Stanford University Press: Stanford, California.

JACKSON, R.R. In press. The biology of primitive web-building jumping spiders (Salticidae). *National Geographic Research Report.*

KAESTNER, A. 1968. *Invertebrate Zoology.* Volume 2. John Wiley & Sons: London.

LAND, M.F. 1969a. Structure of the principal eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. *J. exp. Biol.* 51: 443-470.

LAND, M.F. 1969b. Movement of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. *J. exp. Biol.* 51: 471-493.

LANGER, R.M. 1969. Elementary physics and spider webs. *Am. Zool.* 9: 81-89.

LAWRENCE, R.F. 1981. The cannibal spiders (Mimetidae). *The Naturalist* 25: 4-9.

LEGENDRE, R. 1961. Arachaea: la capture de proies et la prise de nourriture. *Bull. Soc. Zool. Franc* 86: 316-319.

LEVI, H. 1982. Chelicerata. In: Parker, S. (Ed.), *Synopses and classification of living organisms*, pp. 71-95. McGraw Hill: New York.

LLOYD, J.E. 1965. Aggressive mimicry in *Photuris*: firefly femme fatales. *Science* 149: 653-654.

LLOYD, J.E. 1980. Male *Photuris* fireflies mimic sexual aspects of their female's prey. *Science* 210: 669-671.

LLOYD, J.E. 1981. Firefly mate-rivals mimic their predators and vice versa. *Nature* 290: 498.

MAIN, B.Y. 1976. *Spiders.* Collins: London.

MARPLES, B.J. & MARPLES, M.J. 1972. Observations on *Cantuaria toddi* and other trapdoor spiders (Araneae: Mygalomorpha) in Central Otago, New Zealand. *J. Roy. Soc. N.Z.* 2: 179-185.

MORSE, D.H. 1981. Prey capture by the crab spider *Misumena vatia* (Clerck) (Thomisidae) on three common native flowers. *Am. Midl. Nat.* 105: 358-367.

MCALISTER, W.H. 1977. The spitting habit in the spider *Scytodes intricata* Banks (Family Scytodidae). *Texas J. Sci.* 50: 17-21.

PARRY, D.A. 1960. Spider hydraulics. *Endeavour* 19: 156-162.

PHIBBS, P. & JACKSON, R.R. 1981. An adaptable cage for behavioural studies of web-building spiders. *Brit. Arach. Soc. Newsl.* 32: 3.

PLATNICK, N.I. 1971. The evolution of courtship behaviour in spiders. *Bull. Brit. Arach. Soc.* 2: 40-47.

ROBINSON, M.H. & ROBINSON, B. 1971. The predatory behaviour of the ogre-faced spider *Dinopis longipes* F. Cambridge (Araneae: Dinopidae). *Am. Midl. Nat.* 85: 85-96.

ROVNER, J.S. 1978. Adhesive hairs in spiders: behavioural functions and hydraulically mediated movement. *Sympos. Zool. Soc. Lond.* 42: 99-108.

ROVNER, J.S. 1980. Morphological and ethological adaptations for prey capture in wolf spiders. *J. Arach.* 8: 201-215.

SAVORY, T.H. 1928. *The Biology of Spiders*. Sidgwick and Jackson: London.

TURNBULL, A.L. 1973. Ecology of the true spiders (Araneomorphae). *Ann. Rev. Ent.* 18: 305-348.

VOLLRATH, F. 1979. Vibrations: the signal function for a spider kleptoparasite. *Science* 205: 1149-1151.

WICKLER, W. 1968. *Mimicry in Plants and Animals.* Weidenfeld and Nicholson: London.

WILSON, E.O. 1975. *Sociobiology: the new synthesis.* Harvard University Press: Cambridge, Mass.

WOOD, D.L. 1982. The role of pheromones, kairomones and allomones in the host selection and colonisation behaviour of bark beetles. *Ann. Rev. Ent.* 27: 411-446.

