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THE ECOLOGY AND ASPECTS OF BEHAVIOUR OF THE INVASIVE ALIEN AMPHIPOD *ARCITALITRUS DORRIENI* (HUNT) IN SOUTH WEST WALES (UK)

by

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A Thesis submitted to the University of Wales in fulfilment of the requirements for the Degree of Doctor of Philosophy

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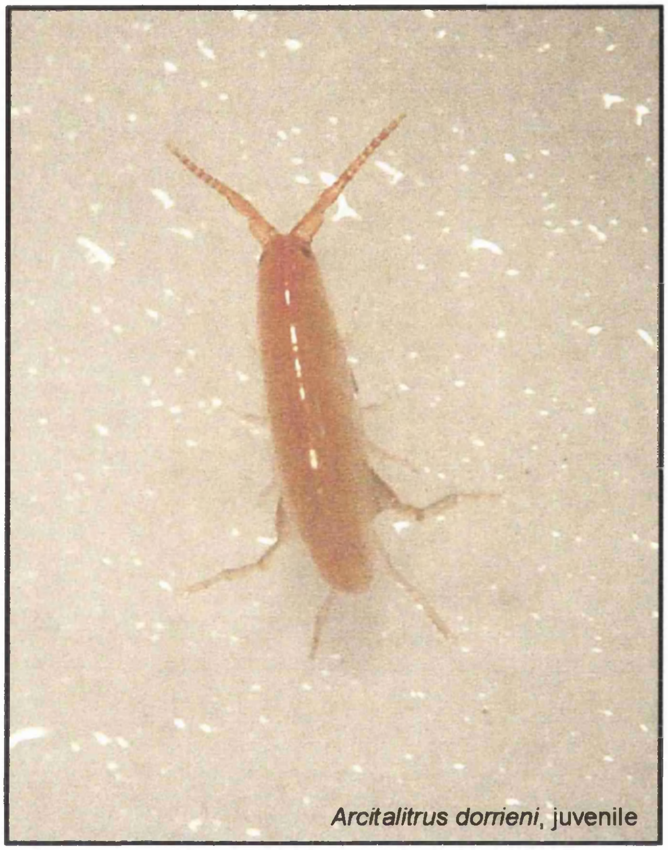

Arcitalitrus dorrieni, juvenile

Preface

This thesis was written with the aim not only to fulfil the requirements for the award of my degree, but to produce a volume that would be of practical use to future researchers who set out to study landhoppers, and in particular *A. dorrieni.* When I was first faced with the challenge myself, I found it very difficult to track down and obtain the relevant literature (which, to this day, remains sparse) and there was virtually no reference material to aid with the practical and experimental aspects of the work I intended to undertake. During the course of this study, I succeeded in making contact with most of the few past and present researchers in this field, virtually all of whom were exceptionally helpful and willing to share their information and literature. I have attempted to incorporate all the material I have thus acquired in this text, so that future workers will be freed from the time-consuming and laborious task of locating suitable references and information sources. Furthermore, I have illustrated and described in detail practical aspects such as handling and maintenance techniques which I had to devise prior to attempting any experimental work. I hope that future experimental work will benefit by being equipped with effective and efficient protocols, thus increasing the time available for the actual experimental investigation. Finally, by translating the most salient parts of this text into German, I hope to enhance the usefulness of the work by increasing its potential audience, particularly since landhoppers are still widely unknown throughout much of Europe.

Overall, the completion of this thesis has been a challenge like no other, not only due to the comparatively obscure nature of the topic but also due to my personal circumstances. I am deeply grateful to my mother, who has stood by me and supported me through everything, and, as the only remaining member of my family, had to do it all by herself. My doctors, particularly Dr. Ludwig Rubin, and my neurologist Dr. Maria Grisold, have been exceptionally kind and supportive. My supervisor, Prof. P. F. Brain, has helped me maintain my enthusiasm by showing his appreciation of my work and was always ready to support my ideas. I could not have done this without them.

Having reached the end of what has been a long and winding road, with its ups and perhaps more than its fair share of downs, I am both sad at having to let it all go, and pleased in the hope that I have achieved something worthwhile, against a good number of odds.

Acknowledgements

I have been very lucky in meeting a number of wonderful people through this study, many of whom have provided me with invaluable advice and assistance. For this I would like to express my gratitude, which, in particular, goes out to:

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Dr. Tony Friend for confirming the native range data of *A. dorrieni*;

Dr. Geraint Owen and the Geography Department for providing me with maps, access to their mapping software and not least provision of experimental space when the going got tough;

The librarians in the Natural Sciences Library for providing me with an endless stream of inter-library loans;

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Dr. Kevin Flynn from Algal Research and Dr. Chris Smith from Biochemistry for allowing me to use their equipment;

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Chris Atkinson for allowing me to use his prize-winning birds in this study;

Summary

This study initially provides a detailed investigation of the population dynamics of the introduced terrestrial amphipod *Arcitalitrus dorrieni* in a coastal deciduous woodland. It also assesses this alien's effect on the native leaf-litter fauna.

The mean population density of *A. dorrieni* in this habitat was 364 individuals/m^2. The maximum densities (around 880 individuals/m^2) occurred in habitat with leaf litter of *Quercus ilex* overlying friable soil. Population density was strongly affected by low temperatures, suggesting that frost is one of the major regulating factors controlling the amphipod's spread. Native invertebrate communities were not significantly altered by the presence of *A. dorrieni*, but some groups seemed to benefit from the landhopper's presence, while others appeared to suffer.

The latter part of this study is devoted to the design of effective handling and maintenance techniques for *A. dorrieni*, and a series of laboratory-based experiments investigating both ecological and behavioural aspects of its biology. These include a determination of the amphipod's feeding rates and food preferences, assessments of the potential predation pressure by native species, and examination of *A. dorrieni's* activity rhythms and dispersal capabilities.

A. dorrieni feeds exclusively on dead plant material, and consumes around 20% of its bodyweight per day at ambient temperatures of 13-20°C. Feeding ceases at temperatures around 4°C. In deciduous woodland, *A. dorrieni* is estimated to consume 25-35% of the annual litter fall at the experimental location. Many native predators accept *A. dorrieni* as a food item, and thus it probably faces considerable predation pressure in Britain. This may be slowing population expansion. It was established that *A. dorrieni* has an essentially crepuscular activity rhythm. Its ability to successfully cross a minimum of 2m of open space in one night was demonstrated.

Overall, the results indicate much potential for a continued spread of the alien amphipod across the British Isles.

Zusammenfassung

Ziel des ersten Teiles dieser Studie ist die Vorstellung einer Population von *Arcitalitrus dorrieni* - eines eingeschleppten terrestrischen Amphipoden – und deren Dichte und Dynamik im Jahreslauf in einem an der Kueste gelegenen Laubwald. Weiters wurden moegliche Einfluesse des Amphipoden auf die einheimische Fauna des Waldbodens untersucht.

Die durchschnittliche Populationsdichte von *A. dorrieni* in dem obengenannten Habitat betrug 364 Tiere/m^2. Die Maximaldichte (ca. 800 Tiere/m^2) wurde an einer Stelle des Waldes erreicht, an welcher eine Schicht von *Quercus ilex* Laubstreu ueber kruemeliger Erde vorherrschend war. Die Populationsdichte wurder stark von tiefen Umgebungstemperaturen beeinflusst, was bedeutet, dass Frost wahrscheinlich einer der Hauptfaktoren ist, welche die Ausbreitung von *A. dorrieni* beeinflussen. Die Zusammensetzung der Wirbellosen des heimischen Laubstreuhabitats wurden durch das Vorhandensein von *A. dorrieni* nicht wirklich veraendert. Es scheint jedoch, dass einige Arten von der Anwesenheit des Amphipoden profitieren, waehrend andere nachteilig beeinflusst werden.

Im zweiten Teil der Studie wurden Techniken bezueglich der Handhabung des Amphipoden bzw. dessen Haltung im Laboratorium entwickelt, und in einer Reihe von Experimenten verschiedene oekologische und verhaltenswissenschaftliche Aspekte der Biologie von *A. dorrieni* untersucht. Die Frassmenge einzelner Amphipoden und Praeferenz der Spezies fuer bestimmte Laubarten wurden untersucht. Weiters wurden heimische raeuberische Spezies auf ihre Akzeptanz von *A. dorrieni* als Nahrung getestet, und das eventuelle Vorhandensein von Aktivitaetsrhythmen sowie die Verbreitungskapazitaet des Amphipoden wurde untersucht.

Diese Untersuchungen ergaben, dass *A. dorrieni* ausschliesslich abgestorbenes Pflanzenmaterial frisst und im Durchschnitt taeglich 20 % seines Koerpergewichts zu sich nimmt, sofern die Umgebungstemperatur zwischen 13°C und 20°C liegt. Bei Temperaturen unter 4°C wird die Nahrungsaufnahme eingestellt. Es wird hier geschaetzt, dass *A. dorrieni* zwischen 25 und 35 % des jaehrlichen Laubfalles im Versuchswald konsumiert. Ausserdem wurde festgestellt, dass *A. dorrieni* von vielen heimischen, raeuberisch lebenden Wirbellosen und Wirbeltieren gefressen wird, was Populationen des Amphipoden in Grossbritannien zweifellos unter einen gewissen Druck setzt und diese eventuell in ihrer Ausbreitung behindert. Es war zu beobachten, dass *A. dorrieni* hauptsaechlich in der Daemmerung aktiv ist, und es konnte bewiesen werden, dass der Amphipode in einer Nacht problemlos eine Distanz von 2 m ohne Deckung bei relativ niedriger Luftfeuchtigkeit ueberwinden kann.

Zusammenfassend zeigen die Resultate, dass *A. dorrieni* starkes Potential besitzt, sich weiter erfolgreich ueber die Britischen Inseln auszubreiten.

Inhalt der Kapitel - Deutsch

Kapitel 1 - Dieses Kapitel stellt den terrestrischen Amphipoden *A. dorrieni* im Detail vor. Zu Beginn wird seine Stellung im Phylum Crustacea erlaeutert. Dann wird die weltweite Verbreitung der terrestrischen Amphipoden, die durch den Menschen in neue Gebiete eingeschleppt wurden, angesprochen. Anschliessend wird die Morphologie und Physiologie terrestrischer Amphipoden, und im speziellen die von *A. dorrieni*, vorgestellt. Als naechstes werden Theorien bezueglich der Einschleppung des Amphipoden besprochen. Es scheint, dass *A. dorrieni* mit Baumfarnen, die als ausgewachsene Pflanzen (oft in einer Lage Laubstreu als Schutz) importiert wurden, unabsichtlich ins Land gebracht wurde. Eine Gaertnerei (Treseder's in Truro, Cornwall) wird als wahrscheinlicher Ursprung der britischen Populationen genannt.

Kapitel 2 - In diesem Kapitel werden die zwei in dieser Arbeit untersuchten Testgebiete vorgestellt. Diese liegen in zwei nahe beieinander liegenden Taelern der Halbinsel 'Gower' im Westen von Swansea. Das Gebiet, in welchem eine eigenstaendige Population von *A. dorrieni* vorkommt, war Bishop's Wood, Caswell. Das Vergleichsgebiet, in welchem *A. dorrieni* noch nicht vorhanden ist, war Bishopston Valley. Die detaillierte Beschreibung der Orte, and denen Bodenproben genommen wurde, inkludiert einen Satz von je drei Fotos fuer jede Jahreszeit, welche sowohl die Flora als auch die Beschaffenheit der Laubstreu illustrieren.

Kapitel 3 - Hier werden die Resultate der Studie der Amphipodenpopulation ueber zwei Jahre in Bishop's Wood, Caswell praesentiert. Die Populationsdichte war geringer als die bisher beobachteten Dichten in Misch- und Nadelwald in Irland. Starke Schwankungen in der Populationsdichte konnten beobachtet werden, und ein moeglicher Zusammenhang mit unerwartet tiefen Temperaturen im Fruehlung wurde festgestellt. Es konnte gezeigt werden, dass *A. dorrieni,* entgegen urspruenglichen Vermutungen relativ ebenmaessig ueber das Versuchsgebiet verteilt ist, und dass diese Ebenmaessigkeit sogar die der heimischen Isopoden uebertrifft. Es konnte weiters bestaetigt werden, dass sich *A. dorrieni* unabhaengig von der Jahreszeit vermehrt, aber dass die im Winter geborenen Juntiere meist nicht ueberleben.

Kapitel 4 - In diesem Kapitel wird die heimische Fauna der Laubstreu im Versuchsgebiet der Fauna im Vergleichsgebiet gegenuebergestellt, um diese auf eventuelle Einfluesse der Anwesenheit von *A. dorrieni* zu ueberpruefen. Statistisch waren keine signifikanten Effekte auf die heimische Fauna (weder positiv noch negativ) festzustellen. Es war jedoch trotzdem klar ersichtlich, dass gewisse Spezies viel haeufiger vorkamen, wo *A. dorrieni* vorhanden war, waehrend andere Spezies seltener zu sein schienen.

Kapitel 5 - Dieses Kapitel widmet sich hauptsaechlich der Beschreibung von Techniken fuer die Handhabung von *A. dorrieni* im Rahmen von Laborexperimenten, welche im Zusammenhang mit dieser Studie entwickelt wurden. Weiters werden Aspekte der Biologie von *A. dorrieni* beschrieben, die hier nur oberflaechlich behandelt werden konnten und noch intensiverer Forschung beduerfen.

Kapitel 6 - In diesem Kapitel wird die Frassmenge einzelner Amphipoden bei verschiedenen Umgebungstemperaturen untersucht. Jeder Amphipode nimmt taeglich im Durchschnitt ca. 20% seines Koerpergewichts an Nahrung auf, sofern die Temperatur zwischen 13 und 20 betraegt. Unter 4°C wird die Nahrungsaufnahme eingestellt. Aufgrund dieser Resultate, und der Daten aus Kapitel 3, wurde der Anteil des jaehrlich von einer typischen Population von *A. dorrieni* gefressenen Laubfalles in einem Laubwald errechnet. Dieser Anteil betraegt zwischen 25 und 35%. Weiters wurde der Anteil einer solchen

Population an der gesamten Biomasse der Laubstreufauna errechnet. Dieser betraegt ca. 7%, aehnlich dem der Schnecken und Tausendfuessler, und ist hoeher als der der Asseln.

Kapitel 7 - Hier wurden eine Anzahl von heimischen raeuberisch lebenden Wirbellosen und Wirbeltieren auf ihre Akzeptanz von *A. dorrieni* als Beutetier untersucht. Es stellte sich heraus, dass Vertreter der meisten Gruppen, welche sich zum Teil von heimischen Isopoden ernaehren, problemlos den eingeschleppten Amphipoden fangen und fressen koennen, und dies auch in Anwesenheit von Isopoden als alternative Futterquelle regelmaessig tun.

Kapitel 8 - In diesem Kapitel werden in einer Anzahl von verschiedenen Experimenten die Verbreitungskapazitaet von *A. dorrieni* und dessen Aktivitaetsrhythmen untersucht. Es konnte gezeigt werden, dass der Amphipode jede Nacht fuer einige Stunden gegen Morgengrauen aktiv wird, auch wenn genuegend Nahrung vorhanden ist und die Luftfeuchtigkeit seinen Anspruechen entspricht. Weiters wurde bewiesen, dass *A. dorrieni* imstande ist, problemlos eine Distanz von zumindest 2 Metern ohne Deckung und bei relativ niedriger Luftfeuchtigkeit zu ueberwinden. Diese Resultate zeigen, wieviel Verbreitungspotential der an und fuer sich kleine und unscheinbare, und physiologisch fragile Amphipode wirklich hat.

Kapitel 9 - Hier werden hauptsaechlich Aspekte im Zusammenhang mit der Handhabung von Problemsituationen aufgrund eingeschleppter Spezies angesprochen und die Dringlichkeit weiterer Forschungen auf diesem Gebiet hervorgehoben.

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1 General Introduction

1.1 *Arcitalitrus dorrieni* in context

The phylum Crustacea consists of predominantly marine and freshwater species. Fully terrestrial representatives have developed in only three orders: the Isopoda, the Decapoda and the Amphipoda (Powers & Bliss, 1983). Overall, the order Amphipoda is a very successful group with around 6000 species in 61 families (Cowling *et al.*, 2004; Spicer, Moore & Taylor, 1987). Amphipods are small, usually laterally flattened, peracarid shrimps that inhabit virtually all permanent waters of the world (Bousfield, 1981). Many amphipods specialise in eating low-quality food such as algal fronds and other dead plant material. Their ability to thrive on such unattractive but vastly abundant material is one of the reasons for their great success (Duncan, 1994).

As is the case in the other crustacean orders which have terrestrial representatives, most amphipod species are marine. Some, commonly known as 'sandhoppers' or 'beachfleas', live on the sea shore, both on rocky and sandy beaches, and thrive there in great numbers despite the difficult living conditions inherent in these habitats. A number inhabit freshwater streams and lakes, and only comparatively few are fully terrestrial, i.e. falling into the highest and second highest of the five grades of adaptation to terrestrial life described by Powers & Bliss (1986) (Table 1-1, Page 2).

Grade	Zone	General description
1	Midlittoral	Habitat frequently inundated; activities greatly influenced by tidal periodicity; organisms may be acitve underwater; use both aerial and aquatic respiration; tolerate dehydration poorly
2	High littoral	Habitat usually damp, occasionally inundated; activities often regulated by tidal cycle; some organisms migrate with changes in water level; terrestrial activity and aerial respiration prevail; many species are diurnal, tolerate mild dehydration
3	Supralittoral	Damp substrates and microclimate of high humidity; organisms require occasional access to standing water; many species are nocturnal, tolerate moderate dehydration; decapods usually have aquatic dispersed larval stages
4	Extralittoral	Habitat typically mesic but microclimates have high humidities; organisms often independent of standing water, but some have aquatic dispersed larval stages; many species are nocturnal; some tolerate prolonged dehydration
5	Terrestrial	Habitat typically mesic, some are xeric; organisms independent of permanent standing water; activity often nocturnal; decapods have direct larval development; cryptozoic habits are common

Table 1-1 Descriptive Scale of Terrestrial Adaptations in Crustaceans

after Powers, L.W. & Bliss, D.E. (1983), Terrestrial Adaptations, pp 273-274; in: The Biology of Crustacea Vol. 8, eds. Vernberg, F.J. & Vernberg, W.B., Academic Press London

All terrestrial amphipods, commonly known as 'landhoppers', belong to the family Talitridae (Cowling *et al.*, 2004; Spicer *et al.*, 1987). This family may be subdivided into four systematic-ecological (polyphyletic and overlapping, but pragmatically useful) units (Bousfield, 1984), as follows:

(1) palustral talitrids - aquatic and semi-aquatic (rarely terrestrial) in estuarine and some freshwater habitats of tropical and antipodean continental areas;

(2) beachfleas - more advanced, semi-terrestrial and terrestrial (but non-substrate-modifying) in supralittoral and coastal rain forest habitats of tropical to boreal marine coastlines of the world;

(3) sandhoppers - specialized fossorial (substrate-modifying), semi-terrestrial, supralittoral on sandy beaches of tropical and temperate marine shores; and

(4) landhoppers - specialized terrestrial (but not usually substrate-modifying), in coastal continental and high-island angiosperm rain forests, mainly of tropical, Indo-Pacific, and antipodean temperate regions.

The Talitridae is the only amphipod family, which has members capable of jumping by sudden extension of their intucked posterior end of the body. This gave rise to the family's old name of 'Saltatoria', distinguishing its members from the swimming forms, the 'Natatoria' (Reid, 1947). The Talitridae consists of over 200 described species, of which more than 120 are landhoppers (Friend & Richardson, 1986; O'Hanlon & Bolger, 1993). It has been suggested that more than 1000 landhopper species are yet to be described worldwide (Bousfield, 1984).

1.2 Distribution of the terrestrial Amphipoda

While the non-terrestrial Talitridae are nearly cosmopolitan in distribution, all the fully terrestrial species originate in, and are in most cases still restricted to, the oceanic areas of the Southern Hemisphere, which once made up the primeval supercontinent known as Gondwanaland (Duncan, 1994; Hurley, 1955; Powers *et al.*, 1983). The fact that a number of synanthropic species have become successfully established in the northern hemisphere suggests that historical biogeographic factors have been the main cause preventing landhoppers from achieving a greater worldwide distribution (Richardson, Swain & Smith, 1991). Fewer than ten species are thought to have been introduced in locations away from their native ranges (Cowling *et al.*, 2004). Introductions have taken place throughout the tropics, sub-tropics and warm temperate regions. Two species of *Talitroides* (namely *T. alluaudi* and *T. topitotum*) have been very widely distributed, their current range including locations in Sri Lanka, India, many of the Indian Ocean Islands, Australia, a number of Pacific Ocean Islands, some Atlantic Ocean Islands and both North and South America, as well as greenhouses in Scandianavia and Europe. Full lists of references regarding their distribution have been compiled both for their worldwide (Friend *et al.*, 1986) and for their European (Vader, 1972) ranges. In areas where native terrestrial amphipods are present, these two species pose a serious threat to biodiversity because they are capable of outcompeting the native species (Friend *et al.*, 1986; Richardson, 1992). Another species, *Brevitalitrus hortulans*, has also been introduced to a number of locations in the tropics and sub-tropics and has been found in the 'tropical pits' of the Royal Botanical Gardens, Kew (near London, UK), but is considerably less widespread than the previous species (Bousfield, 1971; Calman, 1912).

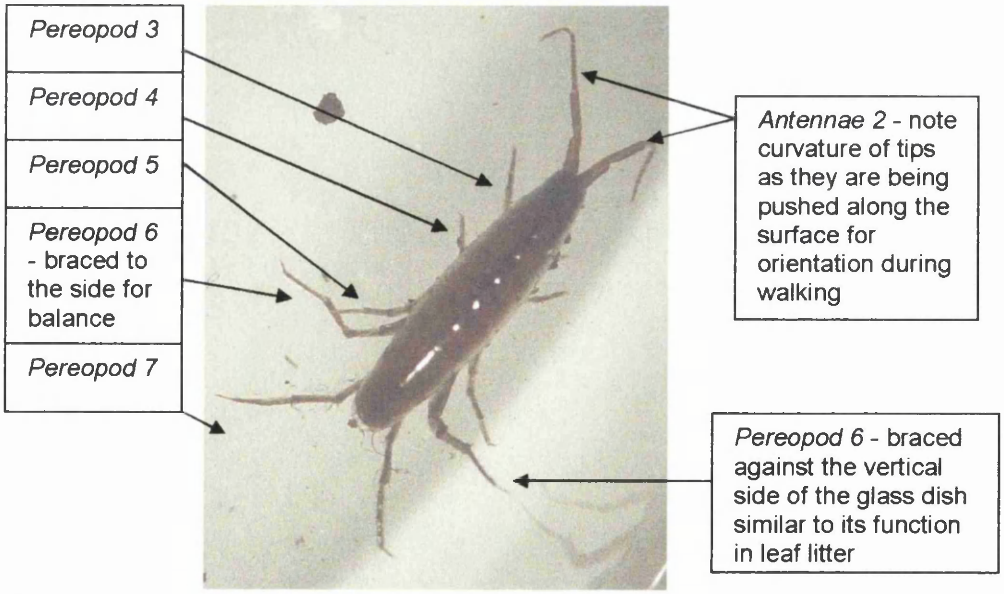
None of the three invasive species described thus far appears to be able to sustain populations outside the shelter of greenhouses in temperate regions. Two species in the genus *Arcitalitrus* have, however, proved capable of forming such self-sustaining, and expanding, populations. *Arcitalitrus* is a small genus with only three species: *Arcitalitrus dorrieni*, *Arcitalitrus sylvaticus* and *Arcitalitrus bassianus.*

The native range of *A. dorrieni* covers an area in mid-eastern Australia on the coastal side of the Great Dividing Range, from Brisbane in southern Queensland to just south of Sydney in New South Wales, Wollongong being at the southern end of the distribution (O'Hanlon *et al.*, 1993; J. A. Friend, pers. comm.). From here, it has been introduced into the North Island of New Zealand, Great Britain and Ireland (Friend *et al.*, 1986). *A. sylvaticus* is native to south-eastern Australia and has been introduced to California (Bousfield & Carlton, 1967), where it occurs in parks and gardens, but has also established populations outside these areas (Lazo-Wasem, 1983). *A. bassianus* has only been recorded from Victoria and Tasmania (Australia) and does not appear to have been introduced to any other locations (Friend, 1987).

1.3 Morphology of terrestrial Amphipoda

In appearance, the terrestrial Talitridae are much like their aquatic and semi-terrestrial counterparts, following the gammaridean body-plan which typically consists of a laterally flattened, top-heavy body which, on land, is prone to fall over sideways, two pairs of antennae and seven pairs of legs on the thoracic segments (or pereon). In the Talitridae, the first antennae are reduced to varying degrees, in *A. dorrieni* reaching no further than the middle of the last segment of the peduncle of the second antenna (Reid, 1947).

The seven pairs of thoracic legs are often referred to as pereopods. The first two pairs (sometimes further distinguished as gnathopods) are almost invariably of a different structure than the posterior five pairs, and are not generally used for walking (Lincoln, 1979). In landhoppers, the small first gnathopods are generally used for passing food to the mouth and for grooming the antennae and the other legs, but occasional use for walking has been reported in at least one species (Lindeman, 1991). The second gnathopods are also used chiefly for grooming, and are carried in a rolled-up position close to the venter during walking, where they are invisible from the side (Lawrence, 1953; Lindeman, 1991). In many species of amphipod, referred to as 'plesiomorphic' species (Bousfield, 1984), the second gnathopod is sexually dimorphic, being larger in the male and playing an important role in amplexus (the carrying of the female by the male prior to mating). Amplexus does not take place in landhoppers, and the sexual dimorphism of gnathopod 2 is consequently often reduced, and in some genera, including *Arcitalitrus* and *Talitrus*, there is no difference in size or appearance of the second gnathopod in males and females (Bousfield, 1984; Reid, 1947). Such species are referred to as 'apomorphic' species (Bousfield, 1984). The five pairs of legs posterior to the gnathopods are used for walking as well as grooming. When standing or walking on a flat surface, the posterior legs have to be braced stiffly outwards to enable the animal to keep its balance (illustrated in Figure 1, below). Occasionally, the penultimate pair of legs is carried vertically upwards during movement (Lawrence, 1953; Lindeman, 1991). Only when observed among leaf litter does a major function of the posterior two pairs of dorsally directed legs, and particularly the penultimate pair, become obvious, namely the provision of a purchase on the substrate all around the animal, not just ventrally. Lindeman (op. cit.) reports that *Cerrorchestia sp.* 'turned somersaults in place by pushing on material above them with pereopods 6 and on the substratum with pereopods 5 and 7'. Thus, the pereopods 6 provide the landhopper with great manoeuvrability in the interstitial spaces of the leaf litter, which it inhabits.



Pereopod 3

Pereopod 4

Pereopod 5

Pereopod 6 - braced to the side for balance

Pereopod 7

Antennae 2 - note curvature of tips as they are being pushed along the surface for orientation during walking

Pereopod 6 - braced against the vertical side of the glass dish similar to its function in leaf litter

Figure 1 ***A. dorrieni* walking in glass dish**

In mature females, the brood plates or oostegites may be found on the inner bases of some pereopods. In *A. dorrieni,* these are present on pereopods 2 to 5 (see section 3.2.2 for description and illustrations). These oostegites form a brood pouch or marsupium in which the eggs are carried. The oostegites of *A. dorrieni* are much reduced in comparison to non-terrestrial talitrids, perhaps to allow sufficient air flow around the eggs, as it is impossible for the female to produce a current by means of her pleopods to fan her eggs, as she would in water (Swain & Richardson, 1993).

In both sexes, the inner bases of pereopods 2 to 6 are the location of the coxal gills. The gills are of an elaborately twisted and convoluted structure, which is believed to confer mechanical resistance to gill collapse in air (Moore & Taylor, 1984). In common with some other landhopper species, in both male and female *A. dorrieni,* the pereopod 6 gills are large and unusually shaped, and gills 3 to 5 are relatively small (Spicer & Taylor, 1986). It has been suggested that the reduction in size of the more anterior gills creates a more open marsupium, thus further facilitating aeration of the eggs, while gills number 2 and 6 play a role in retaining the eggs in the marsupium by closing it off towards the front and the rear (Spicer *et al.*, 1986; Swain *et al.*, 1993). The overall gill area is larger in landhoppers than in intertidal species, indicating that the possible water uptake through the gills in their hypotonic environment is less dangerous than the risk of severe water loss faced by the intertidal species (Morritt, 1988).

The abdomen, also known as the pleon, consists of six segments (the anterior three sometimes referred to as the pleosome and the posterior three as the urosome) (Lincoln, 1979). Each of the anterior three is equipped with a pair of biramous appendages known as pleopods. In the aquatic species, the pleopods are usually well developed and setose, as they are used for swimming and creating the respiratory current across the gills and, in females, the brood pouch or marsupium (op. cit.). In semiterrestrial and terrestrial species, the pleopods are reduced to varying degrees. In *A. dorrieni*, the first and second pleopods are practically normal in form, whereas the third is reduced to a small stump (Reid, 1947). The posterior three pleon segments each possess a biramous appendage or uropod. The uropods are typically robust and rigidly fixed to the body. Their main function is the provision of purchase on the substrate for hopping, but they may also assist in burrowing (Lincoln, 1979) and may be used for 'kicking' in intraspecific antagonistic encounters [Duncan (1969) and pers. obs].

The body surface of landhoppers is very smooth compared to many of their semi-terrestrial and aquatic counterparts. This reduction of setae and other surface structures [including cuticular microstructures (Halcrow & Bousfield, 1987; Holmquist, 1982)] may help to reduce water loss, since landhoppers lose water from the entire body surface (Spicer *et al.*, 1987). A smooth body surface may also allow more efficient movement within the crevices of the leaf litter and prevents pieces of soil and detritus adhering to the animal's body (Lindeman, 1991).

Detailed descriptions of the morphology of the British Talitridae, with comparative descriptions, can be found in Reid (1947), and an overview including non-British species is given in Hunt (1925).

1.4 Physiology of the terrestrial Amphipoda

Physiology is perhaps the most intensively studied aspect of landhopper biology. During the 1980s, a number of studies investigated (often in a comparative way) the water relations, osmoregulatory capabilities and respiratory physiology of a variety of terrestrial and other talitrid amphipods (Lazo-Wasem, 1984; Morritt, 1987, 1988, 1989; Spicer & Taylor, 1987). The late 1980s and early 1990s saw a number of comparative investigations on copper and zinc balance (Moore & Rainbow, 1987; Morritt, 1989; Weeks, 1992; Weeks & Moore, 1991; Weeks & Rainbow, 1994; Weeks, Rainbow & Moore, 1992), coprophagy (Weeks, 1992) and the role of the urosome and anal drinking in the maintenance of water balance (Moore & Richardson, 1992). In 1987, a review of the physiological ecology of semi-terrestrial and terrestrial amphipods, in relation to their adaptations for terrestrial life, was published (Spicer *et al.*, 1987). A number of the above studies include work on *A. dorrieni* (Moore *et al.*, 1987; Moore *et al.*, 1992; Morritt, 1987, 1988, 1989; Spicer *et al.*, 1987; Spicer *et al.*, 1987; Weeks, 1992, 1992; Weeks *et al.*, 1994; Weeks *et al.*, 1992). A review encompassing many of the above studies was later published (Morritt & Spicer, 1998). One recent study focussed on *A. dorrieni* alone, investigating its environmental tolerances with respect to humidity, temperature and sodium levels (Cowling *et al.*, 2003).

One major conclusion from the above investigations was that physiological desiccation tolerance is not an important factor contributing to the success of talitrid landhoppers (Lazo-Wasem, 1984; Morritt, 1987), confirming the view that terrestrial talitrids are adapted behaviourally rather than physiologically to terrestrial life (Edney, 1960; Hurley, 1968). It appears, in fact, that they even possess a rate of water loss in air higher than that of supralittoral talitrids (Morritt, 1987). This fact, coupled with the observation that terrestrial landhopppers have a large - almost 'aquatic' (Morritt, 1987) - gill area (see section 1.3), strengthens the theory that landhoppers - at least the simplydactylate group - evolved not from supralittoral but from palustral species inhabiting the coastal regions of Gondwanaland (Bousfield, 1984). In this scenario, they made their way straight from the rainforest rivers and the mossy riverbanks into the damp woodland leaf litter, without ever facing the desiccation stress to which supralittoral species are prone. Most of the fully terrestrial Talitridae, including *A. dorrieni*, are now, however, incapable of surviving prolonged submersion (Spicer *et al.*, 1987). Survival time in water may be increased by adding some salt, with the optimal concentration apparently around 400 mOsm.l^{-1} (Cowling *et al.*, 2003). This indicates that death on immersion is probably more often caused by difficulty with osmoregulation than by asphyxiation.

Results from the recent investigation into *A. dorrieni's* environmental tolerances confirmed that the landhopper starts to experience desiccation stress at little under 100% relative humidity, and survival is already significantly reduced at 95% (op. cit.). These findings are similar to those produced for *A. sylvaticus* (Lazo-Wasem, 1984), with the difference that *A. dorrieni* appears much less tolerant than *A. sylvaticus* at a RH of 95% (Cowling *et al.*, 2003). It has been further shown that *A. dorrieni* is vulnerable to extremely low salinity, and will not survive exposure to 0°C.

1.5 A. dorrieni in Britain

A. dorrieni was discovered during the winter of 1924/25 in the grounds of Tresco Abbey on the Isles of Scilly by Major A. A. Dorrien-Smith, the governor of the Isles at that time. Specimens were sent to Plymouth Laboratory, where they were identified, and later described as *Talitrus dorrieni*, by O. D. Hunt (Hunt, 1925). In 1933, *A. dorrieni* was first collected from its native range and identified as *Talitroides dorrieni* - the choice of genus a result of an attempt to distinguish between the fully terrestrial members of *Talitrus* and those inhabiting the intertidal zone (Schellenberg, 1934). In 1955, the genus *Talitroides*, which had been created on solely ecological grounds, was moved to a subgeneric level and *Talitrus* was pronounced as the correct genus for the species now known as *A. dorrieni* (Hurley, 1955). Hurley (1955) further stated that *T. sylvaticus* and *T. dorrieni* were synonymous, and treated them both as *T. sylvaticus*. In 1975, *Arcitalitrus* was first erected as a subgenus into which *T. sylvaticus* was placed (Hurley, 1975). In 1980, J. A. Friend and E. L. Bousfield were reported to be in favour of retaining *T. dorrieni* as a separate species (Richardson, 1980). Reports published during the years before the elevation of *Arcitalitrus* to genus level use both the genus '*Talitrus*' and '*Talitroides*' to refer to *Arcitalitrus dorrieni*. There do not, however, seem to be any publications which deal with *A. dorrieni* but mistakenly refer to it as *A. sylvaticus. Arcitalitrus* was finally raised to full generic status in 1982 (Bousfield, 1982), and *A. dorrieni* was described as a species in its own right.

Records of the occurrence of *A. dorrieni* in Britain were published individually until 1988 (Ingle, 1958; Lincoln, 1979; Moore & Spicer, 1986; Murphy, 1973, 1974; Rawlinson, 1937; Reid, 1947; Richardson, 1980; Welch, 1981), when the first distribution map for the alien was produced (Harding & Sutton, 1988). This map was updated in 2002 by Cowling *et al.* (2002) using data from personal communications, surveys by the authors and a number of papers published since 1988 (Anderson & Foster, 1993; Howell, 1988; Jones, 1999; O'Connor, O'Connor & Holmes, 1991; O'Hanlon, 1994; O'Hanlon *et al.*, 1993; Spicer & Tabel, 1996). The resulting map was published in 2004 (Cowling *et al.*, 2004). Until 1988, the spread of *A. dorrieni* was limited, and most recorded populations were small and isolated (Harding *et al.*, 1988).

Recently, records of *A. dorrieni* have become more frequent as well as more numerous. This may be partially due to greater awareness of the existence of terrestrial amphipods and the presence of *A. dorrieni* in Britain, but at least some of the increase in recording appears to be due to a significant increase in the rate of spread of the landhopper. It is now present in many locations in the UK where it was definitely absent only ten years ago (J. Spicer, pers.comm.) and, in many cases, as little as five years ago (H. G. Owen, pers. comm.; F. Harper, pers. comm.; personal observations). A very similar situation has been observed in Ireland (Cawley, 2004).

A number of likely means of introduction have been suggested for *A. dorrieni*, all associated with the importation of exotic plants to British nurseries and gardens (Moore *et al.*, 1986). Richardson (1980) suggested that an introduction with the tree fern *Dicksonia antarctica* was particularly likely. He gave three main reasons for this suggestion:

1. Tree ferns, since they are very slow-growing and hard to raise from spores, were among the few plants which were imported as growing plants rather than seeds. They would therefore require to be packed with a quantity of soil around their roots, and they were often additionally wrapped in leaf litter for protection.

2. The *Dicksonia* trunk provides a multitude of potential humid hiding places for *A. dorrieni* during transit.

3. A very high density of amphipods has been found in tree fern litter in the UK.

Additionally, the use of Wardian cases (similar to today's 'terraria'), which were introduced late last century for the long-distance transport of live plants, is likely to have facilitated landhopper dispersal (Duncan, 1994).

Much of the landhopper's dispersal was probably not a result of direct imports, but occurred *via* large nurseries. For example, Richardson (1980) suggests Cornish nurseries, particularly the long-established Treseder's Nursery at Truro, as the probable source of the landhoppers, which have by now successfully colonized the Isles of Scilly. Treseder's Nursery possessed a 'branch' nursery in New South Wales that dealt extensively with its parent company, and also had dealings with New Zealand (A. Richardson, pers. comm). Treseder's at Truro is known to have provided many gardens with plants during the late 19th century, and a large proportion of these gardens now has thriving colonies of *A. dorrieni* (Richardson, 1980). Furthermore, the populations of *A. dorrieni* in New Zealand mentioned previously, may have been introduced by Treseder's New South Wales (A. Richardson, pers. comm.).

Much of the landhopper's continued spread throughout the British Isles remains synanthropic. The exchange of plants by gardeners is the most obvious, and undoubtedly a very important means of dispersal. A number of less obvious but nevertheless very important mechanisms have, however, been discovered. Perhaps the most effective of these involves the composting strategy of most councils. This involves transporting litter from a variety of locations to a central composting area, which provides perfect conditions for the landhopper, and subsequent distribution of the composted material to a range of council-run parks and gardens. It is very likely that the landhopper has become common in all the larger Council parks in Swansea by these means (personal observations). The same method is believed to have transported the amphipod from Kew Gardens to Battersea Park in London (Cowling *et al.*, 2004). Another possible method of dispersal observed in Australia involves the landhoppers hiding among rubbish bags during the night, and being collected along with the bags. They later appear to make their way out of the refuse collection trucks as they follow their routes (A. Richardson, pers. comm.).

A. dorrieni has proved capable of colonizing a surprising variety of habitats. In Ireland, there are well established landhopper populations in conifer plantations dominated by Lodgepole pine (*Pinus contorta*). The landhopper has also been reported from stands of Sitka spruce (*Picea sitchensis*), albeit at much lower densities (O'Hanlon *et al.*, 1993). It sometimes occurs in grassland under bracken but always in close proximity to a woodland site, with population density declining as one moves away from the wooded area (Patalano, 1999; Bromham 1997; O'Hanlon, 1993). Bracken-free grassland, with or without herbaceous annuals, generally does not harbour any landhoppers (Bromham, 1997; Patalano, 1999 and personal observations). The leaf litter which gathers under hedges along roads is also a favoured habitat, and one facilitating dispersal (personal observations, O'Hanlon, 1993, Richardson, 1980). Mixed and deciduous woodlands seem to be particularly suitable for landhopper colonization, with thriving populations recorded in these habitats in many places around Britain and Ireland. Particularly high densities were observed in a mixed woodland with an understorey of *Rhododendron ponticum* (O'Hanlon *et al.*, 1993). It is likely that the large leathery Rhododendron leaves, which are slow to decompose, help to support large numbers of landhoppers by providing additional shelter and preventing water evaporation from the surface of the soil, since they are only reluctantly taken as food (see Chapter 6).

In parks and gardens, landhoppers have been found under a variety of both native and exotic plants. Richardson (1980) reported particularly high densities among the litter under the tree fern *D. antarctica*, a location also favoured by *A. dorrieni* in the southern hemisphere. Landhoppers have further been reported to inhabit the litter under privet (*Ligustrum ovalifolium*) hedges, under *Acer pseudoplatanus*, *Ulmus spp.*, the ornamental non-native shrub *Euonymus japonicus* and the low-growing non-native Helxine (*Soleirolia soleirolii*) (Murphy, 1973). For some time, Helxine was thought to provide a particularly suitable habitat for *A. dorrieni*, and a possible association with the amphipod was suggested (Murphy, 1973, 1974). It is true that the dense Helxine mounds provide some shelter, shade, increased humidity and a quantity of dead leaf material as a possible food source, and landhoppers have been found among Helxine in this study. Nevertheless, any association appears to be a coincidental rather than a general one, as a number of patches of Helxine searched here did not harbour *A. dorrieni*, although the area around them had already been well colonized. In gardens, landhoppers tend to congregate under dustbins, plant pots, rubble, logs, concrete blocks, doormats, pieces of old carpet used for weed suppression, and in similar places during the day. When such objects are lifted, hundreds of landhoppers can usually be seen hopping frantically for a few seconds, before disappearing into cracks and crevices in the vicinity with astonishing speed and agility. They appear to prefer items resting on soil or, if on a solid surface, objects that are not moved regularly, so that a thin layer of friable compost is formed underneath, into which the landhoppers and other invertebrates can burrow. It seems that landhoppers often use earthworm burrows for shelter and to hide in after disturbance. Occasionally there have been reports of *A. dorrieni* from compost heaps (Richardson, 1980), but there they are generally only found in the surface layer (<5cm) (personal observation). Some typical garden microhabitats in which *A. dorrieni* was observed in considerable numbers are illustrated in Figure 2 (below).

Figure 2 Typical garden habitats of *A. dorrieni*, length of arrows indicates relative numbers of individuals observed.

Generally it may be said that *A. dorrieni* thrives where there is an abundance of mixed leaf litter of adequate (but not excessive) humidity over friable soil (Richardson, 1980), with shelter from full sun (Murphy, 1973) and drying winds. Exposed or waterlogged sites are never colonized (O'Hanlon *et al.*, 1993), but landhoppers have been found among *Phragmites sp.* reeds by the shore of a lake where the surrounding woodland had been colonized (Moore *et al.*, 1986). There do not seem to be any close associations of *A. dorrieni* with any native or non-native plant species that could have an effect on its distribution (Cowling *et al.*, 2004).

1.6 Current distribution of A. dorrieni in Great Britain and the species' invasive potential

As noted earlier, the most recent paper reviewing the distribution of *A. dorrieni* in Great Britain was published in 2004, illustrating the status in 2002 (Cowling *et al.*, 2004). The current updated map is shown as Figure 3 (page 20). The list of all records to date is held at the BRC (British Records Centre, Centre for Ecology and Hydrology, Monks Wood, UK).

Any expansion in the geographical range of a species can be construed as the process of ecological invasion. In its broadest sense, invasion encompasses events as diverse as the recolonization of an area after disturbance and the synanthropic dispersal of species to new areas of the world. It occurs when an individual, or group of individuals, arrives somewhere beyond the range previously occupied by that species (Williamson, 1991). In the case of *A. dorrieni* in Britain and Ireland, the latter definition, which carries with it the potential for the greatest repercussions, has to be applied.

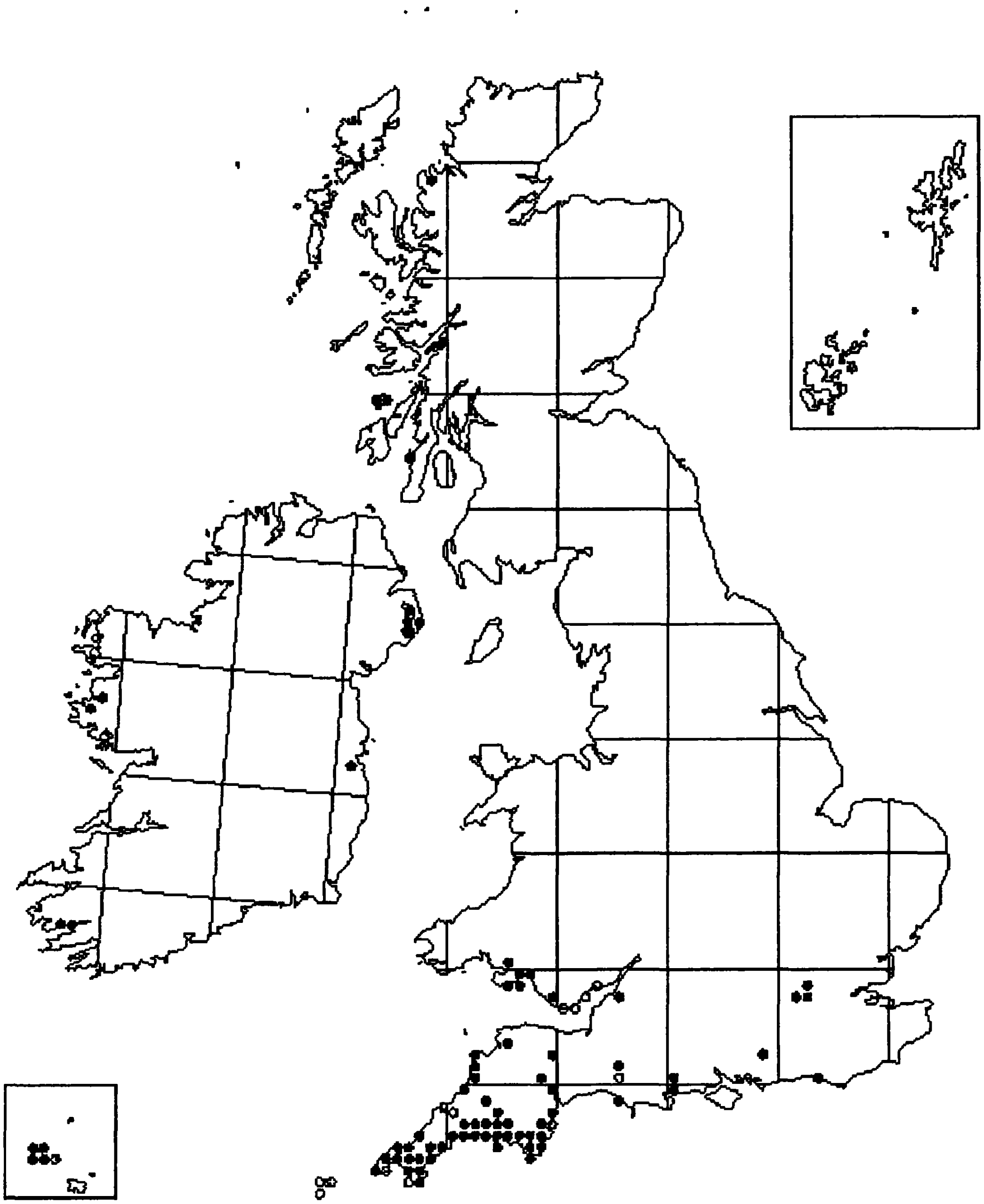


Figure 3 **Distribution of *A. dorrieni* in the British Isles, status summer 2005. Closed symbols indicate post-1980 records, open symbols pre-1980 records.**

reproduced with permission from Biological Records Centre, CEH Monks Wood, UK.

The limit of a species' distribution after invasion defines its invasive potential. Investigating the factors which might control these limits can lead to a better understanding of the invasion process as a whole (Spicer & Gaston, 1999). In addition, it may further lead to possible methods of slowing or stopping invasion, if this process turns out to have detrimental effects on native ecosystems.

Both biotic (e.g. availability of food, presence/absence of competitors or predators) and abiotic factors (e.g. frosts, rainfall, substrate sodium content) may limit a species' potential distribution. In the case of *A. dorrieni* in Great Britain, it has been suggested that the major limiting factors are of an abiotic nature, and that the most important of those is winter frost (Richardson, 1980). When assessing the influence of abiotic factors on a species' distribution, a correlational approach is often taken, where different environmental variables are matched to species' distributions or range limits. This approach can lead to false positive results, as a significant correlation between a certain factor and a species' range does not necessarily mean that the range is defined by the factor in question (Cowling *et al.*, 2004). Factors which do appear to be controlling the colonization of new habitat by landhoppers are a minimum annual rainfall of 600mm/year, a minimum chloride ion precipitation of 25ppm and a relative freedom from ground freezing frosts (Richardson 1980).

Annual rainfall is above this minimum in all parts of the British Isles, so will not pose any limitations on the spread of *A. dorrieni.* Sodium ion concentration, however, may be a significant factor limiting the landhopper's spread. Many landhoppers are restricted to coastal habitats by their requirements for relatively high ion (particularly sodium ion) concentrations in the substrate (Friend, 1987; Morritt *et al.*, 1998; Spicer *et al.*, 1987), and this limitation may well also apply to *A. dorrieni.* Cowling *et al.* (2004) noted severe reductions in landhopper population densities in conditions where mean soil and leaf litter sodium concentrations were below 64 mg/kg. Much further research is required before this aspect of the landhopper's invasive potential will be fully understood. Such research will have to include the determination of litter (as well as soil) sodium concentrations, both in areas colonized by *A. dorrieni* and those where it is still absent, and an investigation of the landhopper's ability to absorb sodium from its food.

As regards temperature, the landhopper populations in Britain and Ireland are subject to strong selection pressure for those individuals best adapted to cope with the temperate climate. It is not unlikely that this has led to an increase in the proportions of individuals capable of surviving the adverse winter conditions compared to the proportion of such animals among the populations when they had only recently been introduced. During this study, landhoppers have been observed near the surface and capable of movement on cold winter days at a time of year when night frosts were a common occurrence. Continued observation and experimentation similar to the experiments described in Chapter 8 and section 9.3 is required to assess the landhopper's potential for future spread into more northerly parts of the British Isles. Additionally, the global increase in temperature has already led to a number of various species with an historically more southerly distribution to establish in Britain (BBC, 2004). This has also enabled British species originally confined to the South to expand their ranges northwards, and will undoubtedly facilitate the spread of *A. dorrieni.*

In situations where conditions for population expansion are favourable, *A. dorrieni* has been estimated to be capable of spreading at a rate of 25m/year (Moore *et al.*, 1986). While some authors suggest that *A. dorrieni* has limited potential to invade further into Britain (Cowling *et al.*, 2003), considerably more work is required before such a statement can be made with any certainty. Until such time, and considering the rapidly increasing speed of invasion observed over the past 25 years, it may be more realistic to assume that *A. dorrieni* is very likely to become a much more commonly and widely encountered member of the leaf litter community as time progresses.

1.7 Study aims

In 1899, a major paper on the taxonomy of the Amphipoda was introduced with the words: "No panegyrist of the Amphipoda has yet been able to evoke anything like popular enthusiasm in their favour. To the generality of observers they are only not repelled because the glance which falls upon them is unarrested, ignores them, is unconscious of their presence" (Stebbing, 1899) and in 1959, Hurley wrote: "Of the few Crustacean groups which have achieved some degree of freedom from the marine or freshwater environment, the Amphipoda have received least attention.". Unfortunately, despite a concentrated research effort by a handful of enthusiastic scientists, only little has changed in the favour of landhoppers since these articles were published. Often the mere existence of fully terrestrial amphipods is news to biologists, especially so in the northern hemisphere. Reasons for this neglect include the distribution of landhoppers, most of which occur in countries where zoological studies, along other than descriptive lines, developed comparatively recently (and much later than in Europe), and the major mechanical problems involved in collection and experimental work. The latter are mainly due to the landhoppers' great agility and to their susceptibility to desiccation (Dresel & Moyle, 1950; Hurley, 1959).

It is very unfortunate that the study of these fascinating animals has been so grossly neglected, because once the basic obstacles have been overcome, researching the terrestrial amphipoda opens up a field of almost endless possibility for discoveries yet to be made. In the case of *A. dorrieni*, the research effort does not only serve the furthering of knowledge for its own purpose but also to advance the understanding of *A. dorrieni's* role as an alien invader, and the effects its introduction may turn out to have.

This study was designed to investigate both ecological and behavioural aspects of landhopper biology, with a view to assessing their possible effects on the landhopper's invasive potential and its subsequent impact on the native fauna.

First, the population densities and population dynamics of *A. dorrieni* in a deciduous woodland are investigated, and the landhopper's impact on the native fauna in this location is assessed. Next, a number of procedures for the collection, handling, laboratory maintenance and other aspects of research involving this species are described. This is followed by the description of a series of laboratory experiments providing first insights into the landhopper's feeding behaviour. These include investigation of feeding rates, food preferences, and calculations of biomass and annual litter consumption. The subsequent section is dedicated to the assessment of the impact of native predatory species on landhopper populations, with several series of experiments exploring the palatability of *A. dorrieni* to a variety of potential predators. Finally, the landhopper's dispersal capabilities and activity rhythms are investigated through different laboratory experiments.

2 The Study Sites

2.1 Introduction

The two study areas used in this investigation were located in adjacent valleys on the Gower Peninsula, to the west of Swansea (Figure 4, page 27). The area in which a self-sustaining population of *A. dorrieni* was known to be present (also termed the 'experimental' area), was Bishop's Wood, Caswell. The area where the landhopper was absent (also termed the 'control' area), was Bishopston Valley.

This chapter introduces first Bishop's Wood, Caswell, and then Bishopston Valley. Included are detailed descriptions of the sampling sites at both locations, with a set of three photographs for each season. Each set of photographs consists of a distance view, illustrating the general properties of the site as well as its vegetation at the shrub layer level; a closer view illustrating the taller ground-cover vegetation; and a close-up view illustrating the leaf litter layer and the conditions at ground level.

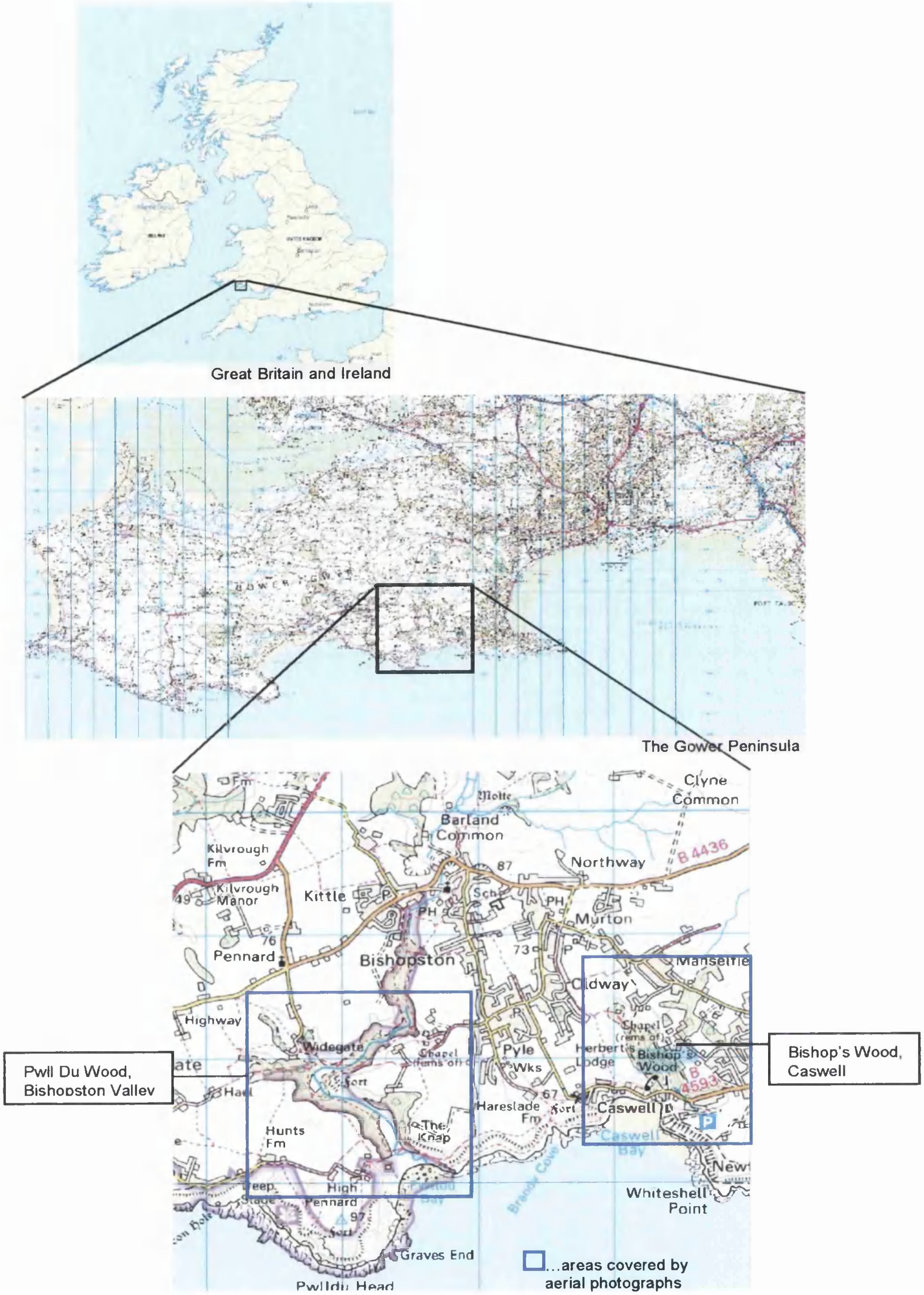


Figure 4 Location of sampling areas.

Great Britain and Ireland map reproduced from ESRI Vmap World Basemap, www.geographynetwork.com. The Gower Peninsula including magnification reproduced from Ordnance Survey mapping by permission of Ordnance Survey © Crown Copyright.

2.2 Bishop's Wood, Caswell

2.2.1 Location, history and choice of sampling sites

Bishop's Wood has been a local Nature Reserve since 1975 and is owned and managed by Swansea City Council. It consists of nearly 12 hectares of limestone-substrated woodland and around 7 hectares of limestone scrubland. There are records of the dry limestone valley already being wooded in the 17th century (Millhouse, 1996) and parts of the upper valley remain undisturbed ancient woodland to this day. During the 18th and 19th centuries, however, large parts (particularly in the lower half of the valley) were used for extracting limestone or grazing. The quarrying finally stopped in 1927 and many of the trees in the valley today constitute the saplings which recolonized the scarred landscape at that time (D. Morris, pers comm).

In the 19th century, the flat, widened base of the valley nearest the beach used to accommodate Caswell Cottage, which was owned by John Dillwyn Llewellyn, an avid gardener and collector of exotic ornamental plants (Figure 5, page 29). Although Caswell Cottage was demolished in 1966 and gardening activity had ceased well before that date, a number of John Dillwyn Llewellyn's plants still survive as escapees in the surrounding woodland.

Figure 5 Caswell Cottage (built 1840), photograph dated late 19th century, building viewed from the south-west; visible in the background: west-facing hillside damaged by limestone quarrying.

(photograph reproduced with permission from City and County of Swansea – Swansea Museum collection)

It used to be widely believed (e.g. Drewett, 1999) that *A. dorrieni* was introduced to Bishop's Wood along with some of the aforementioned ornamental plants, but the research for this study led to some conflicting evidence. The three major arguments are discussed below.

Firstly, there is no mention of *A. dorrieni* on Gower, or in Bishop's Wood, in Mary Gillam's comprehensive 1977 'The Natural History of Gower', which devotes Chapter Six entirely to 'Smaller Woodland Creatures' and describes the Gower soil invertebrates in some detail. The work does highlight the centipede *Geophilus osquidatus,* describing it as having been recorded as a new species for Britain 'in 1961 from Bishop's Wood at Caswell' (Gillham, 1977). It seems very unlikely that, had *A. dorrieni* been present in this location in any numbers at that time, it would have failed to attract the recording scientists' attention. This fact, together with the verbal accounts given by a number of scientists and naturalists who have detailed knowledge of the area (e.g. P. King, pers.comm., P. Llewellyn, pers. comm.) permits the conclusion that *A. dorrieni* was introduced to Bishop's wood later than 1961. Caswell Cottage, however, was demolished in 1966, with gardening having ceased some considerable time prior to that date (records show the garden was already overgrown by 1936).

A second piece of evidence in favour of a more recent introduction of *A. dorrieni* into Bishop's Wood may be found in the fact that Penllergare, a large park/garden complex in the north-west of Swansea created by John Dilwyn Llewellyn in 1845, is free from landhopper colonization to this day (the location was last searched for this study in early 2005). John Dilwyn Llewellyn's father, Lewis Weston Dillwyn, was also an avid gardener and collector of rare plants, and built up an exceptional plant collection at his property at Singleton (just to the west of the centre of Swansea) (Walker, 2003). The family was well known for exchanging plants (Morris, 1999), and a quantity of the stock of the garden at Caswell Cottage, came from the family's collection at Singleton. Plants from both Singleton and Caswell were later moved to Penllergare. Had there been well-established landhopper populations at either Singleton or Caswell at the time of the plant movements (ca. 1845-1860), they would, in all probability, have been introduced to Penllergare at the time.