YAMASHITA, S. & TATEDA, H. 1976. Spectral sensitivities of jumping spider eyes. *J. comp. Phys.* 105: 29-41.

APPENDICES

General

Statistical formulae used:

McNemar's Test for Significance of changes with Yates' Correction,

χ^2 Test of Independence with Yates' Correction,

and χ^2 Test of Goodness of Fit with Yates' Correction.

APPENDIX A. Experiment II.

Test prey	2nd Test-prey Item Eaten			
	Yes		No	
	3rd test item eaten		3rd test item eaten	
	yes	no	yes	no
Theridiid	2	8	5	14
Salticid	21	7	1	1
Trapped flies	22	6	0	2
Free flies	10	5	6	9

		Amaurobiid			
		Eaten	Not eaten	Σ	McNemar's Test
Theridiid	Eaten	7	0	7	χ^2adj = 12.071
	Not eaten	8	0	8	$p < 0.001$
	Σ	15	0	15	

		Amaurobiid			
		Eaten	Not eaten	Σ	McNemar's Test
Salticid	Eaten	28	0	28	N.S.
	Not eaten	8	0	8	
	Σ	36	0	36	

APPENDIX A continued

		Amaurobiid			
		Eaten	Not eaten	Σ	McNemar's Test
Fly on Web	Eaten	22	0	22	N.S.
	Not eaten	8	0	8	
	Σ	30	0	30	

		Amaurobiid			
		Eaten	Not eaten	Σ	McNemar's Test
Fly off Web	Eaten	16	0	16	χ^2adj = 7.111 $p < 0.01$
	Not eaten	14	0	14	
	Σ	30	0	30	

	Eaten			
	Yes	No	Σ	χ^2 Test of Independence
Salticid	28	1	29	$\chi^2 = 16.883$ $p < 0.001$
Theridiid	10	14	24	
Σ	38	15	53	

APPENDIX A continued

	Eaten			
	Yes	No	Σ	χ^2adj Test of Independence
Salticid	28	1	29	N.S.
Fly on Web	28	2	30	
Σ	56	3	59	

	Eaten			
	Yes	No	Σ	χ^2adj Test of Independence
Theridiid	10	14	24	14.682
Fly on Web	28	2	30	$p < 0.001$
Σ	36	16	54	

	Eaten			
	Yes	No	Σ	χ^2adj Test of Independence
Salticid	28	1	29	χ^2adj = 7.846
Fly on Web	15	9	24	$p < 0.01$
Σ	43	10	53	

	Eaten			
	Yes	No	Σ	χ^2adj Test of Independence
Theridiid	10	14	24	N.S.
Fly off Web	15	9	24	
Σ	25	23	48	

APPENDIX A continued

	Eaten			
	Yes	No	Σ	χ^2adj Test of Independence
Fly on Web	28	2	30	χ^2adj = 6.029 p <0.025
Fly off Web	15	9	24	
Σ	43	11	54	

APPENDIX B. Experiment III.

		Initial			
		Amaurobiid	Control	Σ	χ^2adj Test of Independence
Final	Amaurobiid	3	3	6	N.S.
	Control	1	1	2	
	Σ	4	4	8	

		Initial			
		Theridiid	Control	Σ	χ^2adj Test of Independence
Final	Theridiid	2	1	3	N.S.
	Control	1	4	5	
	Σ	3	5	8	

		Initial			
		Amaurobiid	Control	Σ	χ^2adj Test of Independence
'Most of Time'	Amaurobiid	5	1	6	N.S.
	Control	0	2	2	
	Σ	5	3	8	

APPENDIX B continued

		Theridiid	Control	Σ	χ^2adj Test of Independence
Most of time	Theridiid	3	1	4	N.S.
	Control	0	4	4	
	Σ	3	5	8	

APPENDIX C. Experiment IV.