The third, and final, piece of evidence for the original point of introduction of *A. dorrieni* lying outside Bishop's Wood is the fact that the landhopper's main range includes a wide and even distribution across the west of Swansea, [with the addition of the County-run parks (see section 1.5)]. Information on the extent of the area currently colonized by *A. dorrieni* was compiled from a number of sources:

- the verified responses to two newspaper appeals for sightings of landhoppers that had been published for this study;
- communication with local scientists;
- data contained in previous undergraduate projects;
- personal searches.

Bishop's Wood lies at the western boundary of this distibution. In fact, the most westerly wooded hillside that runs along the coast (situated on the opposite side of a wide road to the main woodland) did not yield any landhoppers in numerous searches in conjunction with this study between 2000 and 2002, and it was only in 2004 that, for the first time, small numbers were found.

There was, however, a large and well-known plant nursery dealing in exotic plants, near the centre of the current distribution (at West Cross) between ca. 1950-1970 (P. Llewellyn, pers. comm.). It is therefore suggested that *A. dorrieni* was introduced through this nursery, and, of course further distributed by the nursery's customers, thus explaining the numerous localized populations across the region (pers. obs.).

Initial investigations into the distribution and population density of *A. dorrieni* in Bishop's Wood were first performed by undergraduates in the late 1990s (Drewett, 1999; Millhouse, 1996). Four of the sampling sites chosen in this present study were common to those used in the preceding investigations. The original sites had been chosen to represent the four major microhabitats found in Bishop's Wood.

While the litter layer of forests is the typical habitat of most terrestrial amphipods, some species such as *T. sylvaticus* (Haswell, 1879; Hurley, 1955) and *Orchestia patersoni* (Hurley, 1957; Stephenson, 1938), often invade the litter of the long grass habitat (Duncan, 1969). In order to investigate whether the range of *A. dorrieni* also includes such habitats, a fifth site was added representing an additional type of microhabitat (grassy woodland edge). Quadrats of 10x10m were established at each of the sites and all samples were taken from within these areas. Figure 6 (page 33) illustrates the positions of the sampling quadrates.

Figure 6 Aerial photograph of Bishop's Wood, Caswell indicating the positions of the ten-meter sampling quadrats. The area depicted in this photograph is indicated on the Ordnance Survey map in Figure 4. Orange circles indicate location of sampling sites.

Digital aerial photograph reproduced from 'getmapping', Hartley Wintney, UK.

2.2.2 Site descriptions

Site 1

Site 1 is located on the west side of the valley. The quadrat is on a gentle slope. There is a dense canopy with Sycamore (*Acer pseudoplatanus*) being the predominant species. The ground is fairly rocky due to limestone debris, a leftover from the old limestone quarries in the valley. Ground cover is 100% throughout the year, made up during spring and summer by a large proportion of living plants as well as fallen leaves, during autumn and winter mainly by fallen leaves as well as Ivy (*Hedera helix*) and Bramble (*Rubus fruticosus*). Table 2-1 (below) shows the botanical composition of the canopy, shrub layer and ground cover of Site 1 (the order of plant species roughly reflects each species' abundance). Figure 7 (page 35) and Figure 8 (page 36) show the changing conditions at Site 1 through the seasons.

Canopy	*Dom:* Sycamore (*Acer pseudoplatanus*) *Also:* Ash (*Fraxinus excelsior*) Small-leaved lime (*Tilia cordata*) Pedunculate oak (*Quercus robur*)
Shrub layer	saplings of 1 and 2 above Spindle tree (*Euonymus europaeus*) Hawthorn (*Crataegus monogyna*) Guelder rose (*Viburnum opulus*) Hazel (*Corylus avellana*) Elder (*Sambucus nigra*)
Ground cover	Ramsons (*Allium ursinum*) Bramble (*Rubus fruticosus*) Dog's mercury (*Mercurialis perennis*) Bluebells (*Hyacinthoides non-scriptus*) Ivy (*Hedera helix*) Hart's tongue fern (*Phyllitis scolopendrium*) Male fern (*Dryopteris filix-mas*) Soft shield fern (*Polystichum setiferum*) Stinging nettle (*Urtica dioica*) Wood avens (*Geum urbanum*) Wood melick (*Melica uniflora*) Mosses

Table 2-1 Vegetation at Site 1, Caswell.

Figure 7 Caswell, Site 1 – left: spring (March), right: summer (June).

Figure 8 Caswell, Site 1 – left: autumn (September), right: winter (December).

Site 2

Site 2 is also located on the west side of the valley. It is on a steep slope which means that leaf litter accumulates less easily than (and does not remain as long as) on more level sites. The slope also results in the canopy being somewhat less dense. It consists of a variety of deciduous trees. Ground cover fluctuates between 60 and 85%. The higher level is reached during the Summer and Autumn, when low growing perennials (including woodland grasses) and fallen leaves, respectively, are common. Table 2-2 (below) shows the botanical composition of the canopy, shrub layer and ground cover of Site 2. Figure 9 (page 38) and Figure 10 (page 39) show the changing conditions at Site 2 through the seasons.

Canopy	*Mix of:* Ash (*Fraxinus excelsior*) Wych elm (*Ulmus glabra*) Hazel (*Corylus avellana*) Hawthorn (*Crataegus monogyna*) Pedunculate Oak (*Quercus robur*)
Shrub layer	sparse, with saplings of the above
Ground cover	Ivy (*Hedera helix*) Male fern (*Dryopteris filix-mas*) Broad buckler fern (*Dryopteris dilatata*) False brome (*Brachypodium sylvaticum*) Bramble (*Rubus fruticosus*) Wood melick (*Melica uniflora*) Bluebells (*Hyacinthoides non-scriptus)* Ramsons (*Allium ursinum*) Rose (*Rosa arvensis*) Wood anemone (*Anemone nemorosa*) Common dog-violet (*Viola riviniana*) Arum (*Arum maculatum*) Wood sedge (*Carex sylvatica*)

Table 2-2 Vegetation at Site 2, Caswell.

Figure 9 Caswell, Site 2 – left: spring (March), right: summer (June).

Figure 10 Caswell, Site 2 – left: autumn (September), right: winter (December).

Site 3

Site 3 is located on the seaward end of the valley, near the base of its western slope. The canopy is almost entirely made up of mature introduced Evergreen Oak (also known as Holm Oak) *Quercus ilex*, an escapee from the gardens around Caswell cottage. The canopy is very dense and little light penetrates to the ground. This is reflected in a very sparse layer of low growing plants. Due to the slope, ground cover is patchy, approximately 60% all year round, and is mainly made up of dead *Q. ilex* leaves. However, it is rather thick in places, and there supports a thriving community of leaf litter invertebrates with exceptionally high numbers of landhoppers. Table 2-3 (below) shows the botanical composition of the canopy, shrub layer and ground cover of Site 3. Figure 11 (page 41) and Figure 12 (page 42) show the changing conditions at Site 3 through the seasons.

Canopy	*Dom*: Evergreen Oak (*Quercus ilex*)
Shrub layer	Young sycamore (*Acer pseudoplatanus*) Young wych elm (*Ulmus glabra*)
Ground cover	Arum (*Arum maculatum*) Hart's tongue (*Phyllitis scolopendrium*) Dandelion (*Taraxacum officinale*) Spear thistle (*Cirsium vulgare*) Sterile brome (*Brachypodium sp.*) Lesser burdock (*Arctium minus*) Male fern (*Dryopteris filix-mas*)

Table 2-3 Vegetation at Site 3, Caswell.

Figure 11 Caswell, Site 3 – left: spring (March), right: summer (June).

Figure 12 Caswell, Site 3 – left: autumn (September), right: winter (December).

Site 4

Site 4 is located on the east side of the valley. It is on a very gentle slope where leaf litter accumulates easily. The canopy is dense and consists mainly of Ash (*Fraxinus excelsior*). The ground is very rocky due to limestone debris. Ivy is the predominant groundcover plant, providing at least 60% of the total ground cover all year round. Overall, ground cover is between 80% and 100%, depending on season. Table 2-4 (below) shows the botanical composition of the canopy, shrub layer and ground cover of Site 4. Figure 13 (page 44) and Figure 14 (page 45) show the changing conditions at Site 4 through the seasons.

Canopy:	*Dom:* Ash (*Fraxinus excelsior*) *Also*: Wych elm (*Ulmus glabra*) Sycamore (*Acer pseudoplatanus*) Hazel (*Corylus avellana*) Holly (*Ilex aquifolium*) Field maple (*Acer campestre*) Hawthorn (*Crataegus monogyna*) Elder (*Sambucus nigra*) Honeysuckle (*Lonicera periclymenum*)
Shrub layer:	Saplings of 1-4 above Spindle (*Euonymus europaeus*)
Ground cover:	Ivy (*Hedera helix*) Soft shield fern (*Polystichum setiferum*) Intermediate polypody (*Polypodium interjectum*) Hart's tongue fern (*Phyllitis scolopendrium*) Bramble (*Rosa fruticosa*) Common dog-violet (*Viola riviniana*) Ramsons (*Allium ursinum*)

Table 2-4 Vegetation at Site 4, Caswell.

Figure 13 Caswell, Site 4 – left: spring (March), right: summer (June).

Figure 14 Caswell, Site 4 – left: autumn (September), right: winter (December).

Site 5

Site 5 is located centrally at the bottom of the valley, approximately 400m into the valley. It represents typical 'woodland edge' habitat, a community of mostly perennials and ferns which is cut back once a year by Swansea Council. The quadrat is fringed by trees and shrubs, but there is no canopy directly overhead. The ground is fairly heavy with a large proportion of clay, and it is often quite damp. Ground cover is 100% during spring, summer and autumn but can drop to 80% in late winter. Table 2-5 (below) shows the botanical composition of the canopy, shrub layer and ground cover of Site 5. Figure 15 (page 47) and Figure 16 (page 48) show the changing conditions at Site 5 through the seasons.

Fringe:	Hawthorn (*Crataegus monogyna*) Field maple (*Acer campestre*) Wych elm (*Ulmus glabra*) Sycamore (*Acer pseudoplatanus*)
Ground cover:	Hogweed (*Heracleum sphondylium*) Bracken (*Pteridium aquilinum*) Broad leaved dock (*Rumex obtusifolius*) Stinging nettle (*Urtica dioica*) Cleavers (*Galium aparine*) Ramsons (*Allium ursinum*) Herb robert (*Geranium robertianum*) Wood speedwell (*Veronica montana*) Yellow pimpernel (*Lysimachia nemorum)* Lesser celandine (*Ranunculus ficaria*) Creeping buttercup (*Ranunculus repens*) Dandelion (*Taraxacum officinale*) Wild angelica (*Angelica sylvestris*) Meadowsweet (*Filipendula ulmaria*) Meadow buttercup (*Ranunculus acris*) Ground ivy (*Glechoma hederacea*) Dog's mercury (*Mercurialis perennis*) Creeping thistle (*Cirsium arvense*) Red campion (*Silene dioica*) Male fern (*Dryopteris filix-mas*) Soft brome (*Bromus hordeaceus*)

Table 2-5 Vegetation at Site 5, Caswell.

Figure 15 Caswell, Site 5 – left: spring (March), right: summer (June).

Figure 16 Caswell, Site 5 – left: autumn (September), right: winter (December).

2.3 Bishopston Valley - Pwll-du Wood

2.3.1 Location, history and choice of sampling sites

The Pwll-du wood area of Bishopston Valley was chosen as the location for the 'control' sites (*A. dorrieni* absent) because it is less than two kilometres to the West of Bishop's Wood, and it closely resembles the study locale in several respects, namely:

1. This valley, too, leads down to a small bay (in fact, the next bay along the coastline from Caswell)
2. The underlying rocks are identical and extensive limestone quarrying has also been carried out at this locality in the past.
3. It is also made up of a mixture of ancient and recent woodland

The main difference is that Caswell is a dry valley in which the stream runs underground, whereas in Bishopston Valley it runs on the surface. The consequence is that overall humidity in Bishopston Valley is somewhat higher and this, in turn, is reflected by a somewhat higher proportion of mosses and moisture-loving plants.

The sampling sites were chosen to resemble their respective counterparts in Caswell as closely as possible. Particular attention was given to the ground itself, the composition of species of low growing plants and the amount of ground cover through the seasons. Where possible, the tree species in the canopy were also matched to achieve maximum similarity in the composition of the leaf litter. Figure 17 (below) illustrates the exact locations of the sampling sites. Since *A. dorrieni* was virtually absent from Site 5 in Caswell, there was no 'control' woodland edge site in Bishopston Valley.

Figure 17 Aerial photograph of Pwll Du Wood, Bishopston Valley indicating the positions of the ten-meter sampling quadrats. The area depicted in this photograph is indicated on the Ordnance Survey map in Figure 4. Orange circles indicate location of sampling sites.

Digital aerial photograph reproduced from 'getmapping', Hartley Wintney, UK.

2.3.2 Site description

Site 1

Site 1 is on a gentle slope facing north-west. The canopy consists of a mixture of Elm, Small-leaved lime and Ash interspersed by a number of large hawthorns. The ground is somewhat rocky. Ground cover is 100% all year round, with the exception of a small number of isolated, steep slopes. During spring and summer, most of the ground cover is made up of living plants as well as fallen leaves. During autumn and winter, the ground cover consists mainly of fallen leaves, as well as some bramble and mosses. Table 2-6 (below) shows the botanical composition of the canopy, shrub layer and ground cover of Site 1. Figure 18 (page 52) and Figure 19 (page 53) show the changing conditions at Site 1 through the seasons.

Canopy:	*Mix of:* Wych elm (*Ulmus glabra*) Small-leaved lime (*Tilia cordata*) Ash (*Fraxinus excelsior*) Hawthorn (*Crataegus monogyna*)
Shrub layer:	saplings of the above Hazel (*Corylus avellana)*
Ground cover:	Bramble (*Rubus fruticosus*) Dog's mercury (*Mercurialis perennis*) Ivy (*Hedera helix*) Bluebells (*Hyacinthoides non-scriptus*) Ramsons (*Allium ursinum*) Soft shield fern (*Polystichum setiferum*) Hart's tongue fern (*Phyllitis scolopendrium*) Male fern (*Dryopteris filix-mas*) Wood anemone (*Anemone nemorosa*) Wood speedwell (*Veronica montana*) Stinging Nettle (*Urtica dioica*) Herb robert (*Geranium robertianum*) Wood avens (*Geum urbanum*) Common dog-violet (*Viola riviniana*) Arum (*Arum maculatum*) Red campion (*Silene dioica*)

Table 2-6 Vegetation at Site 1, Bishopston Valley.

Figure 18 Bishopston Valley Site 1 – left: spring (March), right: summer (June).

Figure 19 Bishopston Valley Site 1 – left: autumn (September), right: winter (December).

Site 2

Site 2 is located on a reasonably steep west-facing slope which, as in Caswell, prevents leaf litter from settling in certain areas of the site. The canopy is not very dense and the shrub layer is thin. Ground cover fluctuates between 60 and 90%, depending on season. Table 2-7 (below) shows the botanical composition of the canopy, shrub layer and ground cover of Site 2. Figure 20 (page 55) and Figure 21 (page 56) show the changing conditions at Site 2 through the seasons.

Canopy:	*Mix of:* Wych elm (*Ulmus glabra*) Syacmore (*Acer pseudoplatanus*) Hawthorn (*Crataegus monogyna*)
Shrub layer:	sparse, with saplings of the above
Ground cover:	Soft shield fern (*Polystichum setiferum*) Ramsons (*Allium ursinum*) Hart's tongue fern (*Phyllitis scolopendrium*) Male fern (*Dryopteris filix-mas*) Bramble (*Rubus fruticosus*) Rose (*Rosa arvensis*) Ivy (*Hedera helix*) Dog's mercury (*Mercurialis perennis*) Wood speedwell (*Veronica montana*) Common dog-violet (*Viola riviniana*) Herb robert (*Geranium robertianum*) Wood melick (*Melica uniflora*) Wood avens (*Geum urbanum*) Wild strawberry *(Fragaria vesca)* Wood sedge (*Carex sylvaticus*) Creeping buttercup (*Ranunculus repens*) Mosses

Table 2-7 Vegetation at Site 2, Bishopston Valley.

Figure 20 Bishopston Valley Site 2 – left: spring (March), right: summer (June).

Figure 21 Bishopston Valley Site 2 – left: autumn (September), right: winter (December).

Site 3

There is no dense stand of evergreen trees in Bishopston Valley which exactly resembles the patch of Holm Oak which characterizes Site 3 in Caswell. This site, however, possesses a similarly dense canopy of wind-pruned trees and, as a result, resembles Site 3 in Caswell to the extent that its low-growing vegetation is similar and its leaf litter layer is thick and persists throughout the year. The leaves of the deciduous trees in this site do break down faster than those of the evergreen trees in Caswell. However, a large proportion of woody debris along with the decaying leaves ensures that the ground remains covered all year round in most places. Site 3 is located on the east side of the valley, on a gentle slope near the sea. Table 2-8 (below) shows the botanical composition of the canopy, shrub layer and ground cover of Site 3. Figure 22 (page 58) and Figure 23 (page 59) show the changing conditions at Site 3 through the seasons.

Canopy:	*Mix of:* Hawthorn (*Crataegus monogyna*) Ash (*Fraxinus excelsior*) Hazel (*Corylus avellana*)
Shrub layer:	sparse, with saplings of the above Blackthorn (*Prunus spinosa*) Spindle (*Euonymus europaeus*)
Ground cover:	Ivy (*Hedera helix*) Hart's tongue fern (*Phyllitis scolopendrium*) Soft shield fern (*Polystichum setiferum*) Arum (*Arum maculatum*) Ramsons (*Allium ursinum*) Herb robert (*Geranium robertianum*) Male fern (*Dryopteris filix-mas*) Bramble (*Rubus fruticosus*) Bracken (*Pteridium aquilinum*) Black Bryony *(Tamus communis)*

Table 2-8 Vegetation at Site 3, Bishopston Valley.

Figure 22 Bishopston Valley Site 3 – left: spring (March), right: summer (June).

Figure 23 Bishopston Valley Site 3 – left: autumn (September), right: winter (December).

Site 4

Site 4 is located on a west facing slope. The canopy is fairly dense and consists of Elm, Ash and Sycamore. The ground is very rocky due to limestone debris. Ground cover varies between 50 and 70%, depending on season. The substrate at this site is unstable and thus not optimal for colonisation. Table 2-9 (below) shows the botanical composition of the canopy, shrub layer and ground cover of Site 4. Figure 24 (page 61) and Figure 25 (page 62) show the changing conditions at Site 4 through the seasons.

Canopy:	*Mix of:* Wych elm (*Ulmus glabra*) Ash (*Fraxinus excelsior*) Sycamore (*Acer pseudoplatanus*)
Shrub layer:	sparse Hawthorn (Crataegus monogyna) Holly (*Ilex aquifolium*)
Ground cover:	Soft shield fern (*Polystichum setiferum*) Hart's tongue fern (*Phyllitis scolopendrium*) Ivy (*Hedera helix*) Arum (*Arum maculatum*) Bramble (*Rubus fruticosus*) Dog's mercury (*Mercurialis perennis*) Ramsons (*Allium ursinum*) Mosses

Table 2-9 Vegetation at Site 4, Bishopston Valley.

Figure 24 Bishopston Valley Site 4 – left: spring (March), right: summer (June).

Figure 25 Bishopston Valley Site 4 – left: autumn (September), right: winter (December).

3 Population densities and population dynamics of *A. dorrieni*

3.1 Introduction

A major essential step on the way to understanding an alien species' invasive potential is the investigation of the population densities this species is capable of reaching in different habitats and under different environmental conditions. Population dynamics may be defined as the regular and recurring fluctuations in densities that occur due to the birth and death of individuals. Furthermore, the term population dynamics is applied to the study of the factors influencing these changes (Solomon, 1976). The three basic questions which population studies aim to answer (Dempster, 1975) are:

1. What causes the fluctuations in a species' numbers, particularly those from one year to another?
2. What determines the extent of these fluctuations?
3. What limits the distribution of the species under investigation?

In a spreading alien species such as *A. dorrieni,* the third question is obviously the most commonly asked and the one carrying the greatest immediate need for an answer. Thus, population study has been one of the most researched areas of the biology of *A. dorrieni.* Nevertheless, there have, to date, not been any comprehensive studies investigating landhopper population dynamics in deciduous woodland. Virtually all population density data for deciduous locations are results from spot-sampling on one or two days (Richardson, 1980; Spicer *et al.*, 1996). O'Hanlon & Bolger (1993) investigated the population dynamics of *A. dorrieni* in a coniferous plantation and a mixed woodland in some detail.

This chapter is devoted to the determination of the population densities reached by *A. dorrieni* at different times of the year and in different habitats within the coastal deciduous woodland at Bishop's Wood, Caswell, and the analysis of its population dynamics in this location.

3.2 Methods

3.2.1 Collection of Samples

Sampling quadrats of 10m x 10m were initially measured out at each site using string and tent pegs. As both Bishop's wood and Bishopston Valley are accessible to the public, the markers could not be left in place. Instead, landmarks along the outline of the quadrats were recorded and, on subsequent visits, these were used to determine the position of each quadrat. During the last week of each calendar month, five samples were collected at random from each quadrat. In line with previous Australian studies (Clark, 1954; Duncan, 1969) as well as the Swansea undergraduate projects, the samples were taken using a custom-made cylindrical metal corer (Mumbles Light Engineering, Castle Road, Swansea, UK). One of the advantages of using a corer instead of a quadrat is that the entire litter fauna is sampled, including those animals that take refuge in the larger interstices of the surface layer of the soil. The inside diameter of the corer was 7 cm (meaning that the surface area of each core as calculated by the formula πr^2 was around 38.5 cm^2), and the corer's length was 13.5 cm. In order to take a sample, the corer was pushed vertically through the leaf litter into the soil using a twisting motion. Where possible, it was pushed in until it had reached a depth of more than 5 cm below soil level, since landhoppers have been reported as being able to burrow to this depth (Clark, 1954), and other leaf litter fauna is also very scarce below this level (Dunger, 1958). Sometimes, however, the presence of rocky ground made penetration to such a depth impossible. In those cases, as thick a layer of soil as possible was taken and the area below the removed core was thoroughly examined to ensure no animals were present at that level. The corer was withdrawn with a twisting motion and the sample placed in an A4 sized resealable plastic bag with a write-on strip for labelling each sample ('Minigrip', Fisher Scientific UK Ltd., Loughborough, UK). Previous undergraduate projects (Drewett, 1999; Patalano, 1999) stress the importance of keeping the corer covered at all times to prevent landhoppers from jumping out. This proved unnecessary, since landhoppers only jump when uncovered, while any other kind of disturbance (such as core sampling) only motivates them to remain still or burrow deeper into the substrate. In fact, during the course of this study, not once did any invertebrate attempt to escape out of the top of the corer. It also turned out that it was unnecessary to use Clark's (1954) intricate method of removing the corer from the soil (he removed all litter and soil to one side of the cylinder and slid a metal plate under the cutting edge of the corer before lifting it up). In this study, the soil proved consistently sticky and firm enough to remain in the corer, concomitantly preventing animals escaping out of the bottom of the cylinder. The soil in the rainforest, where Clark (op. cit.) undertook his study, would doubtless be of a more friable texture, probably due to its higher proportion of organic matter.

The sample bags were sealed, labelled and, immediately on return to the laboratory, frozen at -20°C for a minimum of 48 hours or until they were processed.

3.2.2 Processing of Samples

Samples were processed in batches of five. Immediately after removal from the freezer, every sample was weighed on a torsion balance ('Torbal', *The Torsion Balance Co.* now *Fulcrum Inc.*, Clifton, N.J., USA) to determine its wet weight. The samples then were left to defrost at room temperature before being emptied into white plastic trays. Each sample was meticulously examined with the aid of a Luxo fluorescent lamp with a x 2 magnification lens, and all animals were removed by hand. Hand sorting, as used by the Swansea Honours students and many national and international workers (Dunger, 1958; Moore *et al.*, 1986; O'Hanlon *et al.*, 1993; O'Hanlon & Bolger, 1997) was used in preference to other extraction methods despite the considerably greater amount of work involved because of its greater accuracy. Other, less labour intensive extraction methods, such as use of a Tullgren funnel (as used for two related species of terrestrial amphipods by Duncan (1969)) and even a specially adapted Berlese-funnel-type arrangement (as used for a tropical terrestrial amphipod by Lindeman (1991) had been found comparatively unreliable and inefficient, since many animals (particularly *A. dorrieni* and most gastropods) died during the extraction procedure while still in the litter.

Special live insect handling forceps (F.S.T., Haverhill, UK) were used in order to avoid damaging the very fragile landhoppers and other soft-bodied small invertebrates. The animals were transferred to small glass jars with white write-on lids containing 70% ethanol (both from Fisher Scientific UK Ltd., Loughborough, UK) for later processing. Had long-term storage of specimens been an aim, a small quantity of chalk could have been added to the alcohol to prevent fatty acid destruction of the landhoppers' calcium-impregnated exoskeletons (Duncan, 1994). The samples, still in the trays, were placed in a drying oven (origin unknown) at 50°C, a standard temperature for drying sediment samples (Luczak, Janquin & Kupka, 1997), for a minimum of 48 hours. This time period had initially been determined with a set of five test samples (1000g, 80% water content), which had completely dried after that period of time (weight at end of the drying period was constant after an additional 48, 72 and 96 hours). Immediately after removal from the oven, the samples were weighed in order to determine their dry weight. Next, the organic matter content of the samples was determined by means of the Difference-On-Ignition (D.O.I) method (Luczak *et al.*, 1997). The samples were placed into large crucibles and ignited at 450°C for 240 minutes in a muffle furnace (Carbolite, Hope Valley, UK), an ashing regime regularly used for leaf litter/soil samples (Richardson & Devitt, 1984; Richardson & Mulcahy, 1996; Richardson *et al.*, 1991). When the samples had cooled, they were weighed a final time in order to determine their content of inorganic matter.

The preserved animals were placed into a petri dish and examined under a binocular microscope with zoom function of x 6.5 - x 50 magnification (Zeiss Stemi 2000 on Stemi DV4 base from Carl Zeiss Ltd., Welwyn Garden City, UK). Landhoppers in the samples were measured to the nearest millimetre. This was done by gently straightening the animals and viewing them over graph paper. Their length was measured along the median axis of the dorsal surface of the body, from the anterior edge of the cephalon to the tip of the telson.

Since there is no sexual dimorphism of gnathopod 2 in *A. dorrieni* (see section 1.3), the sexes were determined as follows: Males were identified by the presence of a pair of genital papillae on the sternal plate of the seventh/last thoracic segment (illustrated in Figure 26 and Figure 27, page 70). Females were identified by the presence of oostegites attached proximo-medially to the coxae of pereopods 2 to 5 (Friend *et al.*, 1986; Moore *et al.*, 1986) (illustrated in Figure 29, page 71; Figure 30 and Figure 31, page 72). Animals with neither of these structures and up to and including 5 mm in length were classed as juveniles. In most cases this classification was straightforward to apply. A number of individuals were found, however, which possessed neither genital papillae nor oostegites, but were significantly larger than 5 mm and consequently had to be adults. In some other species, oostegites only form at certain moults, and are lost or much reduced at others (A. Richardson, pers.

comm.) It is possible to differentiate between mature females in which the first three pairs of oostegites bear setae, and immature females with non-setose oostegites (Moore *et al.*, 1986; O'Hanlon *et al.*, 1997). It is therefore possible that an intermittent non-setose condition exists in adult female *A. dorrieni* that may sometimes result in such a reduction of the oostegites that they are rendered indiscernible under a dissecting microscope (up to x 50 magnification). Those individuals possessing neither genital papillae nor visible oostegites were therefore classed as females. Presence and number of eggs or larvae were noted (Figure 28, page 71; Figure 32, page 73) . The number of eggs recorded was not, however, used in any analysis, as a variable number are regularly lost from the brood chamber during capture and on the death of the mother (Duncan, 1969).

All other animals in the samples were identified to order level, and, where practical, to family and genus levels. These data are described in Chapter 4.

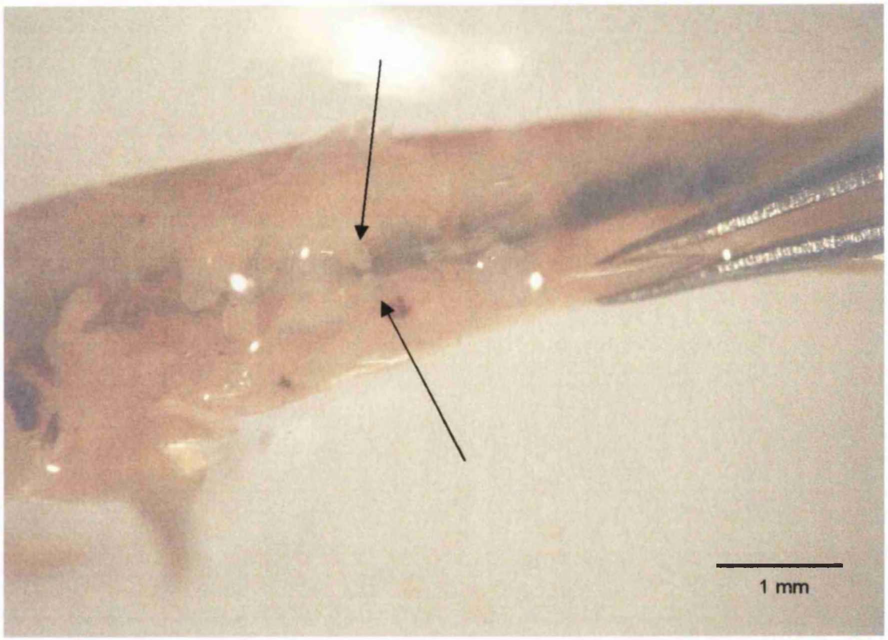


Figure 26 Arrows positioned at bases of genital papillae on seventh thoracic somite in an alcohol preserved male *A. dorrieni* (viewed under incident light, with the legs removed).

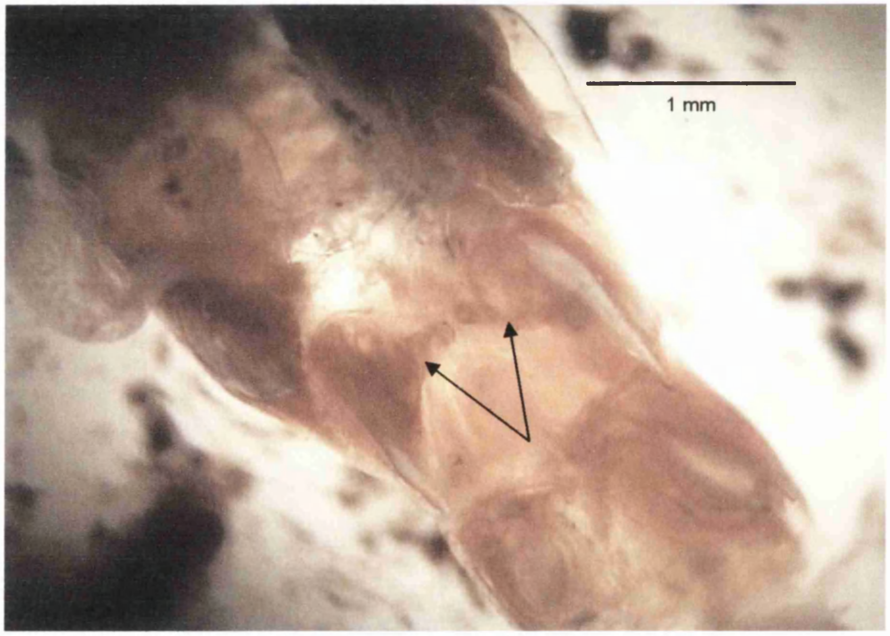


Figure 27 Arrows positioned to indicate position of genital papillae on seventh thoracic somite in an alcohol preserved male *A. dorrieni* (viewed under transmitted light, with the legs, urosome and intestine removed).

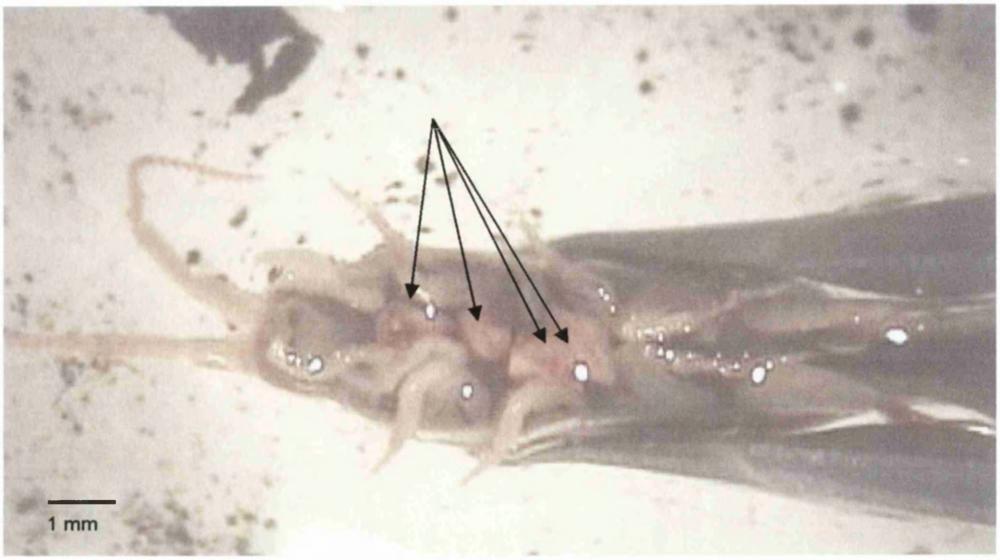


Figure 28 Arrows indicating position of eggs in an alcohol preserved female *A. dorrieni*, viewed under incident light.

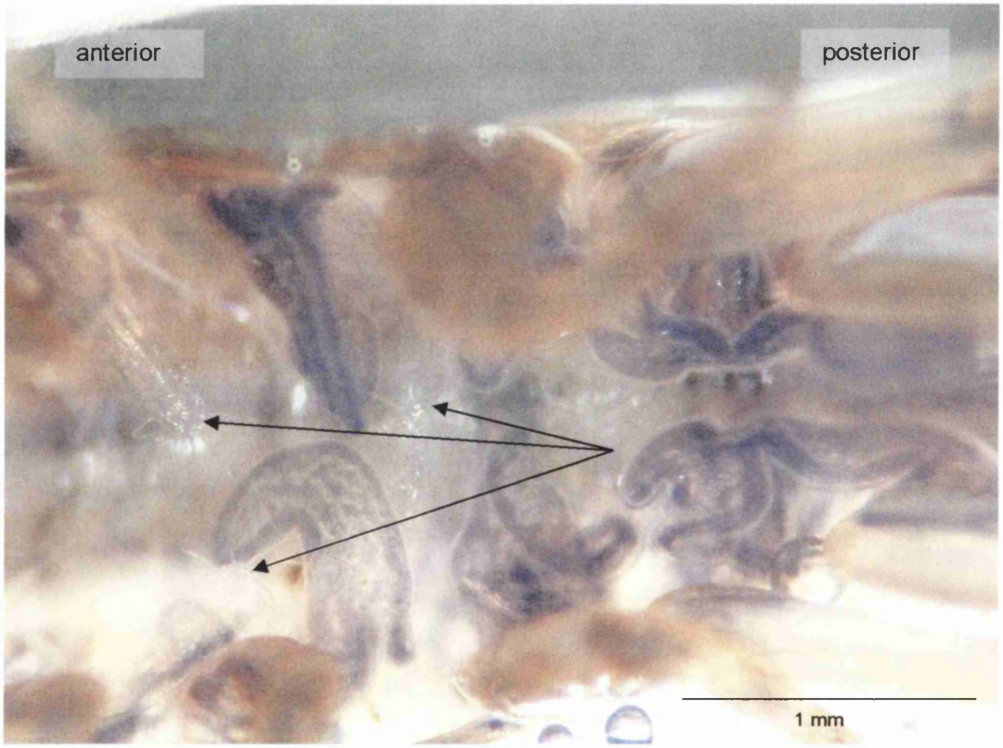


Figure 29 Arrows indicating tips of some of the setose oostegites on thoracic segments of a live anaesthetized female *A. dorrieni*, ventral view using transmitted + incident light.

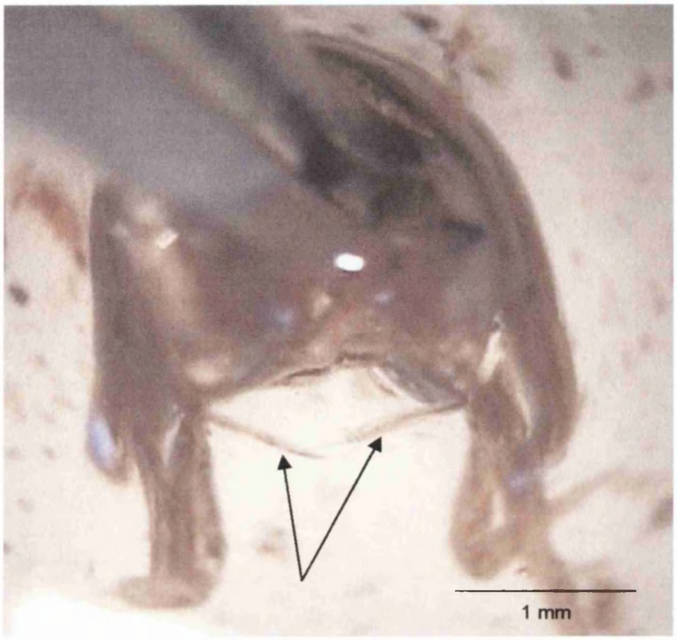


Figure 30 Arrows indicating oostegites forming the brood pouch (marsupium) on dissected fourth thoracic segment of alcohol-preserved female *A. dorrieni*, caudal view using transmitted light.

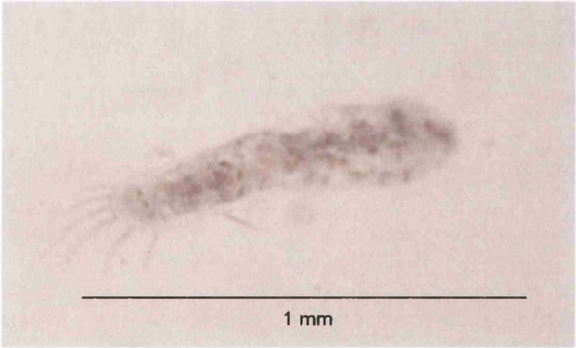


Figure 31 A single setose oostegite dissected from a female *A. dorrieni*, viewed under low level transmitted light.

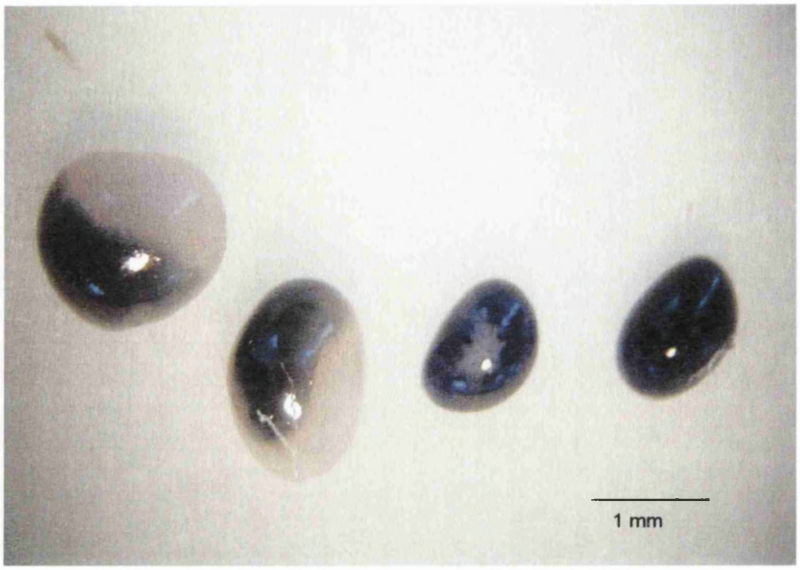


Figure 32 *A. dorrieni* eggs, removed from the brood pouch of two different live anaesthetised females. The pair on the left is of an advanced, and the pair on the right is of an early developmental stage, viewed using incident light.

3.3 Results

The results described here include the corresponding data from the control sites at Bishopston Valley, which are predominantly used in the next chapter. In order to assess the comparability of the sites, however, the data from both Bishop's Wood, Caswell and Bishopston Valley have to be analyzed in conjunction, and this is best accomplished at this stage.

A total of 600 samples was collected from Bishop's wood, Caswell and 420 samples from Pwll Du wood, Bishopston Valley. The difference in numbers is a result of two factors. Firstly, as explained previously (see section 2.2.1) only four sites were sampled in Bishopston Valley. Secondly, access to Bishopston Valley was precluded from February to May 2001 as a result of the national outbreak of Foot and Mouth disease (Bourn, 2002).

3.3.1 Substrate properties

3.3.1.1 Water content

The water content of the litter/soil layer is of the utmost importance for landhopper colonization of a site, due to the animal's dependence on high ambient humidity (see section 1.4). The proportion of water on the basis of wet weight was consequently determined for each sample, and monthly values for each site were calculated. These are summarized in Table 3-1 (page 75).

	C 1	C 2	C 3	C 4	C 5	BV 1	BV 2	BV 3	BV 4
May-00	0.37	0.37	0.36	0.43	0.56	0.41	0.44	0.51	0.41
Jun-00	0.39	0.35	0.32	0.39	0.29	0.31	0.32	0.46	0.2
Jul-00	0.33	0.3	0.28	0.35	0.3	0.28	0.33	0.32	0.3
Aug-00	0.35	0.21	0.34	0.31	0.31	0.35	0.35	0.39	0.42
Sep-00	0.4	0.62	0.44	0.51	0.39	0.35	0.53	0.44	0.29
Oct-00	0.37	0.47	0.54	0.36	0.38	0.32	0.45	0.54	0.37
Nov-00	0.49	0.51	0.44	0.18	0.36	0.39	0.46	0.51	0.27
Dec-00	0.39	0.44	0.45	0.39	0.39	0.39	0.42	0.48	0.3
Jan-01	0.4	0.44	0.43	0.39	0.34	0.4	0.41	0.49	0.3
Feb-01	0.4	0.45	0.4	0.29	0.33				
Mar-01	0.47	0.4	0.48	0.3	0.39				
Apr-01	0.5	0.41	0.41	0.43	0.38				
May-01	0.4	0.36	0.4	0.25	0.29	0.44	0.4	0.43	0.08
Jun-01	0.4	0.34	0.37	0.33	0.33	0.34	0.37	0.44	0.13
Jul-01	0.35	0.28	0.35	0.22	0.35	0.33	0.62	0.33	0.84
Aug-01	0.42	0.24	0.34	0.28	0.26	0.37	0.29	0.36	0.18
Sep-01	0.47	0.33	0.43	0.36	0.35	0.44	0.43	0.46	0.21
Oct-01	0.41	0.46	0.51	0.38	0.37	0.36	0.39	0.43	0.09
Nov-01	0.38	0.45	0.43	0.41	0.36	0.36	0.41	0.48	0.33
Dec-01	0.41	0.49	0.4	0.39	0.37	0.34	0.43	0.45	0.18
Jan-02	0.42	0.49	0.44	0.42	0.41	0.38	0.44	0.51	0.45
Feb-02	0.36	0.43	0.41	0.42	0.36	0.4	0.43	0.44	0.34
Mar-02	0.38	0.4	0.31	0.28	0.32	0.36	0.22	0.4	0.17
Apr-02	0.37	0.39	0.5	0.33	0.33	0.36	0.38	0.46	0.38
Means	**0.4**	**0.4**	**0.41**	**0.35**	**0.36**	**0.37**	**0.41**	**0.44**	**0.3**

Table 3-1 Proportion water content in the litter/soil samples from Bishop's Wood, Caswell (C) and Bishopston Valley (BV).

A series of Friedman tests were conducted in order to test for differences in water content among the sites of each location. The first test incorporated the proportion of water content monthly data from Caswell sites 1 to 5. The P value calculated was <0.001 ($\chi^2_{(4)}$=24.191), denoting that there is a highly significant variance between the medians calculated for the sites. In order to determine which sites were different and which similar, the data were examined. It appeared that sites 4 and 5 were drier than sites 1-3. The Friedman test was repeated excluding first both sites 4 and 5 then site 4 and then site 5 separately. When both sites were excluded, the P value was 0.876

($\chi^2_{(2)}$=0.264), indicating no significant differences between sites 1, 2 and 3. Where either site 4 or site 5 was incorporated, the P value was less than 0.05, ($\chi^2_{(3)}$=9.478, P=0.024 and $\chi^2_{(3)}$=10.31, P<0.001, respectively) indicating that both site 4 and site 5 are significantly different from, i.e. drier than, the other three sites. Finally, a Wilcoxon signed ranks test confirmed that there was no significant difference between sites 4 and 5 (W=8, P=0.881).

A Friedman test for the data from the four sites at Bishopston Valley also revealed significant overall variance ($\chi^2_{(3)}$=31.646, P<0.001). However, when each site was excluded in turn as above, the P values remained below 0.05, indicating that no three sites have the same median values. In order to determine whether there were any pairs of sites that were not significantly different from each other, six Wilcoxon signed ranks test were performed. The results are summarized in Table 3-2 (below). All P values are smaller than 0.05, indicating that the proportion of water in the litter/soil layer at each of the four sites in Bishopston valley is significantly different from the other three sites. This means that the proportion of water in the litter/soil layer is more variable at Bishopston Valley than it is at Caswell.

Site pair	**1&2**	**1&3**	**1&4**	**2&3**	**2&4**	**3&4**
Test statistic W	4	2	6	3	3	2
P Value	**0.025**	**<0.001**	**0.019**	**0.009**	**0.002**	**0.001**

Table 3-2 Results of Wilcoxon signed ranks tests comparing pairs of sites at Bishopston Valley.

In order to assess the degree of similarity in water content and retention between the matched sites (Caswell 1 - Bishopston 1 etc.), scatter graphs were constructed and correlations were performed. The graphs indicated a high degree of correlation in at least two cases. This was confirmed by calculation of the Pearson product-moment correlation, the results of which are displayed in Table 3-3 (page 78). The correlation for Sites 2 is not significant at the 0.05 level, but it is obvious that a considerable degree of correlation nevertheless exists. The surface layer of the soil of Site 4 Bishopston Valley (illustrated in Figure 24, page 61 and Figure 25, page 62) contains a greater number of small rocks than Site 4 Caswell (illustrated in Figure 13, page 44 and Figure 14, page 45), so that a larger proportion of samples contained significant amounts of inorganic material. This resulted in a reduction of recorded proportion of water and is the likely reason for the apparent lack of correlation between the Sites 4. Overall, the corrrelations show that the sites at Caswell and Bishopston were reasonably well matched in terms of the proportion of water in the soil/litter layer.

Only three of the nine sites showed a significant correlation of water content and rainfall when analyzed by Pearson product-moment correlation. The results are summarized in Table 3-4 (page 78). These results indicate that the woodland litter/soil layer offers comparatively stable conditions for its inhabitants throughout the seasons. In Figure 33 (page 79) an area graph is used to illustrate the monthly rainfall in the area (data obtained from Agro/Met station 8411 at Penmaen, Gower) and the percent water content of the litter/soil layer, encompassing data from all sites.

Although not strictly appropriate, this chart type best expresses the high level of constancy of the conditions in the litter/soil layer during widely fluctuating environmental conditions.

	Sites 1	**Sites 2**	**Sites 3**	**Sites 4**
r	0.508	0.356	0.657	-0.084
P	0.019*	0.114	0.001**	0.717

Table 3-3 Pearson product-moment correlation results for water content of matched sites.

*.....significant at the 0.05 level
**...significant at the 0.001 level

	C 1	**C 2**	**C 3**	**C 4**	**C 5**	**BV 1**	**BV 2**	**BV 3**	**BV 4**
r	0.193	0.550	-0.524	0.026	-0.252	0.092	0.385	-0.593	0.110
P	0.366	0.005*	0.015*	0.911	0.271	0.699	0.094	0.012*	0.644

Table 3-4 Pearson product-moment correlation results for sampling sites and rainfall.

*.....significant at the 0.05 level

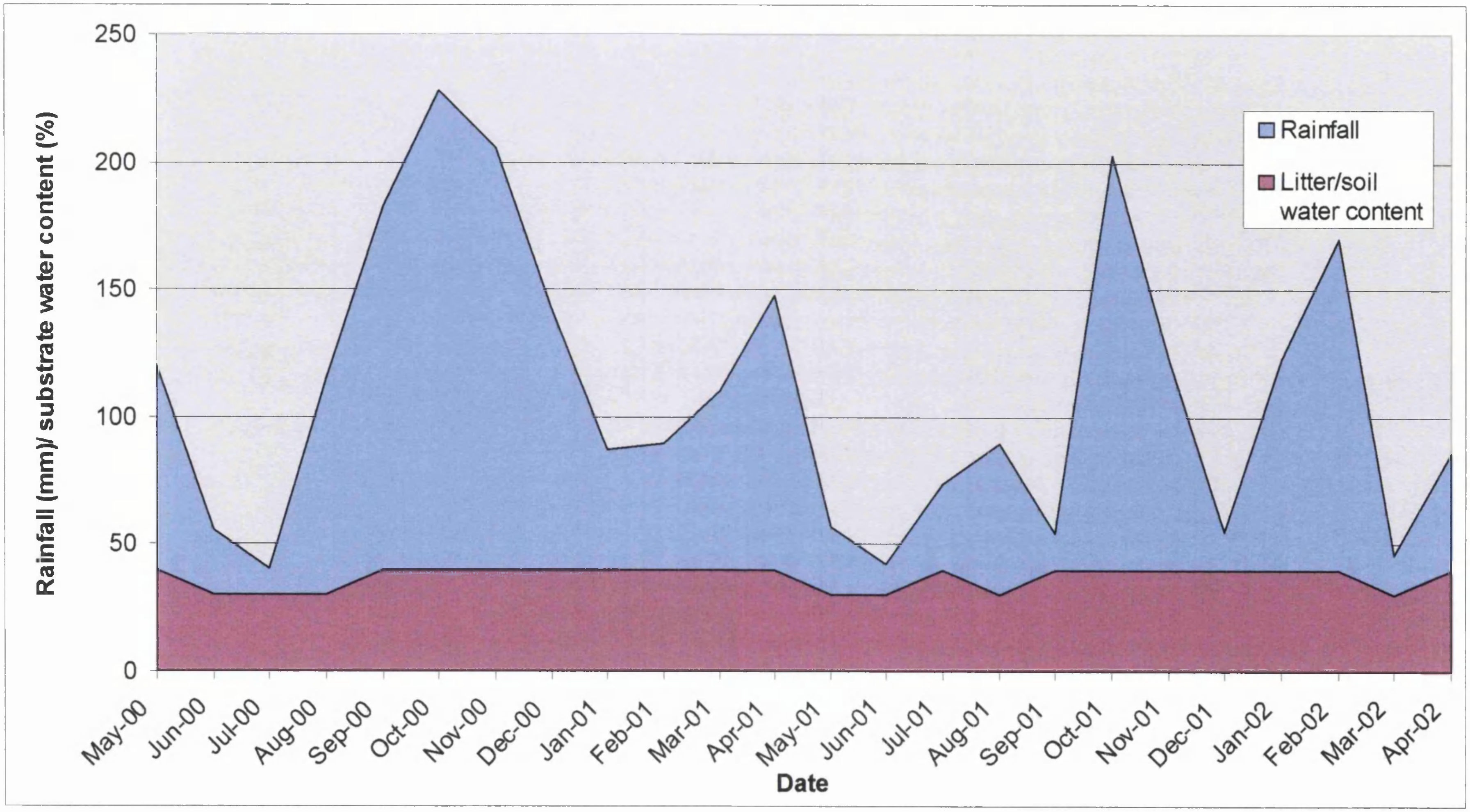


Figure 33 Area graph illustrating levels of rainfall and changes in % water content of the litter/soil layer at Bishop's Wood, Caswell and Bishopston Valley over the study period.

3.3.1.2 Organic matter content

The organic matter content of the litter/soil layer is a vital factor determining the suitability of a particular habitat for landhopper colonization, as it represents the presence and quantity of potential food material. Such data always have to be examined, however, in conjunction with the type of habitat, as the properties of the organic matter vary with habitat type. In grassland, for example, a large proportion of the organic matter in the sample will be made up of growing grass and its roots, which is unsuitable for landhoppers.

	C 1	**C 2**	**C 3**	**C 4**	**C 5**	**BV 1**	**BV 2**	**BV 3**	**BV 4**
May-00	0.16	0.17	0.18	0.13	0.07	0.08	0.11	0.14	0.15
Jun-00	0.13	0.12	0.15	0.11	0.05	0.08	0.13	0.18	0.06
Jul-00	0.13	0.15	0.2	0.11	0.07	0.07	0.14	0.17	0.07
Aug-00	0.11	0.06	0.22	0.12	0.05	0.08	0.12	0.21	0.34
Sep-00	0.09	0.05	0.16	0.14	0.1	0.08	0.09	0.16	0.07
Oct-00	0.08	0.11	0.15	0.15	0.05	0.07	0.12	0.16	0.06
Nov-00	0.13	0.14	0.15	0.04	0.06	0.08	0.11	0.15	0.03
Dec-00	0.11	0.15	0.21	0.1	0.06	0.08	0.12	0.16	0.07
Jan-01	0.12	0.13	0.25	0.18	0.06	0.07	0.12	0.16	0.08
Feb-01	0.1	0.09	0.21	0.16	0.05				
Mar-01	0.12	0.1	0.2	0.19	0.06				
Apr-01	0.12	0.11	0.17	0.12	0.05				
May-01	0.2	0.14	0.2	0.1	0.06	0.12	0.11	0.18	0.04
Jun-01	0.16	0.14	0.2	0.16	0.06	0.08	0.13	0.16	0.12
Jul-01	0.11	0.14	0.21	0.12	0.07	0.01	0.14	0.23	0.04
Aug-01	0.15	0.12	0.2	0.16	0.05	0.09	0.13	0.21	0.04
Sep-01	0.11	0.1	0.19	0.12	0.07	0.08	0.16	0.21	0.05
Oct-01	0.11	0.15	0.14	0.17	0.06	0.09	0.11	0.21	0.03
Nov-01	0.09	0.14	0.21	0.13	0.05	0.08	0.11	0.17	0.08
Dec-01	0.1	0.16	0.14	0.14	0.05	0.08	0.15	0.16	0.04
Jan-02	0.1	0.15	0.21	0.12	0.06	0.08	0.12	0.17	0.17
Feb-02	0.09	0.09	0.22	0.12	0.05	0.09	0.13	0.15	0.08
Mar-02	0.11	0.14	0.2	0.15	0.05	0.08	0.13	0.23	0.07
Apr-02	0.09	0.13	0.28	0.15	0.06	0.08	0.12	0.19	0.11
Means	**0.12**	**0.12**	**0.19**	**0.13**	**0.06**	**0.08**	**0.12**	**0.18**	**0.09**

Table 3-5 Proportion organic matter content in the litter/soil samples from Bishop's Wood, Caswell (C) and Bishopston Valley (BV).

The organic matter proportions on the different sampling sites are summarized in Table 3-5 (page 80). Mann-Whitney U tests confirmed that both Site 1 and Site 4 at Caswell have a statistically significant higher proportion of organic matter than their corresponding counterparts at Bishopston Valley. This could partly be due to the fact that those two sites are located on a somewhat steeper slope in Bishopston Valley than in Caswell, which leads to reduced leaf litter buildup and a less dense layer of groundcover plants (illustrated for Caswell in Figure 7 & Figure 8, pages 35&36 and Figure 13 & Figure 14, pages 44&45 and for Bishopston Valley in Figure 18 & Figure 19, pages 52&53 and Figure 24 & Figure 25, pages 61&62). Part of the difference, however, is likely to be a result of the texture of the top layer of the soil in Bishopston Valley (mentioned previously in section 3.3.1.1). This is characterized by a somewhat greater proportion of small pieces of limestone than that in Caswell, particularly so on Sites 2 and 4. As a result, samples from these sites tended to show greater total sample weights, greater proportion of inorganic matter and thus apparently a smaller proportion of organic matter. Overall, and particularly taking the above into account, the corresponding sites (Caswell 1-Bishopston 1, etc.) were well matched regarding their organic matter content. The results of the Mann-Whitney U Tests are summarized in Table 3-6 (below).

	Sites 1	**Sites 2**	**Sites 3**	**Sites 4**
U	79.5	219.5	198	86
P	<0.001**	0.455	0.215	<0.001**

Table 3-6 Results of Mann-Whitney U tests comparing the proportion of organic matter at the matched site pairs in Caswell/Bishopston Valley.

**...difference significant at the 0.001 level

3.3.1.3 *Soil pH*

The soil pH at the sampling sites was determined using a Westminster pH NPK Soil Test Kit (West Meters Ltd., Corwen, LL21 0DR, UK). Two samples were analyzed for each site, one at the end of spring (after a large proportion of the leaf litter had decomposed, thus possibly acidifying the soil) and one in the autumn (before a thick layer of leaf litter had formed). The results were identical or very similar at both sampling times, namely neutral to slightly alkaline, and are typical of a mull type forest soil (Wallwork, 1970). They are further indicative of the closely underlying limestone (at Site 4, Bishopston Valley, where especially large numbers of limestone particles are among the surface layer, the pH was particularly high). Caswell Site 5 showed a pH more typical of grassland habitat, which most of the site closely resembles. The results are summarized in Table 3-7 (page 83). The soil pH was so similar between the sites, that further investigations into correlations of landhopper numbers and soil pH were not undertaken. There was an apparent correlation between the low pH at Site 5 Caswell and the site's landhopper density. The low numbers of landhoppers found there were, however, probably only indirectly related to the site's pH value, since the main factors contributing to the low landhopper densites at this site are to be found among the unsuitability of the vegetation, absence of food and lack of adequate cover at the site (see Figure 15, page 47 and Figure 16, page 48).

Site	**Mean pH**
Caswell 1	7.5
Caswell 2	7.5
Caswell 3	7.0
Caswell 4	7.5
Caswell 5	5.5
Bishopston Valley 1	7.0
Bishopston Valley 2	7.5
Bishopston Valley 3	7.0
Bishopston Valley 4	8.0

Table 3-7 Mean pH values of the soil at the sampling sites.

3.3.2 Amphipod density

Most publications incorporating landhopper population studies, from Clark (1954) to Patalano (1999) state amphipod densities per m^2 calculated from sets of smaller samples. While this can give a general idea of a particular location's suitability as amphipod habitat and allows comparison of sites, it does not fully account for the fact that landhopper distribution in most habitats is very patchy, and, depending on the site, is patchy to different degrees. In order to minimize errors resulting from the extrapolation, a maximum number of samples covering as much surface area as possible should always be used in landhopper population studies, and the sampling period should also be as extensive as possible. Even where these precautions are taken, densities per m^2 can still result in misleading results. One example of such a result is the landhopper density at Site 5, Bishop's Wood, which was calculated as 9 animals/m^2 (see Figure 34, page 84). This figure implies that, while Site 5 constitutes poor landhopper habitat compared to the other sites, it is still capable of sustaining a low and steady number of individuals. In actual fact, however, landhoppers were only found at this site in 2 of 24 months, and it is thus much more likely that those individuals had accidentally strayed into the sampling area from neighbouring, suitable, habitat, rather than being regular inhabitants of Site 5. This is in keeping with other researcher's findings (e.g. Patalano, 1999, Bromham, 1997) and also applies to other landhopper species, such as *Cerrorchestia hyloraina*, which 'did not venture far from the forest edge' (Lindeman, 1991).