		Initial			
		Amaurobiid	Control	Σ	χ^2adj Test of Independence
Final	Amaurobiid	18	6	24	N.S.
	Control	15	11	36	
	Σ	33	17	56	

		Initial			
		Salticid	Control	Σ	χ^2adj Test of Independence
Final	Salticid	11	8	19	N.S.
	Control	4	7	11	
	Σ	15	15	30	

		Initial			
		Theridiid	Control	Σ	χ^2adj Test of Independence
Final	Theridiid	18	10	28	N.S.
	Control	8	14	22	
	Σ	26	24	50	

APPENDIX C continued

		Initial			
		Pooled data	Control	Σ	χ^2adj Test of Independence
Final	Pooled data	47	24	71	N.S.
	Control	27	32	59	
Σ		74	56	130	

		'Most of Time'			
		Amaurobiid	Control	Σ	χ^2adj Test of Independence
Final	Amaurobiid	22	2	24	χ^2adj = 18.899
	Control	7	19	26	$p < 0.001$
Σ		29	21	50	

		'Most of Time'			
		Salticid	Control	Σ	χ^2adj Test of Independence
Final	Salticid	17	2	19	N.S.
	Control	3	8	11	
Σ		20	10	30	

APPENDIX C continued

		'Most of Time'			
		Theridiid	Control	Σ	χ^2adj Test of Independence
Final	Theridiid	18	10	28	N.S.
	Control	10	12	22	
	Σ	28	22	50	

		'Most of Time'			
		Pooled data	Control	Σ	χ^2adj Test of Independence
Final	Pooled data	57	14	71	N.S.
	Control	20	39	59	
	Σ	77	53	130	

Amaurobiid		Initial			
		Left	Right	Σ	χ^2adj Test of Independence
Final	Left	14	8	22	N.S.
	Right	13	15	28	
	Σ	27	23	50	

APPENDIX C continued

Salticid

		Initial			
		Left	Right	Σ	χ^2adj Test of Independence
Final	Left	8	10	18	
	Right	7	5	12	
	Σ	15	15	30	

		Initial			
		Left	Right	Σ	χ^2adj Test of Independence
Final	Left	12	14	26	
	Right	16	8	24	
	Σ	28	22	30	

Pooled data

		Initial			
		Left	Right	Σ	χ^2adj Test of Independence
Final	Left	34	32	66	N.S.
	Right	36	28	64	
	Σ	70	60	130	

APPENDIX D. Experiment V

		Initial			
		Amaurobiid web	Theridiid web	Σ	χ^2adj Test of Independence
Final	Amaurobiid web	12	5	17	χ^2adj = 6.934
	Theridiid web	2	11	13	$p < 0.01$
	Σ	14	16	30	

		'Most of Time'			
		Amaurobiid web	Theridiid web	Σ	χ^2adj Test of Independence
Final	Amaurobiid web	16	1	17	χ^2adj = 19.024
	Theridiid web	1	12	13	$p < 0.001$
	Σ	17	13	30	

		Initial			
		Amaurobiid web	Theridiid web	Σ	χ^2adj Test of Independence
Final	Amaurobiid web	10	5	15	N.S.
	Theridiid web	4	11	15	
	Σ	14	16	30	

APPENDIX E. Experiment VI

		Initial			
		Amaurobiid web	Theridiid web	Σ	χ^2adj Test of Independence
Final	Amaurobiid web	19	12	31	N.S.
	Theridiid web	5	5	10	
	Σ	24	17	41	

		Initial			
		Left	Right	Σ	χ^2adj Test of Independence
Final	Left	11	11	22	N.S.
	Right	7	12	19	
	Σ	18	23	41	

APPENDIX F. Experiment VII

		Initial			
		Amaurobiid web	Theridiid web	Σ	χ^2adj Test of Independence
Final	Amaurobiid web	13	12	25	N.S.
	Theridiid web	2	3	5	
	Σ	15	15	30	

		Initial			
		Left	Right	Σ	χ^2adj Test of Independence
Final	Left	9	8	17	N.S.
	Right	6	7	13	
	Σ	15	15	30	