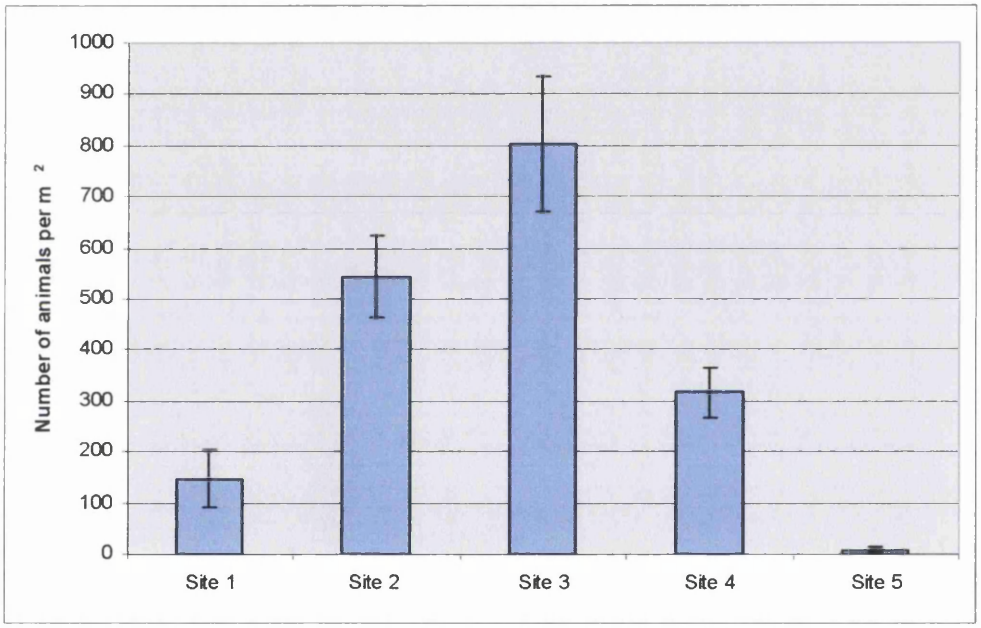


Figure 34 Mean densities of *A. dorrieni* at the different sampling sites at Bishop's Wood, Caswell (+/- SE, n=24).

3.3.2.1 *Landhopper numbers through the seasons*

Figure 35 (Page 86) displays the mean monthly landhopper density at Bishop's wood, Caswell over the 24 months of this study. The population density appears to follow a bimodal distribution pattern. Landhopper numbers generally rose in late spring and were at their highest during the summer months, peaking in August. This peak was followed by a drop in numbers during the autumn, and reached a low in October/November. In early winter, there was a second rise in numbers peaking in December/January before dropping back to an annual low around March. In May 2001 there was an apparently sudden dramatic drop in numbers, after which the landhopper population took until December to recover the levels recorded during the previous year. Investigation of data collected at the closest meteorological station (Agro/Met Station 8411, Penmaen, Gower) revealed that April 2001 had been the fifth wettest this century with 222% of the average rainfall. It had also been the coldest for 12 years with the largest number of ground frosts in that same time period, and the grass minimum temperature well below average for most of the winter and spring (illustrated in Figure 36, page 89). Most importantly, however, the 20th of April saw the grass minimum temperature plummet to -5.6 °C, which is very unusual for this time of year in this location, in fact, values this low had not been recorded since 1996. It is likely that these meteorological factors, particularly acting in combination, resulted in the drastic decline of landhopper numbers, which had already started to rise after their winter decline.

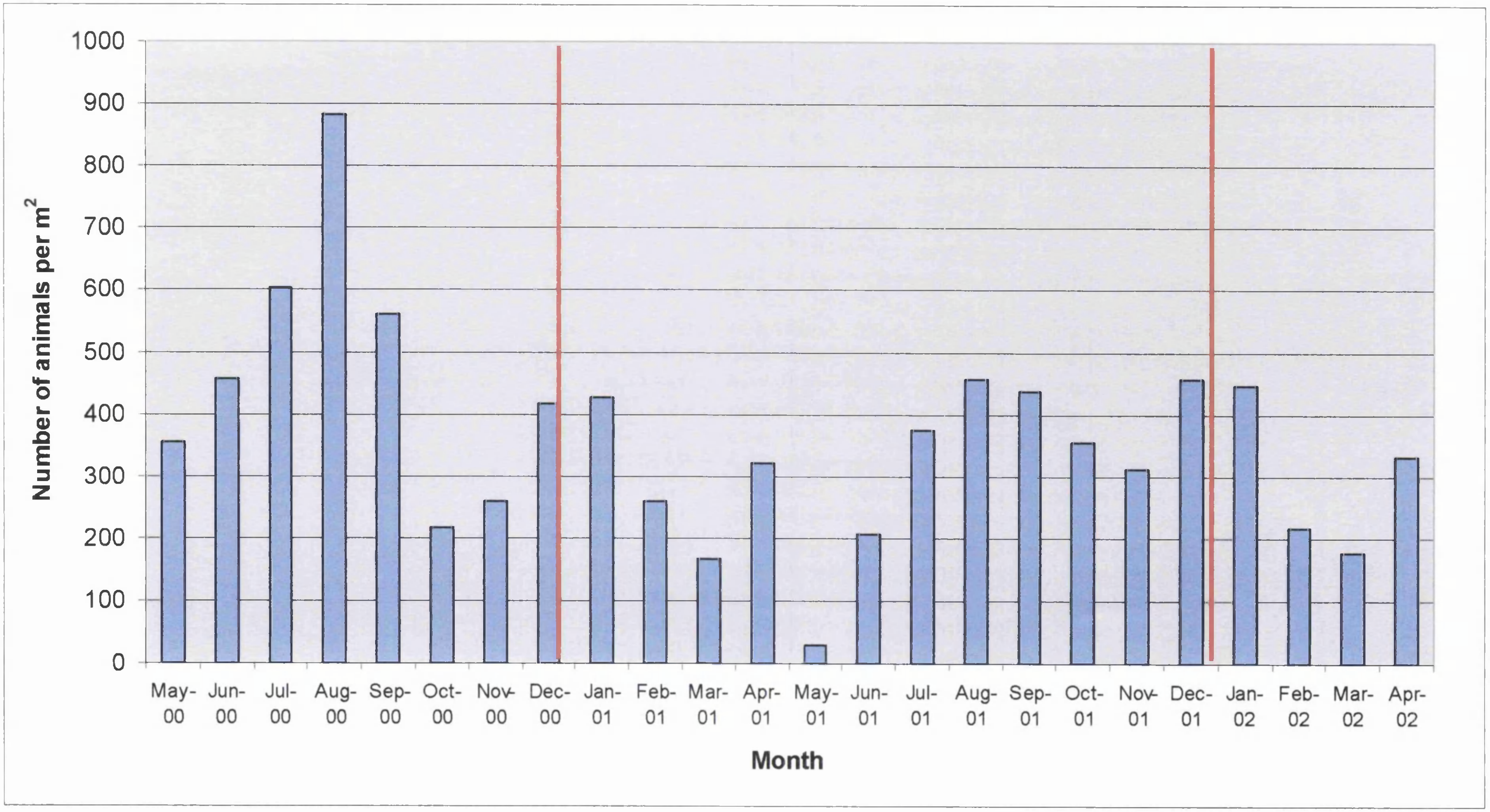


Figure 35 Landhopper density at Bishop's wood over 24 months; vertical lines indicate new calendar years.

3.3.2.2 *Effects of the weather on landhopper numbers*

Detailed meteorological data for the study period (including maximum, minimum and mean air temperatures, grass minimum temperatures, rainfall and number of ground frosts per month) were obtained from Agro/Met Station 8411. The climate at the sampling locations is of a typical temperate oceanic type, with high rainfall throughout the year (on average 102 mm/month), and relatively mild winters. Ground frosts do not generally occur until November, but they usually become frequent (>7 / month) by December. Regular ground frosts rarely occur later than April, but have occasionally been recorded in May. Ground frosts of around -8 °C occur in most years and temperatures of as low as -13.5 °C have been recorded. The temperature data for the sampling period, in comparison with the corresponding mean temperatures from 1971-2000 (also obtained from the Agro/Met station) are summarized in Figure 36 (page 89). The unusually low grass minimum temperatures during early 2001 are illustrated particularly clearly in this figure. Higher than average temperatures during early 2002 are likely to have contributed to particularly successful population growth later in this year, but unfortunately the sampling period ended before any such effects could become noticeable (namely the end of summer, after the main breeding period). Otherwise, the temperatures during the study period were very close to the mean values. Total landhopper numbers were correlated with the corresponding monthly mean, maximum and minimum temperatures, grass minimum temperatures (illustrated in Figure 36, page 89), rainfall (illustrated previously in Figure 33, page 79) and the total number of ground frosts per month.

Table 3-8 (below) summarizes the Spearman's rank-order correlation results. Both monthly minimum temperatures and monthly grass minimum temperatures showed a significant correlation with landhopper numbers. The grass minimum showed the stronger correlation. This result indicates that landhopper numbers are very intimately linked with low temperatures, dropping significantly during the colder months. High temperatures, rainfall and the total number of ground frosts recorded per month did not show a significant correlation with landhopper numbers.

	r_s	P
Mean temperature	0.384	0.064
Maximum temperature	0.347	0.097
Minimum temperature	0.414	0.044*
Grass minimum	0.478	0.018*
Rainfall	-0.112	0.601
Number of ground frosts/month	-0.326	0.120

Table 3-8 Spearman's rank-order correlation results for landhopper numbers with weather data.

* ... significant at the 0.05 level

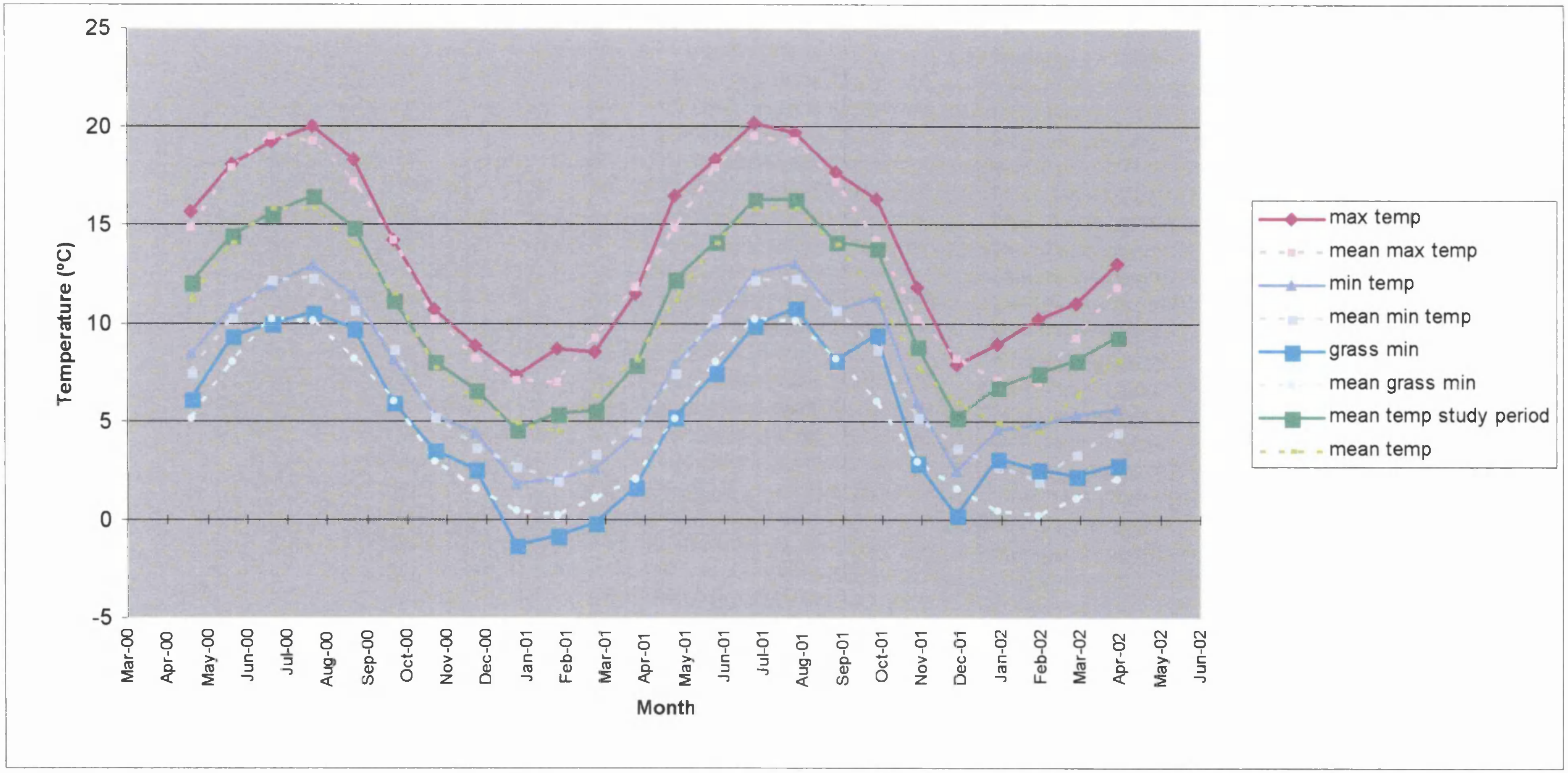


Figure 36 Temperatures on the Gower during the study period (smooth lines) and corresponding mean values 1971-2000 (dashed lines).

3.3.3 The relationships between amphipod populations and the different substrate properties

In order to better understand the effects (if any) of certain substrate properties on the landhopper population, correlations were performed to detect possible associations.

3.3.3.1 Landhopper numbers and water content of the litter/soil layer

The numbers of landhoppers collected monthly and the corresponding substrate water content were correlated separately for each site using Spearman's rank-order correlation. The results are summarized in Table 3-9 (below). Only Site 1 showed a significant correlation, thus indicating a relationship between the fluctuations of the amount of water in the soil/litter layer and the fluctuations in amphipod numbers. At most sites, the fluctuations of amphipod numbers during the year and the changes in litter/soil water content were independent of each other.

Site	r_s	**P**
1	-0.438	0.032*
2	-0.148	0.49
3	-0.081	0.708
4	-0.178	0.407
5	0.225	0.291

Table 3-9 Results of the Spearman's rank-order correlations for monthly soil/litter layer water content and amphipod densities.

* indicates significance at the $P<0.05$ level

When the mean amphipod numbers at each site was examined for correlation with the respective site's mean water content, a non-significant result was returned (r_s=0.8, P=0.2). This indicates that the mean water content at a site does not affect its landhopper population. This result must be viewed with some caution as all water contents observed here were very similar and within the range of potential landhopper habitat. Had sampling been extended to more unsuitable habitat, a larger range of litter/soil layer water contents would have been observed and a significant result would undoubtedly have been returned. A further examination of the data revealed that a significant correlation would have been returned if the data from Site 4 had been excluded. It was decided, however, that the apparently very significant correlation was of no practical value, as it would have meant that a very slight increase in water content would almost double the landhopper density, which obviously is not the case. This is confirmed by the data from Site 4, which possessed a lower water content than any of the other sites and yet contained twice as many landhoppers than Site 1.

3.3.3.2 *Landhopper numbers and the organic matter content of the litter/soil layer*

The numbers of landhoppers collected every month and the corresponding organic matter contents were correlated separately for each site using Spearman's rank-order correlation. The results are summarized in Table 3-10 (page 92). None of the sites showed a significant correlation. This indicates that organic matter content (at the range seen in these study sites) does not affect the landhopper numbers at the different sites.

Site	r_s	P
1	-0.197	0.355
2	0.224	0.293
3	0.024	0.911
4	0.024	0.913
5	0.335	0.110

Table 3-10 Results of the Spearman's rank-order correlations for monthly soil/litter layer organic matter content and amphipod densities.

When the mean amphipod numbers at each site were examined for correlation with the respective site's mean organic matter content, a non-significant result was returned (r_s=0.821, P=0.089). This indicates that the average organic matter content at a site and its landhopper population are independent of each other. The result is, however, sufficiently close to 0.05 to suggest a possible link between organic matter content and landhopper density should not be ruled out. Such an association is not unlikely and warrants further investigation. In particular, more marginal habitats (with lower organic matter content) should be included. This would strongly increase the likelihood of significant associations being found.

3.3.4 Size-frequency analysis

Figure 37 (page 95) and Figure 38 (page 96) present the monthly size-frequency histograms for May 2000 to April 2002. These data are also summarized in Table 3-11 (page 94). The comparatively low densities of *A. dorrieni* at Bishop's Wood, Caswell, and the resulting low numbers of individuals present in the samples, probably result in trends not showing up as well as they would if larger numbers of individuals had been available for inclusion. Nevertheless, two conclusions can be drawn from the investigation of the data, namely:

Young (the 3mm size class) first appear (i.e. they are first released by the females) between April and June, and they continue to make up a proportion of the population until December/January. They are generally absent between January and March.

A large proportion of overwintering animals belongs to the 5mm size class. The proportion of animals in this size class decreases around March/April, with proportions of the larger size classes slowly increasing. This indicates that *A. dorrieni* is capable of resuming growth in early spring.

The proportion of males, females and juveniles in the population is presented in Figure 39 (page 98). There do not appear to be any regular annual fluctuations in the proportion of either of the sexes or the juveniles. It may be of note that during 2001, following the devastating population reduction in early spring, the proportion of juveniles was considerably higher than in the preceding year. This was the case despite the fact that in 2001 the proportion of females was generally lower, and in many months much lower, than in 2000.

Figure 40 (page 99) illustrates the proportions of the three different size classes (3mm, 4mm and 5mm) within the total juvenile population. It can be seen that the smallest juveniles made up a large proportion of the total juveniles during the warmer months, with numbers of larger juveniles increasing during the autumn and peaking in late winter and early spring. The 3mm size class released during late autumn/early winter virtually disappeared by early spring.

Body-length (mm)	**3.0-3.4**	**3.5-4.4**	**4.5-5.4**	**5.5-6.4**	**6.5-7.4**	**7.5-8.4**	**8.5-9.4**	**9.5-10.4**	**10.5-11.4**	**11.5-12.4**	**12.5-13.0**
Size class	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
Jan	1	2	30	9	22	17	6	6	6	0	1
Feb	0	0	42	13	16	13	7	7	2	0	0
Mar	0	5	25	7	15	17	13	13	3	3	0
Apr	4	11	16	11	16	9	7	4	5	16	1
May	0	5	34	16	11	10	1	20	3	0	0
Jun	10	10	4	6	19	18	11	11	7	4	0
Jul	14	22	22	14	14	6	3	3	1	1	0
Aug	2	15	23	17	17	8	4	5	2	5	2
Sep	3	15	27	18	11	11	1	10	1	3	0
Oct	2	13	29	24	16	9	0	5	0	2	0
Nov	9	19	28	11	13	11	7	0	0	2	0
Dec	8	7	28	8	13	7	17	6	6	0	0

Table 3-11 Percentage of total population taken up by each size class of *A. dorrieni* throughout the year at Bishop's Wood, Caswell.

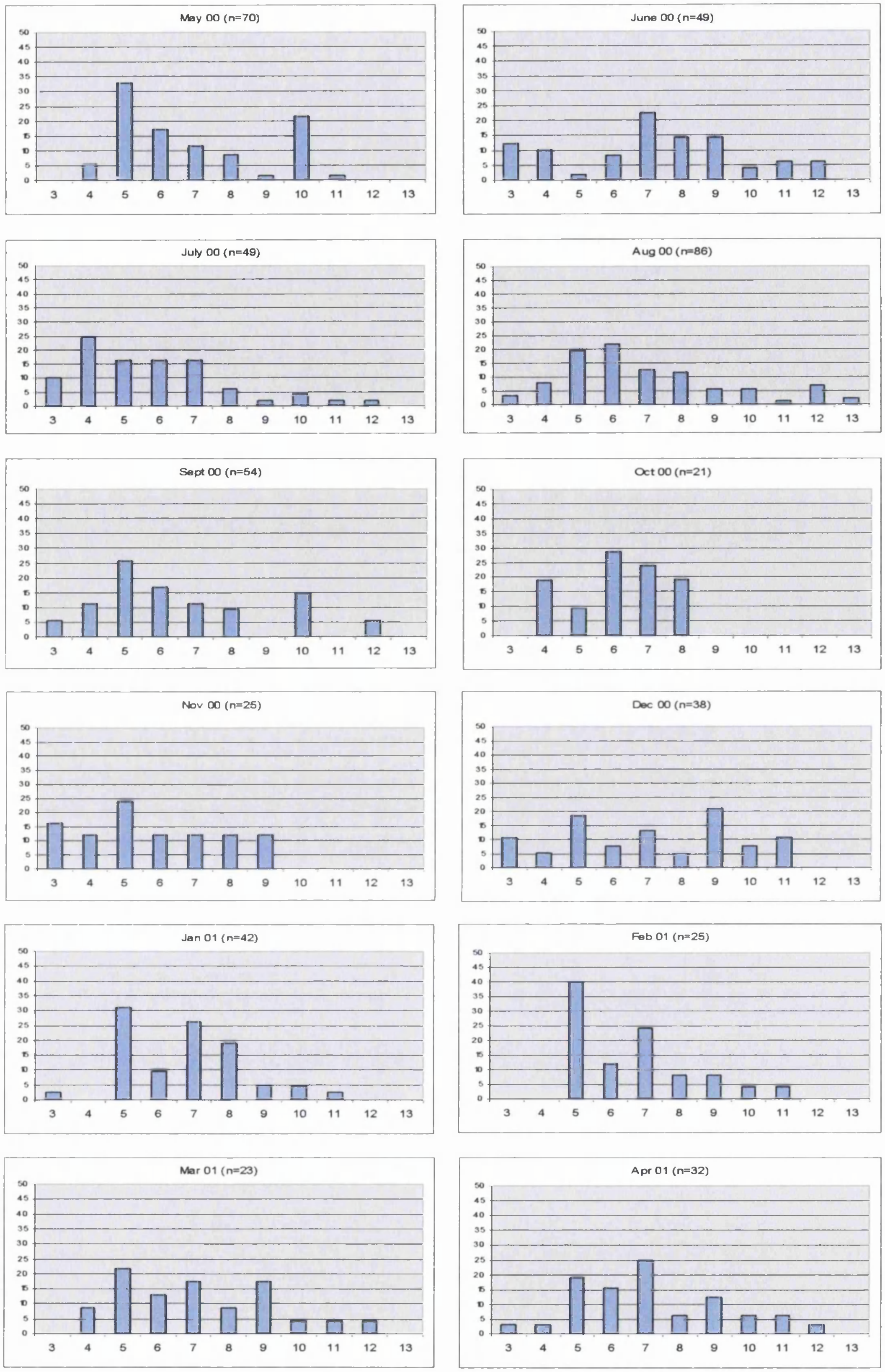


Figure 37 **Size class distribution of the Bishop's wood population from May 2000 to April 2001 (x axes: bodylength in mm, y axes: % of population).**

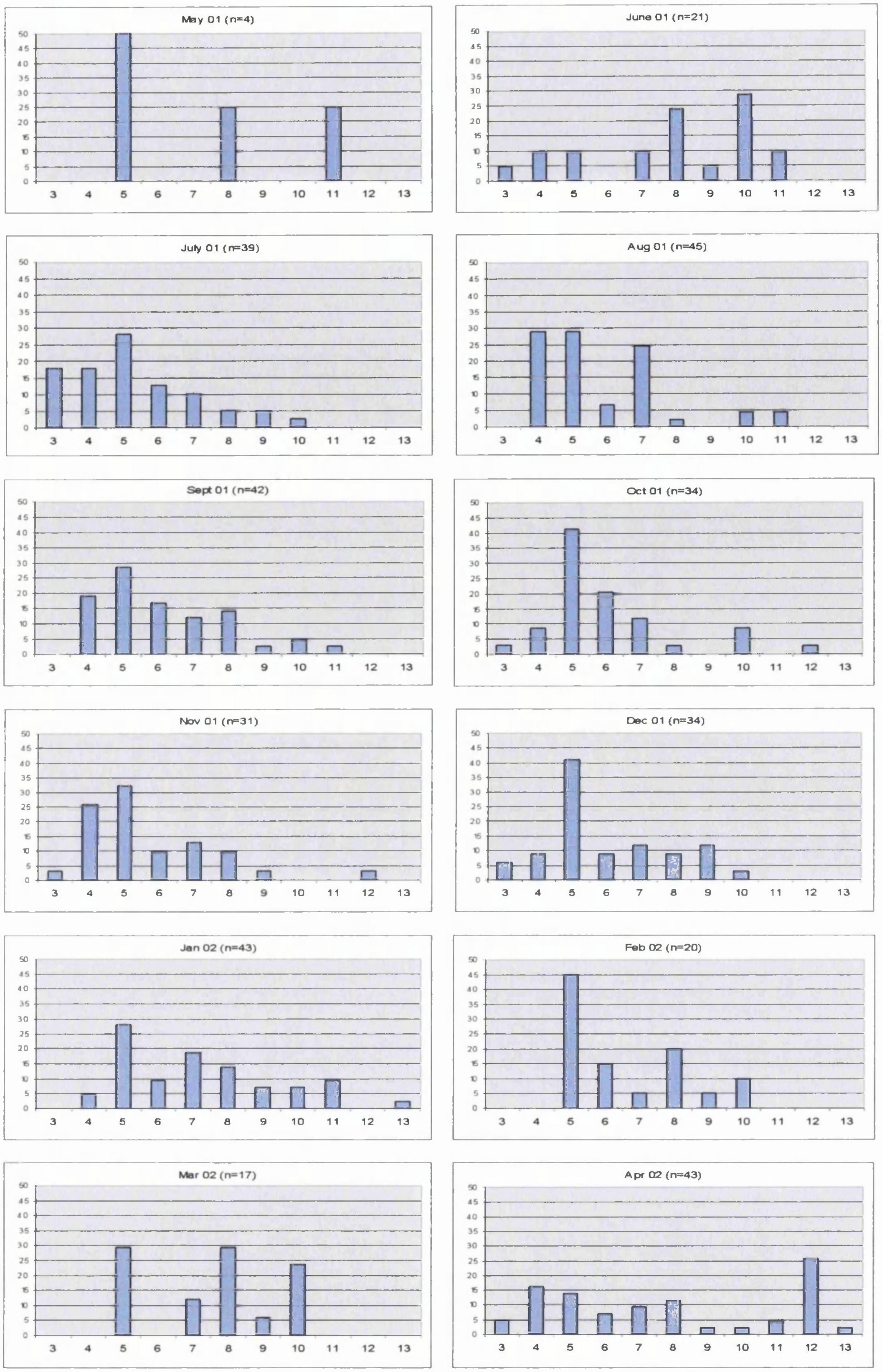


Figure 38 Size class distribution of the Bishop's Wood population from May 2001 to April 2002 (x axes: bodylength in mm, y axes: % of population).

3.3.4.1 Sex ratios and adult sizes

The number of females recorded exceeded that of males in 19 of the 24 months. A Mann-Whitney U test comparing the numbers of males and females recorded every month confirmed that the population consistently contained significantly more females than males (U=143, P=0.002). The male:female sex ratio varied widely from 1:0.5 to 1:9, but averaged 1:2.3. Table 3-12 (below) summarizes the numbers of landhoppers of each sex, juveniles and the total number collected during the study period.

Male	Female	Juvenile	Total
158	358	315	831

Table 3-12 Total numbers of landhoppers recorded between May 2000 and April 2002 at Bishop's Wood, Caswell.

Average female adult size was 7.86mm (n=359, SE=0.1) ranging from 5.5 to 13.0mm. Average male adult size was 6.98 mm (n=160, SE=0.08) ranging from 5.0 to 10.5mm. A Mann-Whitney U test showed that the two means were significantly different (U=22,344.5; P<0.001). Juveniles were released from the marsupium at 3.0 mm bodylength.

Females were observed carrying eggs at a sizes of 9-13mm. This occurred during the months of January, February, March, April, June, August, October. Young were observed in the brood pouch only in August and October.

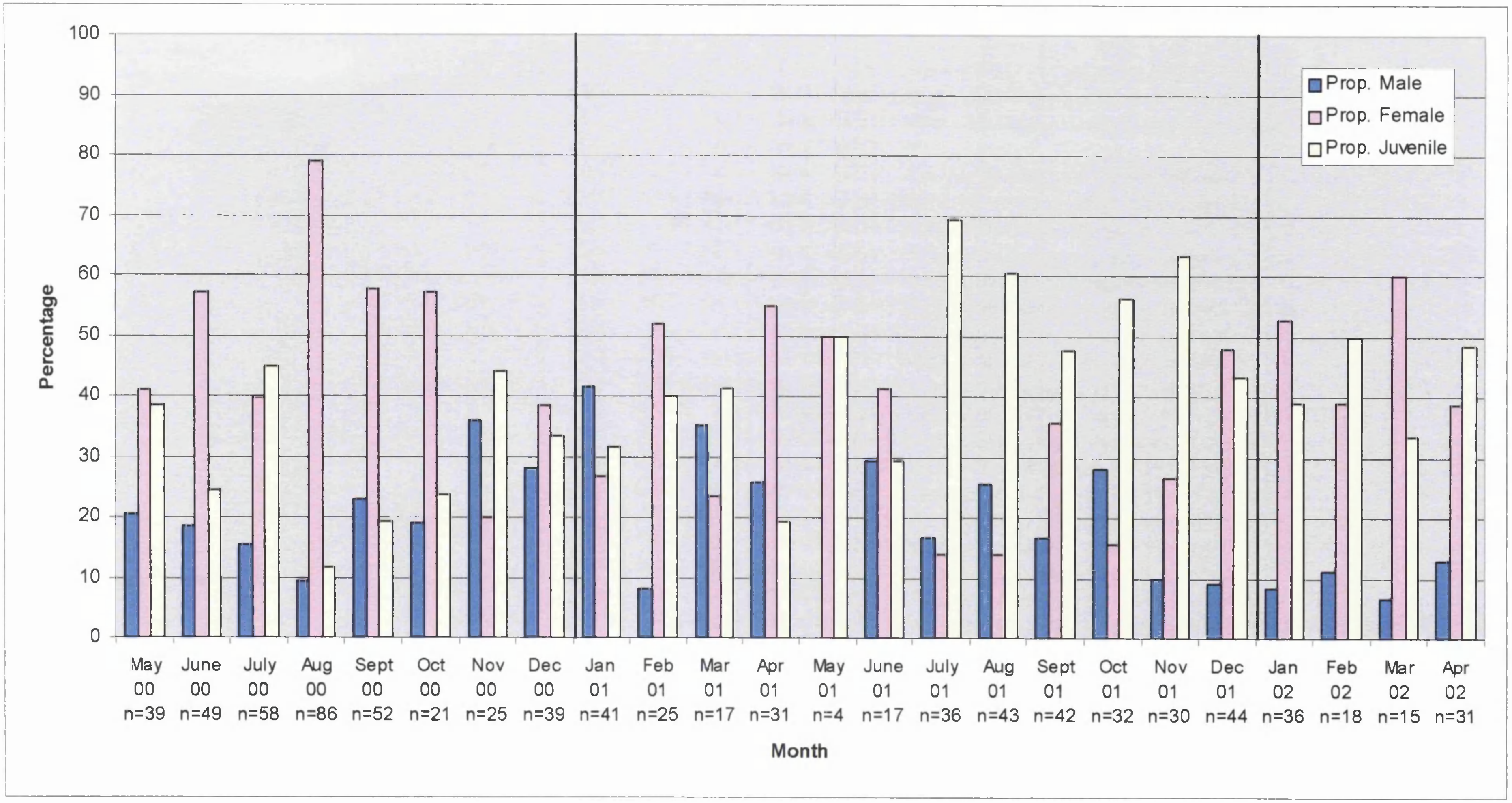


Figure 39 Proportions of male, female and juvenile *A. dorrieni* recorded in monthly samples (Sites 1-5) from May 2000 to April 2002 (vertical lines indicate new calendar years).

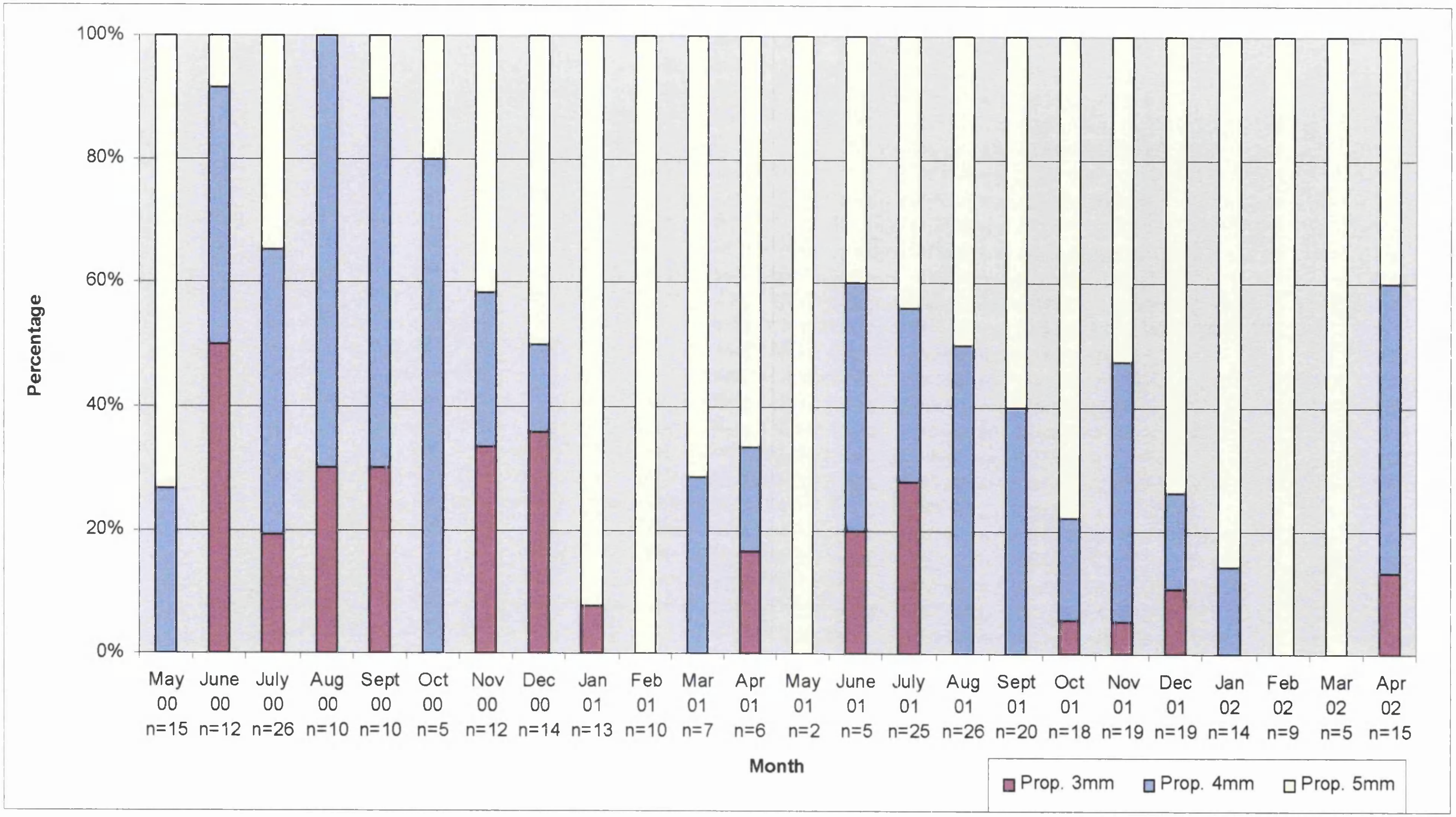


Figure 40 Proportions of different size classes among juvenile *A. dorrieni* from May 2000 to April 2002.

3.4 Discussion

One aim of this study, in addition to investigating the landhopper population at different sites throughout the deciduous woodland of Bishop's Wood, Caswell, was to identify comparable 'control' sampling sites which were not colonized by *A. dorrieni*, in order to compare the native invertebrate assemblages at the two locations (see Chapter 2). This aspect of the study is discussed further in the Chapter 4. In the results section of this chapter, however, comparisons of environmental variables were made not only between the sites at Bishop's Wood, Caswell, but also between the sites at Caswell and those at Bishopston Valley, which was chosen as the 'control' location, in order to assess the degree to which a successful match had been achieved. It could be shown that the sampling sites at the experimental and the control locations were well matched, not only in terms of their aspects, inclinations and plant communities (described and illustrated in Chapter 2), but also in terms of substrate water and organic matter content and soil pH. A good correlation in all these factors is necessary in order to make reliable comparisons between the native animal communities at the two sites, and assess possible influences of *A. dorrieni* on these communities.

The landhopper density at Bishop's Wood, Caswell was shown to be subject to considerable fluctuations, both within and between years. Many animal populations are subject to wide and seemingly erratic fluctuations (Andrewartha, 1971), and similar marked fluctuations in population density have been reported on a number of occasions for other landhopper species as well as for *A. dorrieni* (Lam & Ma, 1989; Margules, Milkovits & Smith, 1994; O'Hanlon *et al.*, 1993). Significant fluctuations between years, similar to those observed here, were a common feature in these reports.

While, in many cases, the causes for these fluctuations remain unknown, here the cause for the sudden and dramatic reduction in population density following April 2001 appears to have been a series of late frosts combined with unusually heavy rainfall. These factors may have killed those animals which had already ventured out of areas of deeper litter (where they would have sheltered from previous frosts) and any young which may just have been released. Frosts have often been cited as the most likely factor (or at least as being among the major factors) limiting the spread and density of landhopper populations in Britain (Cowling *et al.*, 2003; Cowling *et al.*, 2004; Friend *et al.*, 1986; Harding *et al.*, 1988; Richardson, 1980; Vader, 1972). Confirming this are the less dramatic, but regular decreases in population density during the coldest months (January – March), which was also observed by other workers (O'Hanlon *et al.*, 1993; Sherriff, 1986). The finding that landhopper numbers in this study were strongly correlated with grass minimum temperatures and minimum temperatures, but not with other weather parameters, further strengthens the assumption that frosts play a significant part in the population dynamics of *A. dorrieni.*

There have been suggestions that a number of naturalized species, which were originally frost-sensitive (such as the isopods *Porcellio laevis* and *Metoponorthus pruinosus*) survived their first winters following introduction in compost heaps and other accumulations of leaf litter which become heated by bacterial activity, and only later became adapted to the British climate, with the result that they are now able to survive and breed out of doors well away from human habitation (Sutton, 1980). It is possible that *A. dorrieni's* naturalization has also been progressing in such a manner, and initial experiments assessing its current cold tolerance place its tolerances fairly closely to those of native woodlice (see section 9.3).

Overall, the landhopper population showed two peaks, a major one around August and a minor one around December/January. This pattern appears to correlate with the findings by O'Hanlon & Bolger (1993). Unfortunately, however, their samples were not collected monthly, so a direct comparison could not be made.

Most authors only present *A. dorrieni* density figures for one sampling occasion of one or more habitats, rather than means calculated from sampling over a prolonged period of time. Therefore, maximum recorded numbers per m^2 are compared in Table 3-13 (page 103). O'Hanlon & Bolger's (1993) maximum figure of 12,172 individuals/m^2 may be due to sampling error as a result of *A. dorrieni's* patchy distribution, since they report a more moderate density of 5187/m^2 for the same month in the following year. The maximum density observed at Bishop's Wood, Caswell fits in well with the results of the other workers.

Author	Habitat	Maximum recorded density (individuals/m^2)	Time of year of sampling
Richardson, 1980	*D. antarctica* litter, Cornwall	2266	December
Moore and Spicer, 1986	Rhododendron and Oak litter overlying friable soil, Scotland	680	May
O'Hanlon & Bolger, 1993	Mixed woodland, Ireland	12 172	September
O'Hanlon & Bolger, 1993	Coniferous plantation, Ireland	ca. 4000	December
Spicer & Tabel, 1996	Coastal mixed woodland, Guernsey	300	August
Bishop's Wood, Caswell, 2001	**Coastal deciduous woodland over limestone, South Wales**	**883**	**August**

Table 3-13 Maximum recorded densities of *A. dorrieni* in different habitats across the British Isles.

O'Hanlon & Bolger (1993) are, to date, the only other authors who have calculated mean densities for *A. dorrieni* populations from sampling for more than one calendar year. The densities they presented were 4336 individuals/m^2 for mixed woodland and 2078 individuals/m^2 for a *P. contorta* plantation. The mean density for Bishop's Wood, Caswell is 364 individuals/m^2. As may be seen in Chapter 2, the sites at Bishop's Wood did not have a continuous and thick litter layer throughout the year. This contributed to the lower recorded densities, since the distribution of the animals was patchier than it would have been in the presence of a continuous litter layer. Site 3, which had a considerable proportion of patchy, but fairly deep and, more importantly, slowly decaying Holm Oak litter which preserves moisture well, harboured the highest densities of *A. dorrieni*, averaging 803 individuals/m^2. O'Hanlon & Bolger's sites both had continuous and well-developed litter layers of slowly decomposing litter throughout the year, which were due to the proportions of conifers and, in the case of the mixed woodland, *Rhododendron* at the sites. These thick, continuous and persistent litter layers thus provide a likely explanation for the high densities recorded.

Landhopper density did not show a correlation with the litter/soil water content recorded at the sampling sites, nor did it show a correlation with the changing water content throughout the year. Undoubtedly, had other, more marginal habitats been included, a significant correlation might well have been found between the different sites and landhopper densities, since *A. dorrieni* is known to avoid very wet and dry locations (Moore *et al.*, 1986). Among similar sites within a deciduous woodland habitat such as Bishop's Wood, however, where water content is comparatively similar, the differences were not pronounced enough to have an impact on the resident landhopper populations.

Similarly, landhopper population density did not show any significant correlation with organic matter content at the sites, or throughout the year. Mean organic matter content at the different sites correlated with landhopper population density, however, returned a result which was sufficiently close to the level of significance to indicate a relationship. In most studies investigating this aspect of landhopper biology, there has been considerable variation in the rates of correlation of litter depth/amount and amphipod density. It has generally been found that in some locations a correlation applied, whereas in others there were either particularly low landhopper numbers in seemingly large litter accumulations or very high landhopper numbers in areas with very little organic material (Moore *et al.*, 1986; Richardson, 1980; Spicer *et al.*, 1996).

Following the findings of this study, there now appears little doubt that there is a major annual increase in population density of *A. dorrieni* caused by reproduction which peaks around August, depending on sampling location (O'Hanlon *et al.*, 1993; Sherriff, 1986). Nevertheless, a proportion of newly released young is present for most of the year, generally with the exception of the coldest period of the year, January to March.

Where comparison was possible with size-frequency histograms constructed for other populations of *A. dorrieni* in Britain [these, with the exception of O'Hanlon and Bolger (1993) only showed the status in one the month of the year], they largely resembled the size-frequency histograms constructed for the Bishop's Wood population (Moore *et al.*, 1986; O'Hanlon *et al.*, 1993, 1997; Richardson, 1980). It has been suggested by a number of authors (O'Hanlon *et al.*, 1997; Rawlinson, 1937; Richardson, 1980) that *A. dorrieni* is a Type 1 species according to the life history classification of Morino (1978) (described in Table 3-14, page 106), namely a year-round breeder, which, in Britain, is forced to stop releasing young during the most inhospitable time of the year, during which its metabolism is lowered considerably due to the low ambient temperatures. Such behaviour has been recorded for other, normally continuously breeding, landhopper species in New Zealand (Duncan, 1994).

The results for the Bishop's Wood population, further confirm the classification of *A. dorrieni* as a Type 1 species.

It was unexpected that, following a considerable drop in population density in early spring of 2001, the proportion of juveniles in the population was markedly higher than in the preceding year. It is possible that the reduction in number of adults allowed more juveniles to survive, as a result of an amelioration of intraspecific competition.

Breeding	**Description**	**Type**	**Example species**
Year-round breeding	Young released throughout the year	**1**	*A. sylvaticus* (Clark, 1954) *Mysticotalitrus tasmaniae* (Friend, 1975)
Seasonal breeding	Yearly life cycle, two generations	**2**	no examples published to date
Seasonal breeding	Yearly life cycle, one generation	**3**	*Orchestia hurleyi* (Duncan, 1969) *O. patersoni* (Duncan, 1969) *Platorchestia japonica* (Tamura & Koseki, 1974)
Seasonal breeding	Two years or more for breeding	**4**	*Keratroides angulosus* (Friend, 1980) *K. vulgaris* (Friend, 1980)

Table 3-14 Amphipod life history types (Morino, 1978) and species of landhoppers which fall into three of the categories; after O'Hanlon & Bolger, 1997.

A major regular seasonal fluctuation in the proportion of juveniles in the population as observed by O'Hanlon & Bolger (1997) was not apparent in the population at Bishop's Wood. This may be due to the fact that Bishop's Wood is in a very mild location close to the coast, whereas the location sampled by O'Hanlon & Bolger was somewhat more inland and considerably more northerly. Unfortunately, their publication does not contain any weather data for their chosen sampling region.

In most British woodlouse species, breeding is highly synchronized. Their potential to breed throughout the year may give *A. dorrieni* a competitive advantage over the native woodlice, and partly explain the alien's tendency to occur in great numbers when conditions are favourable.

The proportion of males and females in the population varied between months, but these variations did not appear to follow any particular pattern. This was also observed by O'Hanlon & Bolger (1997).

Analysis of the relative proportions of the three different juvenile size classes indicates that the overwintering animals of the 5mm size class are indeed those released during the preceding summer and autumn. The virtual disappearance by February of the 3mm size class released during the late autumn/early winter months indicates that few, if any, of these juveniles survive the winter to reach adulthood.

The female-biased overall sex-ratio recorded here was also noted by other workers (Moore *et al.*, 1986; O'Hanlon & Bolger, 1997; Sherriff, 1986) and appears to be common to a number of terrestrial amphipod species (Friend *et al.*, 1986; Lindeman, 1991; Wildish, 1982) and possibly talitroidean populations in general (Wildish, 1982). The possible involvement of a microsporidian parasite in creation of the female-biased sex ratios should be examined in future studies. Such parasites are known from many related crustacean genera, where they distort the normal sex ratios by feminizing a proportion of the population (Terry *et al.*, 2004).

As is typical for *A. dorrieni*, females were significantly larger on average than were males. The maximum size of both males and females at Bishop's Wood was somewhat greater than that reported by Moore & Spicer (1986), namely 10.5mm for males and 13 mm for females compared to 9.5 mm and 12mm reported in their study. This difference may, however, only be due to the smaller sampling effort of the 1986 study. One study reports even bigger animals, with the largest male measuring 10.9 mm and the largest female 14.9 mm (Sherriff, 1986).

Females carried eggs from a size of 9mm upwards, which agrees with Moore & Spicer's findings (1986), while Sherriff (1986) reports a female of 8mm carrying eggs. This latter measurement was probably accurate, representing the minimum size necessary for reproduction, as Moore & Spicer (1986) report that the smallest female in their study possessing setose oostegites (and thus capable of carrying eggs) was 8mm long.

Overall, it could be shown that *A. dorrieni* population densities are lower in deciduous woodland than at the mixed woodland and coniferous sites investigated to date. The strong population fluctuations observed indicate that density-independent factors (those factors which act equally strongly on a population, however dense this population may be, e.g. frost, drought) are the dominant factors influencing the *A. dorrieni* population at Bishop's Wood, rather than density-dependent factors (those factors whose effects get more pronounced with higher population density, e.g. food shortages, crowding and resulting emigration) which typically result in smaller changes around an equilibrium. It has to be noted that some usually density-independent factors can become density-dependent when, for example, shelter from adverse conditions is in short supply and not all individuals in a population are capable of obtaining a space in a protected area (Sutton, 1980). This is often the case among woodlouse populations, and may also affect populations of *A. dorrieni*, although it does not appear to be currently a factor at Bishop's Wood.

Continued studies over longer periods of time in the same location are needed to produce a clear picture of the long-term population dynamics of *A. dorrieni* in a deciduous woodland habitat. Where possible, sample size should be increased due to the low density of the amphipod in this habitat. Larger numbers of specimens would then allow the production of more detailed and accurate size-frequency distribution histograms, and insights into the animal's reproductive biology could be gained by assessing the reproductive status of larger numbers of females, as attempted by O'Hanlon & Bolger (1997).

4 Responses of the native litter/soil faunal biodiversity to the presence of *A. dorrieni*

4.1 Introduction

Populations and communities, including those of the litter layer and the upper layer of the soil, are influenced by a wide range of abiotic and biotic factors. Climate, nutrients, competitors, natural enemies, symbionts, microscopic decomposers, microhabitat structure and the availability of water are among the many potential forces that determine population change and community structure. It is one of the biggest challenges for the discipline of ecology to quantify the relative strengths of these forces, determine interactions among them, and so explain the patterns of animal and plant distribution and abundance that can be seen in nature (Hunter & Price, 1992). Since soil systems contain some of the most species-rich communities in existence - temperate woodland soils sometimes containing up to a thousand animal species and populations of up to 2 million individuals per square metre - the investigation of inter-and intra-specific relationships alone has proved to be 'one of the most intractable ecological problems' (Anderson, 1975). The arrival of a new species can have powerful effects on an existing, well-balanced ecosystem.

The balance of every ecosystem depends on a combination of forces from two 'directions'. These are the bottom-up forces (for example, nutrient availability) and top-down forces (for example, predators). These forces are potentially active at every trophic level. There is much disagreement over which of these forces contributes more to the maintenance of the balance in nature (for a summary of the various arguments see Hunter & Price, 1992). It is likely that the influences elicited by the two forces will turn out to vary, both from ecosystem to ecosystem as well as over time.

An alien species establishing itself in an existing ecosystem may cause a variety of changes. From those changes, it can be possible to determine which forces are altered by the arrival of the newcomer, and exert the greatest influence in this particular location. In the case of *A. dorrieni*, for example, a decrease in the numbers of native primary decomposers would indicate a bottom-up controlled system, as such a decrease is likely to be caused by competition for resources. An increase in numbers of similar-sized natives, however, would indicate a top-down controlled system, since predation pressure would be shared between the natives and the aliens. It is very likely that such an increase would later be followed by an increase in the number of predators present at the location. This would suggest that the next trophic level was under the influence of bottom-up control prior to the arrival of the landhopper (Bolger & Golden, 2000). An increase in numbers of native decomposers not followed by an eventual increase in predators would indicate that this level, rather than being controlled by top-down forces, had been influenced by a different factor or resource (such as limited microhabitat) which was increased by the presence of the alien.

As a primary decomposer (i.e. an animal feeding primarily on dead plant material that is still in its original state or has only recently been colonized by bacteria and fungi), *A. dorrieni* is in competition with the native primary decomposers. These include the Isopoda, the Diplopoda, the epigeic Lumbricidae and some coleopteran and dipteran larvae. On the other hand, if, like other landhoppers (Richardson & Morton, 1986), *A. dorrieni* contributes to the diminution of leaf litter, the creation of new microhabitats (by burrowing through the loose litter and top layer of the soil) and an increase in the soil microflora, it may stimulate secondary decomposer populations. Finally, by acting as a prey item, the landhopper may influence population densities of native predators.

4.2 Methods

Both collection and processing of samples took place as described in sections 3.2.1 and 3.2.2 (pages 64 and 66, respectively)

4.3 Results

The first part of this section introduces the taxa found during the course of the study at Bishop's Wood, Caswell and Bishopston Valley. The second part is dedicated to analyzing the numerical data collected.

4.3.1 Description of taxa

4.3.1.1 Pulmonata and Prosobranchia- the slugs and snails

Figure 41 ***Oxychilus sp.*** **(left) and** ***Carychium sp.*** **(right), members of the Pulmonata.**

Most commonly encountered snails and all slugs belong to the Pulmonata, their name indicating that they posess a lung. Two examples of pulmonate snails encountered in this study are illustrated in Figure 41 (above). In contrast, the Prosobranchia, although terrestrial, breathe through gills. Their shells can be closed with a deeply retractable horny operculum (Kerney & Cameron, 1996). Like *A. dorrieni*, slugs and snails are dependent on high humidity and are therefore most active at night or in wet weather. Their nocturnal and/or cryptozoic lifestyle also protects them against most visually hunting daytime predators.

Many species of slugs and snails are generalist feeders taking decaying plant material, algae, lichens and fungi, thus to a large extent sharing the landhopper's diet. Some species feed on living higher plant tissues and a few are predatory, feeding on other snails or even earthworms (Wheater & Read, 1996). Unlike many other herbivorous animals, slugs and snails are able to digest cellulose (Kerney *et al.*, 1996), thus possibly sharing a further of the landhopper's characteristics (T. Bolger, pers. comm.).

4.3.1.2 Isopoda – the woodlice

Figure 42 ***Haplophthalmus sp.*****, an Isopod.**

In many respects, woodlice (a typical example illustrated in Figure 42, above) may be considered the northern hemisphere counterparts to the terrestrial amphipods of the southern hemisphere. Isopods are generally regarded as the most successful group of crustaceans with respect to terrestrial exploitation (Edney, 1968). While over 6000 of the 10 000 described isopod species still live in the sea, some species are so well adapted to terrestrial life that they are able to be active in direct sunlight. Most, however, are very sensitive to desiccation, which means that they are restricted to moist microhabitats and have a cryptozoic and/or nocturnal lifestyle. Currently, 37 woodlouse species occur in Britain (Hopkin, 2003).

Like landhoppers, woodlice feed primarily on dead plant material, while also taking a small proportion of fungal hyphae. This makes them important decomposers, each individual eating between 5 and 10 % of its body weight every day (op.cit.). Due to their great similarities with landhoppers, and as the only other terrestrial crustacean in Great Britain, woodlice merit particular attention where possible interaction with the landhopper is concerned (Costello, 1993).

4.3.1.3 *Chordeumatida, Glomerida, Julida, Polydesmida - the millipedes*

Figure 43 Representatives of the orders Chordeumatida, Glomerida (top row) Julida and Polydesmida (bottom row).

The orders Chordeumatida, Glomerida, Julida, and Polydesmida (a representative of each order illustrated in Figure 43, above) all belong to the

Class Diplopoda. Members of this class are commonly referred to as 'millipedes' and are defined by the presence of two pairs of legs per body segment. Members of all four orders have similar habits: they lead a cryptozoic lifestyle, feed mainly on dead plant material, preferring soft or decomposing tissues due to their weak mouthparts (Brade-Birks, 1930), and they are generally confined to habitats with high humidity. They are important litter diminutors and their faecal pellets are an excellent substrate for bacterial growth compared to undigested plant material (Hopkin, 2004). Currently there are sixty-one species of millipede in Britain and Ireland, which includes some recent introductions (op. cit.). Most millipedes possess poison glands capable of producing powerful sedatives (Glomerida), repellents (Julida) and even cyanide (Polydesmida) (op. cit.). These chemicals, along with their well-armoured bodies, make them unlikely candidates for predation. Nevertheless, they are known to be preyed upon by some spiders, frogs, toads and some birds.

4.3.1.4 *Geophilomorpha and Lithobiomorpha - the centipedes*

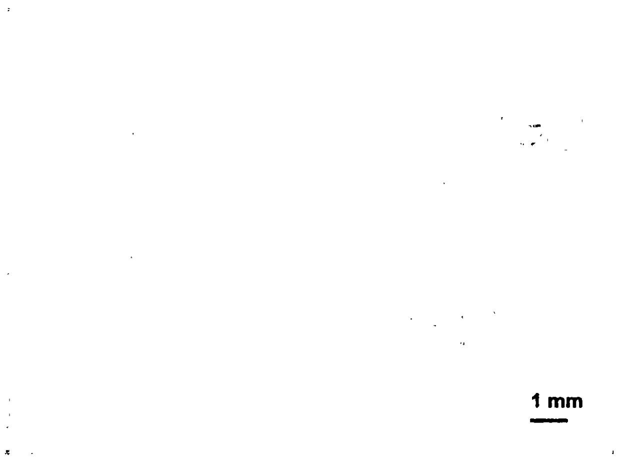


Figure 44 A geophilomorph centipede.

Both the Geophilomorpha and the Lithobiomorpha are commonly referred to as centipedes, despite their rather different appearance. The Geophilomorpha are fragile looking, slow moving, long-bodied, pale animals (a typical specimen illustrated in Figure 44, page 113) inhabiting the lower layers of the leaf litter and the upper layer of the soil, feeding on small, slow moving invertebrates, whereas the Lithobiomorpha are strongly built, fast moving, voracious nocturnal surface predators which shelter in leaf litter and under logs and stones during the day.

4.3.1.5 *Coleoptera - the beetles*

Figure 45 A coleopteran larva.

There are beetles which inhabit the litter layer and the upper layer of the soil during their adult stage, their larval stage or both. Most of the ground beetles (Family Carabidae) and many rove beetles (Family Staphylinidae) spend their entire life living among, or at least sheltering among, dead vegetation on the ground. A large number of these are carnivorous and many are formidable hunters.

Other beetles, such as members of the Elateridae, only spend their larval stages in the leaf litter, in dead wood or in the surface layer of the soil (one such larva is illustrated in Figure 45, page 117). Most of these beetles feed on decaying or living plant material (Chinery, 1993; Wheater *et al.*, 1996).

4.3.1.6 *Collembola - the springtails*

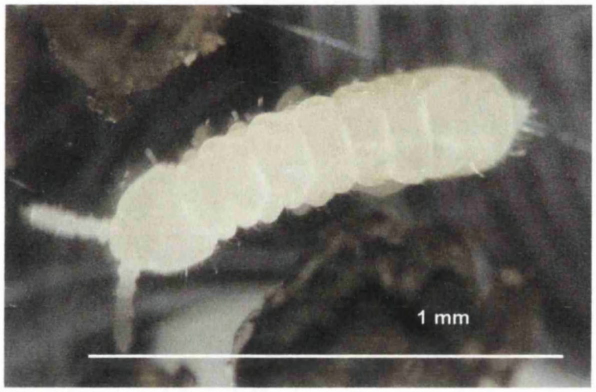


Figure 46 A collembolan.

Collembolans are small, usually cryptozoic insects that feed on decaying plant material and fungal hyphae (one springtail commonly encountered in this study is illustrated in Figure 46, above). They often occur at high densities, in fact they are often considered the most abundant insects in terrestrial ecosystems, reaching densities of more than 40 000 per m^2 (Hopkin, 2000). Most springtails, as their name suggests, utilise an escape mechanism similar to that of landhoppers, namely rapid random jumping. During spot searches for landhopper populations, during which the litter layer is disturbed and/or removed, jumping groups of the largest UK species, *Tomocerus longicornis* (which reaches 6 mm in length) were found to closely resemble landhoppers. *T. longicornis*, however, is generally found in drier habitats than those favoured by the landhopper.

4.3.1.7 *Diptera - the true flies*

Figure 47 Dipteran larva (*Tipula sp.*).

Many flies, particularly crane flies (a larva illustrated in Figure 47, above), midges and fungus-gnats go through their larval stages in the leaf litter layer and/or the upper layer of the soil, feeding on decaying vegetation and occasionally living plant material such as roots. Some Brachycera have predatory litter/soil dwelling larval stages (Wheater *et al.*, 1996).

4.3.1.8 *Hymenoptera – the bees, wasps and ants*

Figure 48 Hymenopteran pupa, removed from pupal case.

Most of the Hymenoptera collected in this study were worker ants. Occasionally, however, pupal (an example illustrated in Figure 48, above) and adult Hymenoptera of other types were also observed.

4.3.1.9 Acari - the mites

Figure 49 *Pergamasus sp.* (male - note modified second legs for grasping the female), a mesostigmatid mite.

Mites are very small leaf-litter/soil inhabitants. They can occur in large numbers and, as a result, are an important component of the ecosystem despite their diminutive size.

Two major groups were common in the woodland samples examined for this study: the cryptostigmatid (oribatid) mites, well-armoured, slow moving animals, sometimes resembling plant seeds, which feed predominantly on decaying vegetation and fungal hyphae, and the mesostigmatid mites (a typical specimen illustrated in Figure 49, above), less well armoured, faster moving animals which feed in nematodes and the eggs of other small invertebrates.

4.3.1.10 *Haplotaxida - the earthworms and potworms*

Figure 50 A potworm, Family Enchytraeidae.

The Order Haplotaxida contains both the Lumbricidae, the family to which the well-known large, pinkish earthworms belong, as well as the Enchytraeidae (also referred to as potworms), a family of much smaller, whitish worms, which is often overlooked, but by no means uncommon (illustrated in Figure 50, above). Members of both families were observed in this study. Both earthworms and potworms are confined to moist microhabitats. Most, if not all, of the Lumbricidae collected in this study will have belonged to species inhabiting primarily the leaf litter layer and surface soil (Wheater *et al.*, 1996) [also referred to as epigeic and epi-endogeic species, respectively (Coleman, Crossley & Hendrix, 2004)]. These species primarily feed on decaying plant material, and do not typically take large quantities of mineral soil. As such, they potentially have to compete with the landhopper for both food and habitat.

The Enchytraeidae take in quantities of very small soil particles, in the process of which they ingest both organic and inorganic matter (including some decaying plant material). Most of their nutrition, however, is received from fungal hyphae and bacteria taken in with the soil, as opposed to the plant fragments (Coleman *et al.*, 2004). Direct competition for resources is less likely between landhoppers and Enchytraeidae. Increased diminution of leaf litter and increased soil respiration as may be the result of landhopper activity (Richardson *et al.*, 1986), may in fact have a positive effect on potworm populations.

4.3.1.11 *The Class Symphyla*

Figure 51 A Symphylan.

The Symphyla (illustrated in Figure 51, above) are small myriapods which look somewhat like lithobiomorph centipedes. However, they are not predatory, but instead feed on dead vegetation in the soil. They may also feed on roots which sometimes results in them becoming minor pests, particularly in greenhouses (Cloudsley-Thompson, 1958; Wheater *et al.*, 1996).

4.3.1.12 *The 'low density inhabitants' – Diplura, Hemiptera, Lepidoptera, Aranae, and Pseudoscorpiones*

Included here are members of leaf-litter dwelling groups which were collected on no more than two occasions. Due to their low densities, these groups are unlikely to be competing significantly with *A. dorrieni* on any level. The locations and dates when members of these groups were observed are summarized in Table 4-1 (page 124).

Diplura - the two-pronged bristletails

The Diplura are small white insects which feed on decaying plant material. They are represented by only one genus in Britain and although not uncommon, they usually occur only at low densities (Wheater *et al.*, 1996).

Hemiptera - the true bugs

Generally, Hemiptera are not typical inhabitants of the leaf litter layer, but they occur on the vegetation above the sampling sites, and their presence in the samples is probably coincidental.

Lepidoptera - the butterflies and moths

Some moths, particularly members of the Noctuidae, spend their larval stages feeding and/or sheltering in the surface layer of the soil, feeding on roots or emerging at night to feed on low-growing herbaceous plants (Chinery, 1993). These moths are more common on open ground and in gardens than in woodland. Other lepidopterans take refuge in the soil for pupation.

Aranae - the spiders

Spiders are voracious predators and common in most habitats. A number of species occasionally seek shelter among fallen leaves, and more commonly under logs and branches, but as they do not spend the majority of their lives in the leaf litter/soil habitat, they were not often encountered during sampling in the present study.

Pseudoscorpionida - the pseudoscorpions

Pseudoscorpions are very small but aggressive predators that belong to the Class Arachnida (Wheater *et al.*, 1996). They feed on very small prey such as collembolans, psocids, thysanurans, symphylans and mites (Cloudsley-Thompson, 1958). Most species require damp microhabitats and lead a cryptozoic lifestyle (Wheater *et al.*, 1996).

Order	**Location**	**Sampling Date**
Diplura	Caswell Site 3	March 2001
Hemiptera	Bishopston Valley Site 2	May 2001
Lepidoptera (larva)	Caswell Site 1	March 2002
Aranae	Caswell Site 4	August 2000
Pseudoscorpiones	Caswell Site 2 & Site 4	September 2001
Pseudoscorpiones	Bishopston Valley Site 3	May 2001

Table 4-1 'low density inhabitants' of the leaf litter/soil layer collected during the study period.

4.3.2 Analysis of data

Table 4-2 (page 126) summarizes the presence and absence at each site of all invertebrate orders recorded between May 2000 and April 2002. Invertebrates are listed by Order with the exception of the Families Lumbricidae and Enchytraeidae and the Class Symphyla. In the Lumbricidae and the Enchytraeidae, which are both members of the Order Haplotaxida, the further separation into families was undertaken due to the marked inherent differences of the two families (see section 4.3.1.10), which may cause them to be differently affected by the presence of *A. dorrieni.* The Class Symphyla is not generally split into orders, but instead consists of only two families, the Scolopendrellidae and the Scutigerellidae. Since identification to family level was not possible with the equipment available, members of the Symphyla were identified to class level only.

Order SITE	C1	C2	C3	C4	C5	BV1	BV2	BV3	BV4
Pulmonata	+	+	+	+	+	+	+	+	+
Prosobranchia	+	+	-	+	+	-	-	+	+
Isopoda	+	+	+	+	+	+	+	+	+
Chordeumatida	+	-	+	+	+	+	+	+	+
Glomerida	+	-	+	+	+	+	-	+	+
Julida	+	+	+	+	+	+	+	+	+
Polydesmida	+	+	+	+	-	+	+	-	+
Geophilomorpha	+	+	+	+	+	-	+	+	+
Lithobiomorpha	-	+	+	-	-	+	-	-	-
Coleoptera	+	+	+	+	+	+	+	+	+
Collembola	+	+	+	+	+	+	+	+	+
Diplura	-	-	+	-	-	-	-	-	-
Diptera	+	+	+	+	+	+	+	+	+
Hemiptera	-	-	-	-	-	-	+	-	-
Hymenoptera	-	+	-	-	+	-	+	+	+
Lepidoptera	+	-	-	-	-	-	-	-	-
Aranae	-	-	-	+	-	-	-	-	-
Acari	+	+	+	+	+	+	+	+	+
Pseudoscorpionida	-	+	-	-	-	-	-	+	-
F. Lumbricidae	+	+	+	+	+	+	+	+	+
F. Enchytraeidae	+	+	+	+	+	+	+	+	+
Class Symphyla	-	+	-	-	-	-	-	-	-
Total number of Groups	**15**	**16**	**15**	**15**	**14**	**13**	**14**	**15**	**15**

Table 4-2 Summary of all invertebrates recorded between May 2000 and April 2002.
+ ... present, - ... absent

There was no statistically significant difference between the number of animal groups at Bishop's Wood, Caswell and Bishopston Valley, whether *A. dorrieni* is included in or excluded from the calculation (Mann-Whitney U test: U= 3, P=0.2 and U=7, P=0.886, respectively). It may therefore be concluded that the presence of *A. dorrieni* does not have a detrimental effect on the overall number of orders (families in the case of the Haplotaxida and class for the Symphyla) present at the experimental site. This comparison of animal groups may be considered equivalent to the commonly used term 'Species richness'.

Figure 52 (page 128) illustrates the numbers of individuals of the major invertebrate groups collected (more than five animals at either location) at Sites 1 to 4 at Bishop's Wood and Bishopston Valley between May 2000 and April 2002. In order to adjust for the reduction in number of samples taken from Bishopston Valley due to the outbreak of Foot and Mouth disease, the data for February – April 2001 were excluded from the Bishop's Wood data set. Two of the sixteen major non-amphipod orders, namely the Isopoda and the Collembola, were present in much larger numbers at Bishop's Wood than at Bishopston Valley. A further six orders were present in marginally larger numbers at Bishop's Wood than at Bishopston Valley. The remaining eight orders were present in considerably lower numbers at Bishop's Wood than at Bishopston Valley, the most marked differences being in the Pulmonata, the Enchytraeidae and the Diptera.

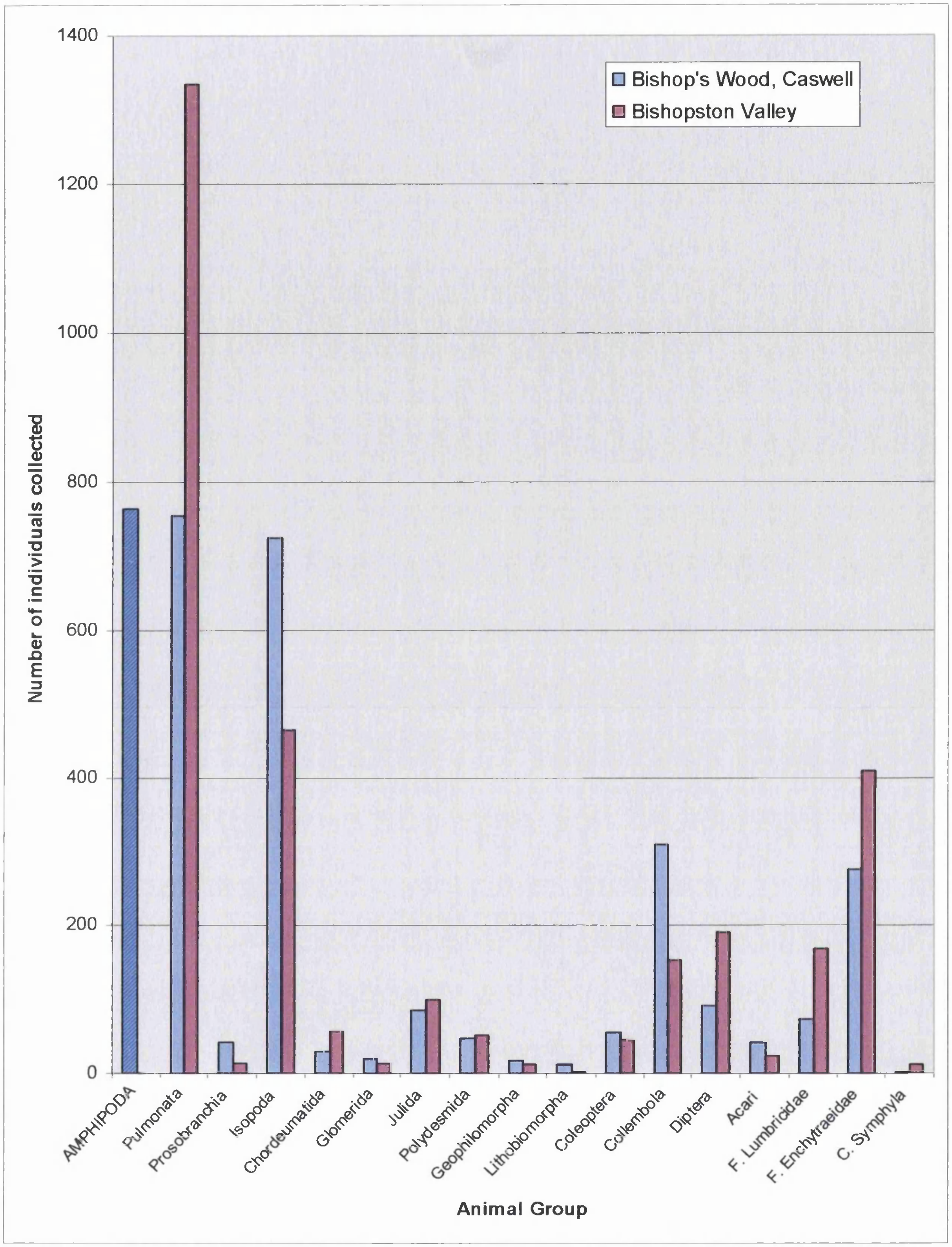


Figure 52 Numbers of the major groups of invertebrates collected at Sites 1 - 4 at Bishop's Wood Caswell and Bishopston Valley between May 2000 and April 2002 (adjusted).

Mann-Whitney U tests investigating the differences in numbers of the various groups for statistical significance returned only insignificant results, with the exception of the Class Symphyla, which was significantly more common in Bishopston Valley. The test results are summarized in Table 4-3 (below).

Group	**U**	**P**
Pulmonata	5.0	0.486
Prosobranchia	4.5	0.343
Isopoda	4.0	0.343
Chordeumatida	3.5	0.200
Glomerida	6.5	0.686
Julida	7.0	0.886
Polydesmida	6.0	0.686
Geophilomorpha	6.0	0.686
Lithobiomorpha	5.0	0.486
Coleoptera	6.5	0.686
Collembola	5.5	0.486
Diptera	3.0	0.200
Hymenoptera	4.0	0.343
Acari	2.5	0.114
F. Lumbricidae	4.0	0.343
F. Enchytraeidae	5.0	0.486
C. Symphyla	0.5	0.029*

Table 4-3 Results of Mann-Whitney U tests comparing numbers of the various invertebrate groups at Bishop's Wood, Caswell and Bishopston Valley.

*** indicates significance at the 0.05 level**

4.3.2.1 Frequency

While the summary of invertebrates in Table 4-2 (page 126) provides information on the groups of animals present at each sampling site, and the comparison of numbers illustrated in Figure 52 (page 128) gives some indication of the different groups' numerical [if not necessarily ecological (Wallwork, 1976)] importance, it does not indicate how widespread the different groups are throughout the sampling locations. Calculating the Frequency of the different groups illustrates this.

Frequency is calculated as follows:

$$\text{Frequency} = a/n * 100$$

where a is the number of sampling units in which the species occurs, and n is the number of sampling units comprising the total sample (Wallwork, 1976).

The results are summarized in Table 4-4 (page 132). Most of the calculated frequencies roughly correlate with the recorded numbers, indicating that most species are distributed fairly evenly across the sampling locations. In both sampling locations, the Coleoptera and the Acari, both of which were recorded in comparatively low numbers, occurred in a larger proportion of samples than their numbers would lead to assume, indicating that their distribution is particularly widely spread (rather than clustered). The distribution of the Polydesmida was slightly more clustered at Bishopston

Valley than at Bishop's Wood. The Collembola were significantly more clustered at Bishop's Wood than at Bishopston Valley, with twice the number of animals and an only marginally larger frequency value for Bishop's Wood. The Acari, too, were more clustered at Bishop's Wood, with larger numbers, but a lower frequency value compared to Bishopston Valley. If a certain animal group occurs at lower frequencies but equal or greater numbers at one of two or more sites, this can indicate that this site offers fewer areas of suitable habitat for this animal group. The high frequency value returned for *A. dorrieni* is remarkable, particularly considering its notoriously patchy distribution (Margules *et al.*, 1994). It indicates that the amphipod is widely and evenly spread throughout the entire wood, to an even greater extent than the native woodlice.

Order	Bishop's Wood, Caswell	Bishopston Valley
Pulmonata	95.8	97.5
Prosobranchia	23.9	8.6
Isopoda	79.2	63.8
Glomerida	10.4	12.5
Polydesmida	26.0	20.0
Julida	46.9	45.0
Chordeumatida	11.4	28.8
Coleoptera	40.6	37.5
Diptera	47.9	60.0
Hymenoptera	1.0	3.8
Collembola	54.2	53.8
Acari	19.8	22.5
Geophilomorpha	21.9	12.5
Lithobiomorpha	8.3	0
F. Enchytraeidae	52.1	55
F. Lumbricidae	40.6	53.8
C. Symphyla	0	12.5
Amphipoda	86.5	0

Table 4-4 Frequencies of invertebrate groups at Bishop's Wood, Caswell and Bishopston Valley.

4.3.2.2 Diversity

Diversity is used to describe the relation between number of species (or other designated groups) and number of individuals in a given community (Lewis & Taylor, 1974). Diversity may be summarized with a single number – a diversity index (Henderson, 2003). All diversity indices try to incorporate both the concept of species richness (the number of species or groups present) and equitability (also referred to as 'evenness', i.e. the pattern of distribution of the individuals between the species or groups). A variety of different diversity indices has been calculated by a range of researchers, and it is generally recommended to apply more than one index to any given data set, in order to make up for the weaknesses of different indices. For example, some indices are biased in favour of species number and others in favour of equitability (op.cit.). Here, the Shannon-Wiener function (*H*), The Simpson-Yule index (*D*), the Margalef Number and the Berger-Parker dominance index were calculated. Calculations were performed using the software 'Species diversity and richness' (Pisces Conservation Ltd., Lymington, UK).

The Shannon-Wiener function is one of the most commonly used diversity indices. It is expressed as *'H'*. The larger the value of *H* the greater the diversity (Solow, 1993). It attempts to express the difficulty of predicting correctly the species of the next individual collected (Krebs, 1999). Typically, values range between 0 (only one species in the community) and 3 (Smith, 2002). The Shannon-Wiener function has been widely criticized and even been referred to as 'a distraction, rather than an asset, in ecological analysis' (Southwood & Henderson, 2000), as it is strongly influenced by species number and the underlying model (op. cit.). It was nevertheless decided to incorporate it here, and compare the values calculated to those of the other, perhaps more reliable indices.

The Simpson-Yule index is expressed as *'D'*. *D* equals 1/λ, where λ equals the result of the (somewhat older) Simpson's Index (Leaver, 1993). As a result, where in the Simpson's Index a higher value indicates greater diversity, in the Simpson-Yule index the smaller the value of *D* the greater the diversity (Solow, 1993). The Simpson-Yule index is based on the probability that a second individual drawn from a population would be of the same species as the first. It is strongly influenced by the few dominant species, but is considered of value particularly as an indicator of interspecific encounters (Southwood *et al.*, 2000).

The Margalef Number is a measure of the number of species (or groups) at the location under investigation (somewhat similar to species richness), but taking into account the total number of individuals present. It is generally expressed as 'R1'. R1 increases with increasing diversity.

The Berger-Parker dominance index is both mathematically and conceptually simple. It is the ratio of the number of individuals in the sample belonging to the most abundant species divided by the total number of individuals caught (Henderson, 2003). This ratio is expressed as *'d'*. The smaller the ratio, the higher the diversity. Despite its simplicity, this index is considered to return valuable and very representative results, which are comparable to, if not better than, those produced by many of the more complex indices (Henderson, 2003; Southwood *et al.*, 2000).

In order to assess whether there are significant differences between the diversities at different locations, the calculated indices were compared by Mann-Whitney U tests. The indices calculated for the Experimental and Control Sites are summarized in Table 4-5 (page 136), and the results of the statistical tests are shown in Table 4-6 (page 136). The Mann-Whitney U tests did not return any significant results, indicating that there is no difference in diversity between Bishop's Wood, Caswell and Bishopston Valley.

In 1993, however, Solow suggested the use of randomization tests for assessing the significance of differences in community structure. These tests were performed with the aid of the 'Species Diversity and Richness' software for each index calculated. The results are summarized in Table 4-7 (page 137). Contrary to the Mann-Whitney U tests, three of the four randomization tests detected differences in the diversities of the two sampling locations. In those cases, the probability of a difference in diversity was 100%. In two of the cases, there was a probablility of 1 that the diversity at Bishopston Valley was less than at Bishop's Wood, Caswell. In the third case, however, the reverse was true. The fourth case, which also indicated a difference in diversity between the sites, but to a lesser level of probablility, also tended to a greater diversity at Bishop's Wood, Caswell.

	Shannon-Wiener function	Simpson-Yule index	Margalef number	Berger-Parker dominance index
Caswell 1	1.90	4.45	1.94	0.41
Caswell2	1.92	5.12	2.43	0.34
Caswell 3	1.55	3.07	1.90	0.52
Caswell 4	2.04	5.38	2.11	0.33
Bishopston Valley 1	2.09	7.24	1.98	0.18
Bishopston Valley 2	1.77	3.39	2.41	0.52
Bishopston Valley 3	1.59	2.88	2.06	0.56
Bishopston Valley 4	1.74	3.88	2.07	0.42

Table 4-5 Calculations of various diversity indices for sites 1 - 4 at Bishop's Wood, Caswell and Bishopston Valley.

Index	*U-value*	*P value*
Shannon-Wiener function	7.0	0.886
Simpson-Yule index	6.0	0.686
Margalef number	7.0	0.886
Berger-Parker dominance index	5.0	0.486

Table 4-6 Results of the Mann-Whitney U tests performed on the diversity indices calculated for Bishop's Wood, Caswell and Bishopston Valley.

Index	*Probability – diversity equal*	*Probability - diversity different*	*Direction of difference*
Shannon-Wiener function	0	1	BV<C
Simpson-Yule index	0	1	BV<C
Margalef number	0.1265	0.0822	BV<C
Berger-Parker dominance index	0	1	BV>C

Table 4-7 Randomization test results for the different diversity indices calculated.

Figure 53 (page 138) shows the Principal Component Analysis plot constructed with the aid of the Community Analysis Package software (Pisces, Lymington, UK) for the native animal communities at Bishop's Wood, Caswell and Bishopston Valley. Site 2, Bishop's Wood and Site 2, Bishopston Valley are located close together, away from the other sites. This indicates that there is little difference in the composition of the fauna between these two sites. Interestingly, however, despite an attempt to select closely matching site pairs at Bishop's Wood, Caswell and Bishopston Valley (see Chapter 2), the fauna at Sites 1, 3 and 4 was quite disparate between the two locations. Overall, the Sites are spread evenly across the plot, without any clustering of either Bishop's Wood or Bishopston Valley sites. This indicates that the presence of *A. dorrieni* has no detectable effect on the native animal communities.

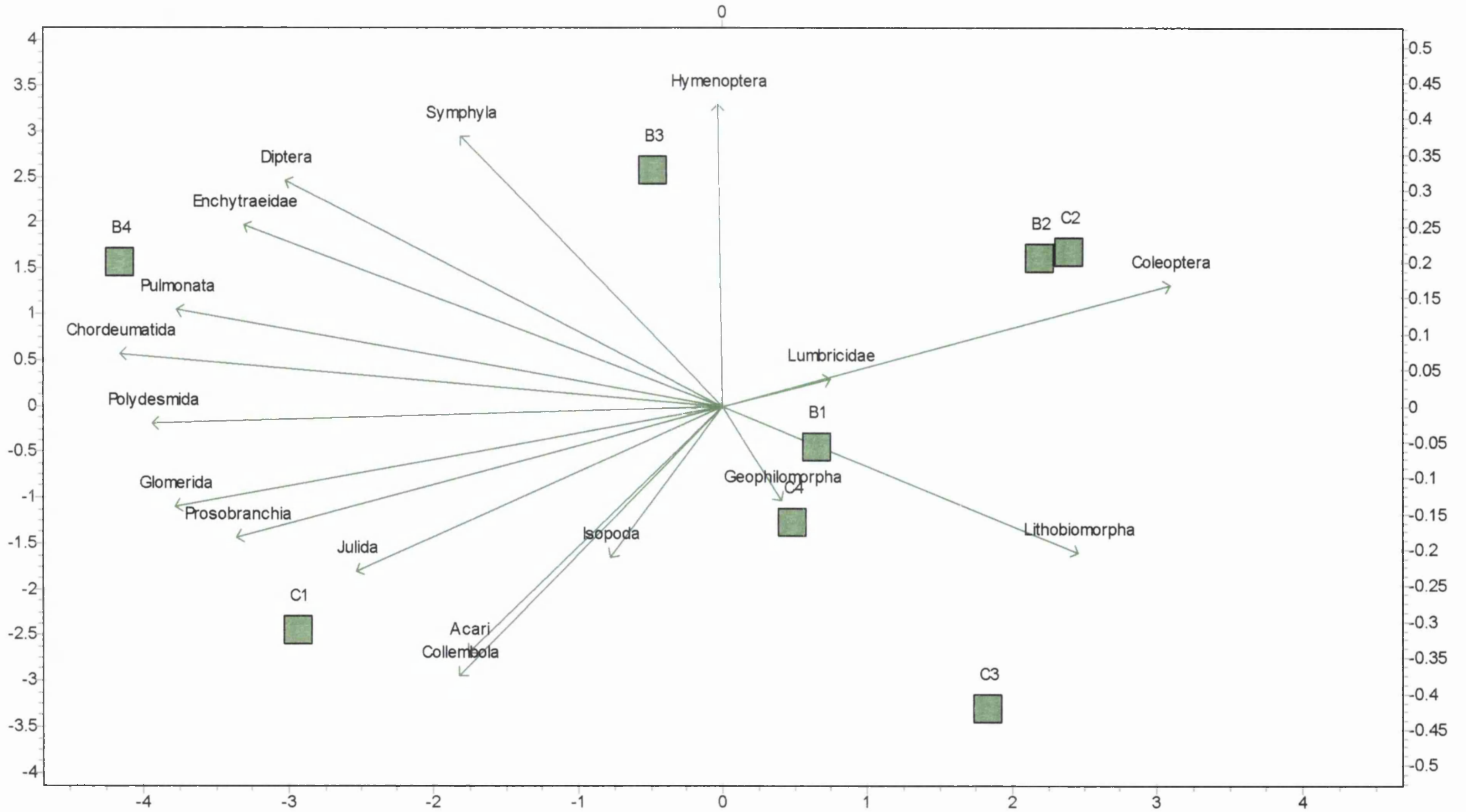


Figure 53 PCA plot for Sites 1-4 at Bishop's Wood, Caswell (C) and Bishopston Valley (B).

4.4 Discussion

A. dorrieni regularly reaches high population densities in the areas where it has been introduced (Chapter 3). The concomitant high proportion of the faunal biomass accounted for by the species (Chapter 6, section 6.1.3.13) and the amphipod's considerable contribution to the breakdown of the annual leaf litter fall (Chapter 6, section 6.1.3.14) make it reasonable to expect that this invader will exert some influences (whether positive, negative, or both) on the native litter-dwelling communities.

The results of this present study, however, indicate that – at least statistically – the amphipod has no such influence at this location. Bolger & Golden (2000), the only researchers to date who conducted a study focussing solely on the examination of possible effects the amphipod's presence may have on native species, also found that the presence of *A. dorrieni* had no significant effects on native species numbers or assemblages. Additionally, two other workers (Leaver, 1993; Sherriff, 1986), who investigated this aspect of landhopper biology to some extent, also failed to detect noticeable changes.

It is possible, therefore, that *A. dorrieni*:

a) Indeed does not affect native communities, perhaps due to its occupation of a niche which has not been previously occupied;

b) Affects groups of the native fauna that could not be examined in this study due to the processing techniques used. Such groups could be members of the micro- and small mesofauna of the leaf litter layer (using the classification of Wallwork, 1970) of even smaller taxa, such as fungi and bacteria;

c) Does have an effect on native species and communities, but this is not (yet?) strong enough to show up through statistical testing.

There are few arguments that can be presented in favour of hypothesis a), other than the statistical insignificance of the findings collected so far. There are no major invertebrate groups among the British leaf litter fauna that are not also present in the landhopper's native habitat (Richardson, 1980). Consequently, the existence of an 'empty niche' ready for *A. dorrieni* to fill on its arrival is very unlikely.

There is more evidence in favour of hypothesis b), namely findings for communities containing other landhopper species indicating that their presence greatly increases soil respiration (Richardson *et al.*, 1986). This may well apply to British populations of *A. dorrieni*, and there is an urgent need for further research in this area.

Examination of the data collected in this study strengthens aspect c). Despite the fact that the differences were not statistically significant, there is little doubt that there were far fewer pulmonates, enchytraeids and lumbricids, as well as many more isopods and collembolans and somewhat greater numbers of lithobiomorphs at the sites containing *A. dorrieni* than at the control sites. A reduction in number of enchytraeids and an increase in lithobiomorphs in the presence of *A. dorrieni* was also reported by Sherriff (1986). Differences in the other animal groups observed here did not show up in Sherriff's study. This could be partly due to the fact that the pH at his sampling locations was far lower than that in this study, leading to Sherriff's samples containing only very few pulmonates, lumbricids and isopods, which prefer more alkaline conditions and require high amounts of calcium in the substrate.

The decrease in pulmonates in the presence of *A. dorrieni* could be due to competition, or due to disturbance of the substrate, possibly increasing exposure of the snails or their eggs to predators. Similar factors may be responsible for the decrease in lumbricids. The decrease in enchytraeids is somewhat more puzzling, as these animals feed on fine, pre-digested litter material and fungal hyphae, both of which would be expected to occur in greater amounts in the presence of *A. dorrieni*, and its associated droppings. Perhaps increased litter disturbance is the causative factor explaining the decrease in their numbers where the landhopper is present.

The increase in numbers of isopods in habitats where *A. dorrieni* is present indicates that there is no detrimental competition between the two groups. This could be due to various factors:

A. dorrieni perhaps prefers leaves of different stages of composition, or it may feed on leaf tissue that is not favoured by the isopods. The ability to digest poorly decomposed leaves avoided by other detritivores has been reported as giving the landhopper *Cerrorchestia hyloraina* a competitive advantage (Lindeman, 1991). Conversely, woodlice, which rely on coprophagy for their long-term survival (Sutton, 1980), may benefit from the amphipod's droppings which may result in their increased densities. Finally, the predation pressure on woodlice may be lessened by the presence of the amphipod if woodlouse predators also take amphipods as part of their diets.

The increased numbers of collembolans could be somewhat more straightforward to explain, since most of these animals feed predominantly on fine leaf litter particles and fungal hyphae (Hopkin, 2000), which will occur in larger quantities in the presence of landhoppers, and thus benefit the collembolans. Additionally, they may benefit from the new microhabitats created by the movements and burrowing of the landhoppers.

It is clear that much more research is needed before the true impact of the introduction of *A. dorrieni* in the British Isles can be fully understood. Ideally, a location where *A. dorrieni* is still absent should be studied extensively, before the amphipod is intentionally introduced. Sampling should then continue through the period of population growth and continue for some time when stable densities are reached. Intentional introduction always carries the risk that it may later turn out to have undesirable consequences. Therefore, it would be best to choose a location which is close enough to the existing range of the ampipod that it is likely to become invaded by natural dispersal within a short period of time. It has to be ensured, however, that the chosen location is indeed still entirely free from invasion prior to the start of the study and it has to be ensured that it will remain so at least until experimental introduction, and ideally for some time beyond that, so that the recorded population growth is not affected by animals moving in from the surrounding area. A project such as this requires considerable long-term effort and resources, but the results gained from it, even if the experimental area were relatively small, would be invaluable in our understanding of this very successful invasive. Such knowledge could turn out to be essential because *A. dorrieni*, once established, is virtually impossible to eradicate.

5 Collection, maintenance, handling and related aspects relevant to laboratory research involving live *A. dorrieni*

This Chapter consists of four separate sections on methodology related to the laboratory investigations involving *A. dorrieni* described in subsequent chapters.

5.1 Collection of large numbers of A. dorrieni

For many experimental investigations, large numbers of *A. dorrieni* were needed, which could not be obtained by collecting random soil samples as described in section 3.2.1. The method used to collect the required numbers of animals involved two steps: Concentration and Extraction.

5.1.1 Concentration of animals

Initially, a large amount of leaf litter was collected in locations where *A. dorrieni* was abundant. The leaf litter was transferred from the ground into buckets as quickly as possible, to stop the animals from escaping into the loose top layer of the soil from which they could not be retrieved without damage. Next, a portion of the litter was placed into a bucket whose bottom had been cut out and replaced by a metal insert with holes of 5 mm diameter (actually the middle section of vegetable steamer). This bucket was suspended over another (intact) bucket containing damp paper towels. A lamp with a 60W bulb was placed ca. 20 cm above the surface of the litter to raise the temperature of the surface of the leaf litter in order to encourage the animals to move downwards. A 60 W bulb was chosen as there is a report of a 100W bulb killing the animals before they could escape into the collecting vessel in a similar arrangement (Lindeman, 1991). It was important to use only relatively small amounts of leaf litter and to put it in loosely, in order to enable the animals to make their way through it quickly and without obstruction. Generally, an extraction time of 2-3 hours was sufficient to remove most of the landhoppers from a portion of litter, and the procedure was then repeated with fresh litter.

5.1.2 Extraction of animals

Landhoppers are very prone to stress-related damage (see also section 5.3). They are physically very delicate and exceptionally agile, so that most handling methods used for invertebrates of a similar size, e.g. picking up by hand or with a damp paintbrush, are out of the question. Many authors have referred to the difficulty involved in catching individual *A. dorrieni* (O'Connor *et al.*, 1991). Reid (1947) describes the collecting of talitrid amphipods such: 'Sometimes hundreds are disturbed [by turning over stones or weed] but they hop so rapidly and erratically that to get half a dozen before they disappear is rather a feat'. The only effective way to pick up and move landhoppers without damaging them was found to be an electric entomological aspirator (Figure 54, page 146), also known as 'pooter' (Hausherr's machine works, Tom's River, N.J. 087053, USA and available in the UK from Watkins & Doncaster, Cranbrook, TN18 5EZ). The landhoppers can be picked up safely by this method and can also be collected in some numbers in the collection barrel. It is important, however, not to leave the suction on for too long when there are animals already in the barrel, as the moving air dries their gills and can easily lead to desiccation.

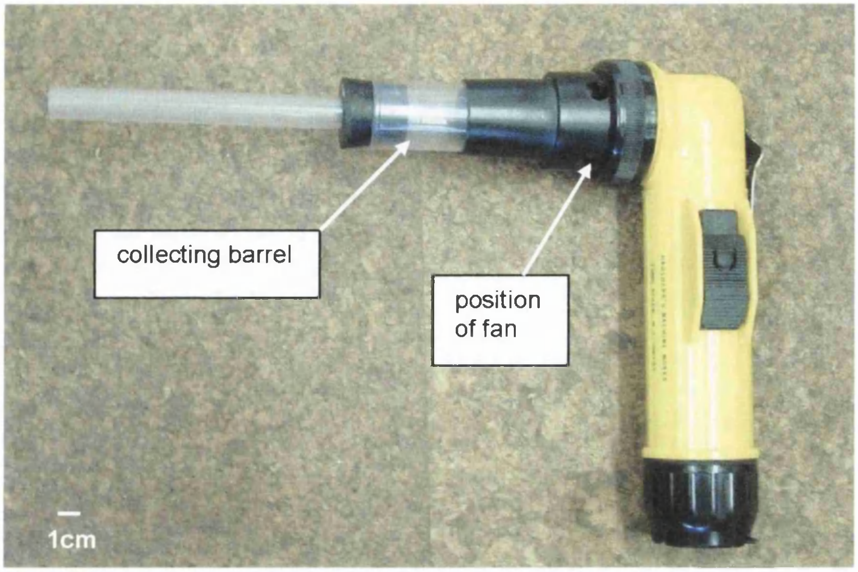


Figure 54 Electric entomological aspirator used for collection of *A. dorrieni*.

5.2 Long-term laboratory maintenance of <u>A. dorrieni</u>

No published information is currently available on maintaining *A. dorrieni* in the laboratory. This has actually proved to be both simple and very challenging, depending on the circumstances.

5.2.1 Basic maintenance in leaf litter

If maintenance in leaf litter is acceptable, for example in order to simply 'store' a number of animals, this is relatively easy to accomplish. The best results are achieved by using a plastic bucket with a number of small holes (2-3 mm diameter) in the lid, a thin layer (ca. 2 cm) of potting compost or similar material and a layer of fallen mixed deciduous leaves (ideally some that have been on the ground for a period of time). This arrangement (see Figure 55, page 148), if kept at room temperature (around 20°C), will need dampening by spraying with water approximately every three days (the surface of the compost has to stay damp at all times) and new leaves should be added on a weekly basis. The fact that leaf litter and compost are both present allows the landhoppers to choose between different levels of humidity to regulate their water balance. Most animals will hide where the leaf litter layer meets the compost, and where humidity is generally 100% (Dunger, 1958; Friend, 1980).

Landhoppers (as well as woodlice and other leaf litter fauna) will survive in such an arrangement for several months and, during the course of this study, *A. dorrieni* as well as some isopods released young, which went on to reach maturity. It is essential that large predatory invertebrates, such as members of the Chilopoda, are excluded and, ideally, any leaf litter should initially be frozen at -18°C or lower before being added to the maintenance vessel to avoid contamination by unwanted invertebrate species.

Figure 55 Long-term maintenance arrangement for *A. dorrieni* using mixed deciduous leaf litter.

5.2.2 More complex maintenance without leaf litter

When the presence of leaf litter is unacceptable, such as in feeding and metabolism experiments or during behavioural observations, maintenance is much more difficult. *A. dorrieni* will only survive for a matter of minutes when put at room temperature into an ordinary petri dish with no substrate, due to its sensitivity to low humidity. *A. dorrieni* is prone to an exceptionally high rate of water loss, largely as a result of its relatively large gill area (Morritt, 1987). When a sheet of damp filter paper is added to the dish, survival is markedly extended. The actual duration depends on the temperature but can exceed 6 hours. Eventually, however, the water evaporates through the small gap that is formed where the larger half of the petri dish overlaps the smaller. This evaporation can be slowed by placing the dish on a stage or in a small bowl and putting these into a closed container with some water in the bottom. Polystyrene cube boxes (such as those used for mailing frozen chemicals) have been found to be ideal receptacles and just the right size for the shallow 'Pyrex' glass bowls used for holding the petri dishes. Airholes are unnecessary (and indeed undesirable) provided the cubes are opened for a few moments once a day. Humidity inside the cube must remain at 95-100%. If it drops for any reason (such as an improperly replaced lid), even by as little as 15%, the damp filter paper in the petri dishes will again dry out very quickly and the animals will die. While this arrangement (see Figure 56, page 150) may seem ideal, one more problem remains to be overcome: the damp filter paper stops air entering the petri dish and the oxygen becomes exhausted within one or two days depending on the size of dish, the temperature and the number of animals in the dish. This problem can be solved by making holes in the larger half of the petri dish (i.e. the lower half, into which the filter paper is placed). These holes are best made with a soldering iron. Three holes of 2 mm diameter were found to be sufficient for a 3.5 cm dish, four holes for a 5.5 cm dish and five holes for a standard size (9 cm) dish. The dish is then raised off the surface by approximately 3 mm by means of small ridges of 'BLUTACK' (Bostik Ltd., Leicester, UK).

In such an arrangement, *A. dorrieni* can be kept almost maintenance-free for a week and, if necessary, even for several weeks. At temperatures above 5°C, it can prove difficult to maintain a humidity of 100% in the cube. In those cases, it may be necessary to add water to the petri dishes every few days and/or install an airpump to speed up evaporation of the water in the cube. In very draughty constant temperature rooms the entire cube may additionally have to be wrapped in plastic in order to maintain the required humidity. At low temperatures (below 10°C) it was found that water tended to condense on the lid of the petri dishes, making them appear sufficiently damp, while the filter paper was actually dry. Wherever possible, condensation droplets should be prevented from forming and/or regularly removed, as the animals can get trapped in them by surface tension and often die as a result (Cowling *et al.*, 2003; Moore *et al.*, 1992; Morton & Richardson, 1984 and pers. obs.), probably due to hyperosmotic stress caused by flooding of the ventral channel (Cowling *et al.*, op. cit.).

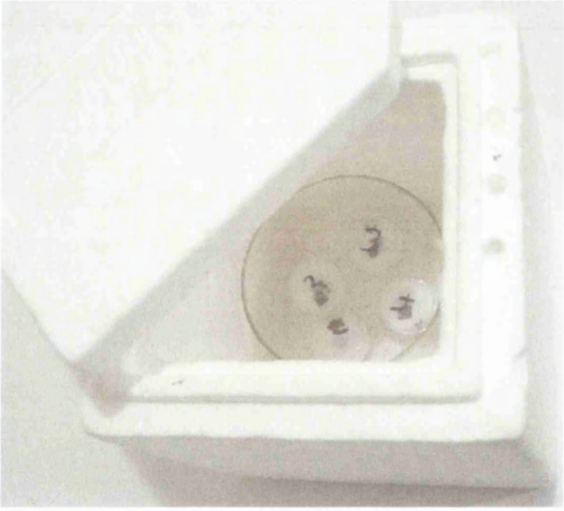


Figure 56 Long-term maintenance setup for *A. dorrieni* without leaf litter.

In experiments where landhoppers had to be housed singly, 3.5 cm diameter dishes were used. In those, the animals stayed mostly around the edges, where they could remain in contact with the sides, unless they were hiding under their pieces of leaf. In larger petri dishes they performed in a similar fashion, hardly ever utilising the space available near the centre. It was consequently reasonable to maintain them in the smallest available dishes.

The longest recorded holding period for a landhopper in somewhat similar conditions was 32 days (Lindeman, 1991). Using the method developed for this study, this period could be extended more than fourfold to 147 days. Even after that period, a large number of subjects was still alive and would undoubtedly have survived much longer had the experiment been allowed to continue. Successfullly maintaining landhoppers for prolonged periods of time in the way described here is a very important prerequisite for experiments investigating moult intervals and laboratory rearing attempts.

5.3 CO_2 Anaesthesia

This technique was developed in order to examine, measure, sex and mark live landhoppers under the microscope while minimizing the risk of injury to the animal. Unanaesthetized landhoppers that are fully conscious show a very vigorous escape response when handled and appear to suffer significant, frequently lethal, levels of stress when restrained, no matter how gently. Two other reports to date refer to similar methods being used (Duncan, 1981; Moore *et al.*, 1992), but unfortunately, in both cases, descriptions of the methodology were omitted.

Anaesthesia involved CO_2 administration from a 600g Welding Gas bottle fitted with a regulator and needle valve. The flow rate was 100 cm^3/min. The animals to be anaesthetized were introduced into a flat-bottomed test tube (diameter 2cm, height 8cm) and the gas was added to the bottom of the tube by means of airline tubing. During the exposure period, the top of the test tube was covered loosely with a thumb.

Initially, in order to determine the amount of exposure to CO_2 necessary to reach an adequate depth of anaesthesia, three groups of five animals were exposed for 30/20/10 seconds respectively. The exposure period was deemed to start after the cessation of the initial vigorous movements. Typically, the animals showed an increased escape response for several seconds (never more than 10) immediately after the start of the introduction of the gas. After this, they lay still on their sides (usually curled up), with slight movements of legs and antennae. From this point onward, they were not responsive to touch. At the end of the relevant exposure period, the animals were placed in a petri dish lined with damp filter paper and observed/manipulated/marked under the microscope for a maximum of four minutes. All animals were non-responsive to manipulation for a minimum of three minutes. After three minutes, the landhoppers that had been exposed to CO_2 for 10 seconds started to become active again, followed by the 20-second group, which began to recover after approximately 6 minutes. Interestingly, small individuals seemed to recover faster than larger ones, but there was insufficient data to allow statistical comparison. The 30-second group took over 30 minutes to recover and seemed more sluggish than usual for many hours. Both short-term (still alive after 48 hours at 13 °C) and long-term survival (still alive after 14 days at 13 °C) were very poor in all groups with only five individuals alive after 48 hours (2,2,1 from the 10,20,30-second groups respectively) and only one individual (from the 20-second group) still alive after 2 weeks.

A number of the animals that had been anaesthetised and manipulated showed a colouration consistent with that of animals under desiccation stress (Figure 57, page 154), and it was noted that during anaesthesia, pleopod movement was much reduced or absent.

Figure 57 *A. dorrieni* showing colouration typical of severe desiccation stress.

As a result, it was proposed that the reason for the poor survival rates may lie with the conditions under which the manipulation took place, rather than the exposure to the CO_2.

In order to test this view, another three groups of 5 landhoppers were exposed to the CO_2 and manipulated as described above, only this time, immediately after the exposure period, they were placed in the deep half of a small petri dish (3.5 cm diameter) filled with cold (approx. 2 °C) distilled water. It was decided to use cold water in order to reduce the animals' metabolic rate, and to thus possibly also prolong the anaesthetic effect of the CO_2. Among these three groups, the short time survival rate was 100% and the long time survival rate was 93% (one animal from the 20 second group died after 10 days). It was therefore concluded that the high lethality in the first round of experiments was due to the unsuitable conditions under which the anaesthetised animals had been handled rather than due to the anaesthesia itself.

Overall, when subsequent handling is performed correctly, CO_2 anaesthesia proves a quick and easy way to temporarily immobilise landhoppers with a minimal amount of stress and very good long-term survival. It was used extensively throughout this study in order to determine the sex and length of individuals, and results have been consistent with the above findings throughout. It is advisable, however, not to exceed the 30 second exposure limit, as recovery has proven to be very slow at that level of exposure, and it is therefore reasonable to assume that even higher doses could easily cause permanent damage to the animal.

5.4 Whitey Disease

A. dorrieni is regularly described as occasionally producing yellow/light brown, even reddish brown to pink individuals (Rawlinson, 1937). Such specimens, predominantly of an orange and pale yellow, almost white, colouration, were also recorded during this study (Figure 58, below and Figure 59, page 157). Where any mention to these colour variations are made, it is usually ascribed to a recent moult (Rawlinson, 1937), also P. Llewellyn, pers. comm. This is, however, not the case, as newly-moulted animals are always of a brownish colour, sometimes with a slight blue hue due to the haemocyanin showing through the soft cuticle. Additionally, there may be an opaque sheen. Newly-moulted animals are illustrated in Figure 60 and Figure 61 (page 157).

Figure 58 *A. dorrieni*: diseased orange specimen.

Figure 59 ***A. dorrieni*****: diseased white specimen.**

Figure 60 Newly-moulted *A. dorrieni,* showing bluish hue due to haemocyanin.

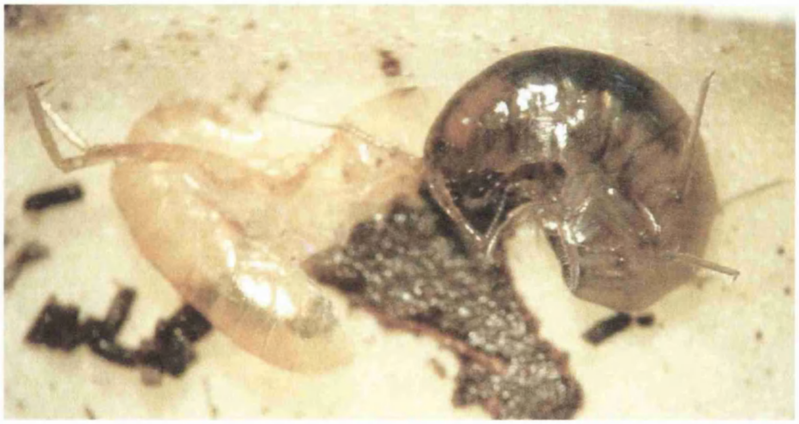


Figure 61 Newly-moulted *A. dorrieni* with shed cuticle.

There is no evidence for this being a genetic phenomenon, however, there have been reports of a bacterial disease caused by *Bacillus subtilis* which affects amphipods and which results in the infected individuals' bodies becoming progressively lighter until they reach an opaque white colour (Duncan, 1981). Other symptoms reported in this paper, which focusses on the effects of the disease on the grassland landhopper species *Orchestia hurleyi*, include: progressive weakening and wasting; inability to jump or walk quickly; inability to brood; and internally initially a massive increase of haemocytes in the circulation (op. cit.). The number of haemocytes is then reported to decline during the course of the infection, until in very diseased individuals no haemocytes are present in the haemolymph, which is instead packed with motile bacteria, which give the diseased animals their creamy white colour (op. cit.).

This disease of *O. hurleyi* was first detected in 1968 near Christchurch, New Zealand, from where it has been spreading, causing considerable reduction in landhopper population density in the affected areas (op. cit.). Another landhopper species which is apparently affected is *T. sylvaticus*, whose colour, when first described in 1879, was described as 'usually dark slate, but occasionally dull yellow', indicating that Whitey disease was already prevalent in this species at that time (Haswell, 1879). It is therefore very likely that the pale individuals of *A. dorrieni* observed in Britain are also affected by *B. subtilis* infection. It may be of note that virtually all diseased individuals observed in this study originated from the West Cross population of *A. dorrieni*, which is located in a woodland surrounding a small stream inhabited by native amphipods. This landhopper population appears to be strongly affected by the disease, whereas hardly any diseased individuals were collected from the dry valley at Bishop's Wood. There may be a possibility that the native freshwater amphipods could be carrying the bacterial infection. Much further research is required to determine whether the causative organism is indeed *B. subtilis*, and whether such an organism is indeed carried by the native freshwater amphipods. For the purpose of all other experimentation, however, it is important to be able to recognize and exclude diseased individuals, as results produced by such specimens would not be representative due to altered behaviours of diseased animals.

6 Feeding and food preferences of *A. dorrieni*

It has been estimated that *A. sylvaticus*, a close relative of *A. dorrieni*, is responsible for utilizing up to 24% of the annual litter fall in the sub-tropical rainforests of its native New South Wales (Clark, 1954). It is therefore possible that *A. dorrieni* has an important, and as yet unquantified, role in litter dimminution and breakdown in the UK. While most publications on *A. dorrieni* contain data on its distribution and often very detailed descriptions of the localities in which it can be found, few so much as make reference to the animal's feeding behaviour. Information about *A. dorrieni's* feeding behaviour and food preferences would be essential in order to gain an insight into the landhopper's potential role in British forests.

It appears to be generally assumed that *A. dorrieni* feeds on whichever litter it happens to find itself in. This assumption ignores possible food preferences as well as the great heterogeneity of the leaf litter in terms of species of origin, stage of colonization with fungi and bacteria as well as changes in chemical composition of the leaf tissue (such as the leaching of tannins) (Sutton, 1980). In the few studies on the feeding biology of other species of landhoppers, it has been observed that they show significant preferences for certain leaf species (usually softer varieties) over other (usually tougher ones, such as *Eucalyptus spp.*) (Devitt, 1981; Morton *et al.*, 1984). It has also been found that they prefer partially (both microbially and chemically) digested leaves to freshly fallen ones (Morton *et al.*, 1984). The first paper touching on the varying palatability of leaf litter from different sources to *A. dorrieni* was published in 1996 (Spicer *et al.*, 1996). The authors found differences in palatability of the litter depending on the plant of origin and pointed out the urgent need for more rigorous studies on the feeding biology of *A. dorrieni*. The only study to date investigating an aspect of the feeding behaviour of *A. dorrieni* in any detail was conducted in 1998 by O'Hanlon and Bolger (1998). They estimated the annual percentage of litter fall utilized by *A. dorrieni* at a coniferous woodland site of predominantly Lodgepole pine (*Pinus contorta*) in Ireland. In this study, they performed some initial experiments to estimate ingestion, assimilation and egestion rates of *A. dorrieni* feeding on *P. contorta* litter, and estimated that the landhopper may consume as much as 25% of the annual litter production at this site. The following series of experiments was designed to provide initial insights into the feeding habits of *A. dorrieni* and to provide answers to the following questions:

1. What is the typical food intake of *A. dorrieni*?
2. Does the food intake of *A. dorrieni* vary with different ambient temperature?
3. Does the assimilation rate of the food vary at different ambient temperatures?
4. What effect does food deprivation have on the weight and longevity of *A. dorrieni*?
5. Does food intake depend on the species of origin of the leaf tissue provided?
6. Does the assimilation rate depend on the type of leaf tissue consumed?
7. Does food intake depend on the freshness of the leaf tissue provided?

8. Is the Konsumquotient (as calculated by Dunger, 1958) applicable to *A. dorrieni* and does it allow a representative estimate of the landhopper's importance in the ecosystem and a comparison with other members of the detritivorous macrofauna?

9. Does *A. dorrieni* show a varied preferences for leaf tissue from different origins?

10. Is it possible to produce estimates for the biomass and proportion of annual litter fall consumed by *A. dorrieni* at Bishop's Wood, Caswell?

6.1 Ingestion, assimilation and egestion under three different temperature regimes

6.1.1 Introduction

Despite the fact that *A. dorrieni* originates from areas of subtropical climate, it is now clear that it is capable of feeding efficiently enough to sustain growth and breeding, even in a temperate climate. It is unknown, however, how the different temperature regimes found in such a climate affect the landhopper's metabolism and feeding behaviour. In order to examine whether there is a relationship between change in temperature and feeding rates, landhoppers were maintained at 4°C, 13°C and 20°C for 15 weeks or until their death (whichever was the earlier). During this time, their weights, the weights of the food ingested and the weights of their droppings were monitored on a weekly basis. Gere (1956) noted considerable increases in metabolism (measured by food intake) with increases in temperature in Diplopoda and Isopoda, and it seemed not unreasonable to expect a similar pattern here.

6.1.2 Materials and Methods

The animals were kept singly in small petri dishes as described in section 5.2.2 (Figure 62, page 165). Birch leaf that had been on the ground for a minimum of 12 weeks had been previously observed to be readily consumed and was chosen as the staple food. The leaves were cut into rough squares (avoiding the midrib) and dried at 60°C for 48 hours, a drying regime commonly used for this type of study (Mackay & Kalff, 1973; Morton *et al.*, 1984). This treatment does not affect the palatability of the leaves, in contrast to drying at higher temperatures (Dunger, 1958). Immediately prior to use, the leaf pieces were weighed using a Sartorius analytical balance to the nearest 0.1 milligram. The leaf pieces were then soaked in hot water (ca. 60°C) for ten minutes before being introduced into the petri dishes. All animals were kept at 13°C for 48 hours before the experiment and weighed prior to introduction into the experimental dishes. Eight animals were subsequently placed into each of the 4°C, 13°C and 20°C conditions. Eight control petri dishes, lacking a landhopper, were set up for each of these conditions.

Food was not withheld prior to the start of the experiment as recommended by some authors (Gere, 1956; van der Drift, 1951), since the aim of the experiment was to obtain representative feeding rates. After starvation, the feeding rates would probably have been above normal (Gere, 1956), falsifying any quantitative findings. Every seven days, new petri dishes with fresh leaf pieces were set up. This prevented any feeding on possible mould/bacterial growth on the leaf pieces or filter paper and reduced the likelihood of considerable weight loss of the food due to bacterial/fungal digestion. The animals were weighed before transfer to the new dishes. The previous dishes (and their controls) were dried at 60°C for 48 hours and the remaining food and the droppings produced (where appropriate) were weighed to the nearest 0.1 milligram (Figure 63, page 165).

Figure 62 Maintenance arrangement for feeding experiments with landhoppers.

Figure 63 Petri dishes arranged for introduction into drying oven.

In order to compare results from this study (which are based on live weight of the experimental animals) with results of those other workers who based their results on dry weights, a formula had to be calculated to transform live (wet) weight into dry weight. This formula was based on data from 50 freshly caught individuals which were weighed immediately on removal from the leaf litter, then killed by freezing at -18°C for 6 hours, and re-weighed after drying (using the procedure described previously for leaf litter). The data were then plotted and a line of best fit calculated Figure 64 below. The regression showed that dry weight was highly dependent on wet weight (r^2=-.8853, $P<0.001$). Thus the equation used to calculate dry weight from live weight was:

$$y=0.2477x+0.6134$$

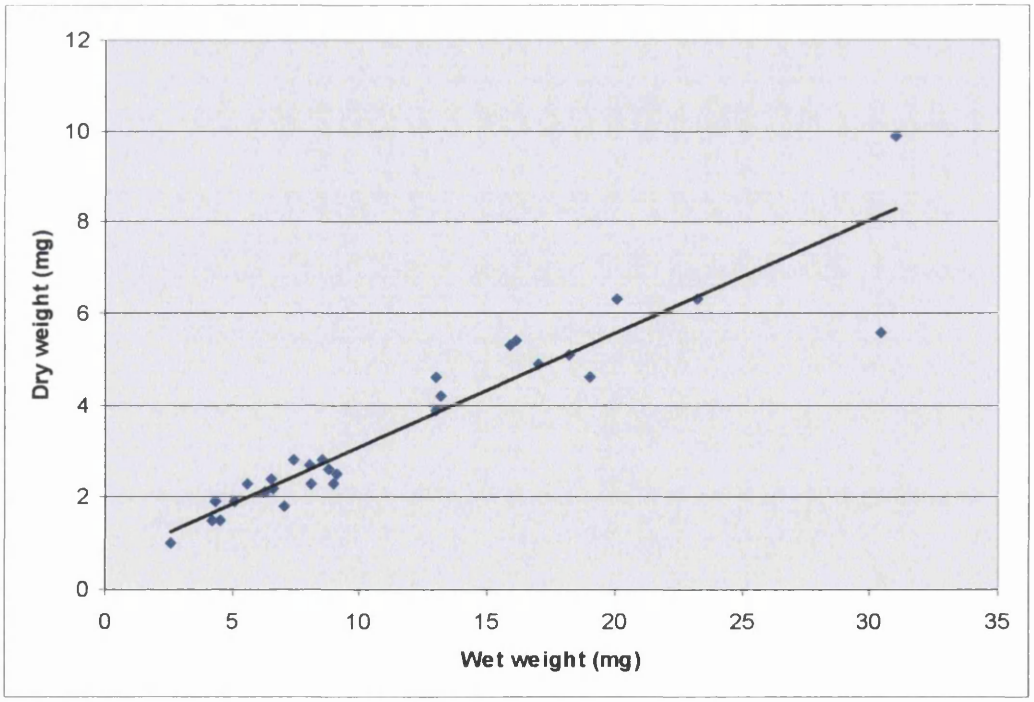


Figure 64 Plot of wet weights and dry weights of 50 *A. dorrieni*, showing line of best fit.

6.1.3 Results

6.1.3.1 Controls

All control fragments lost a small proportion of their original weight, probably as a result of leaching of soluble substances from the leaf tissue during the rehydration process. The slightly higher weight loss at the higher temperature regimes indicates, however, the possible additional involvement of some bacterial digestion. The proportion of weight loss is illustrated in Table 6-1 (page 168) . The great variability of weight loss within the different treatments meant that applying an average correction factor to the leaves fed on by the experimental animals would have led to some invalid (negative) data points. The calculation of a correction factor was therefore decided against. Instead, it was kept in mind that the amount of leaf tissue consumed by the individual landhoppers would be consistently slightly overestimated, and this was taken into account when drawing conclusions from the results. A similar highly variable weight loss of control leaves was observed by Dunger (1958), who also concluded that calculation of a correction factor would be unrepresentative of actual weight loss. Gere (1956) stated that he calculated and applied a correction factor from the weight loss of his control leaves, but the value was not given. Dunger (1958) noted that leaf types with a low C/N ratio were generally subject to greater fluctuations in weight loss than those with higher ratios. Gere (1956) may have succeeded in producing a valid correction value by using one of the latter leaf types (it is not stated clearly what species was used). O'Hanlon and Bolger (1999), working with *P. contorta*, also calculated and applied a correction factor without reporting any undue variations in weight loss of their control samples. The C/N ratio of

P. contorta (50.4) is very high, and considerably higher than that of the *B. pendula* (30) tissue used here (Zimmer & Topp, 2000).

Temperature regime (°C)	**Mean weight loss (%)**	**Minimum weight loss (%)**	**Maximum weight loss (%)**
4	5.9	3.7	7.6
13	7.8	4.9	12.4
20	10.8	4.4	13.4

Table 6-1 Proportion of weight loss of control leaves.

6.1.3.2 *4°C*

Survival rate to 5 weeks: 75%

Survival rate to 10 weeks: 20%

Survival rate to 15 weeks: 0%

Throughout the experiment, only minute traces of faeces were produced, all of which were <0.1mg/week. Only one animal showed evidence of feeding, but this was to a very minor extent and not followed by any increase in production of faeces. What little feeding took place was during weeks 4, 5, 8 and 11. It is of perhaps of note that the animal that fed was one of the largest, being considerably heavier than the rest of the group. The weight loss of the leaves was similar to that of the control group, a mean 4.1%, with a minimum of 2.1% and a maximum of 8.8%.

Despite the fact that the animals were not feeding, in most cases their weight remained constant or slightly increased from week to week over the period of the experiment (Figure 65, below). When the initial weight on day 0 was compared with the last recorded weight, the increase was statistically significant (Wilcoxon's signed ranks test, W=0, P=0.008). On average, the weight gain was 36% (minimum weight gain: 1.7%, maximum weight gain 85%). A similar unexpected weight gain on starvation has been recorded in a woodlouse and a millipede species (Gere, 1956).

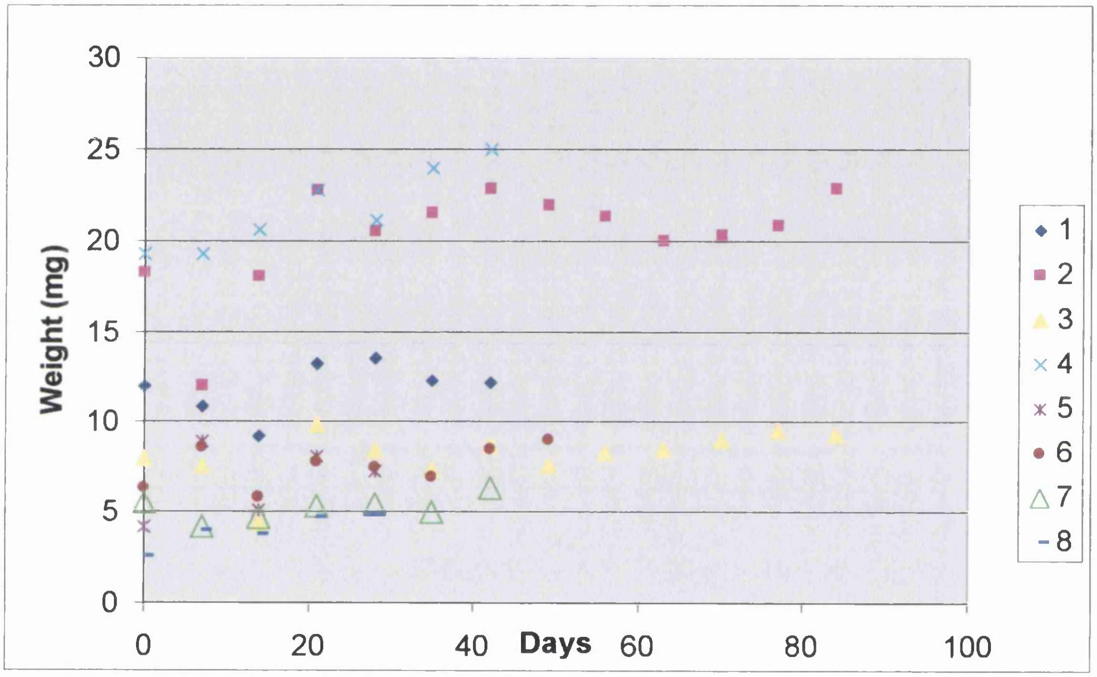


Figure 65 Weights over time in *A. dorrieni* specimens 1-8 at 4°C.

6.1.3.3 13°C

Survival to 15 weeks: 100%

At 13°C, all animals fed and regularly produced quantifiable amounts of droppings. There was considerable fluctuation in bodyweight over time in most individuals, with an upward overall trend. Food intake also fluctuated widely. The nature of these fluctuations is illustrated for a typical individual in Figure 66 (below). When the bodyweight of the experimental animals on day 0 was compared with day 105, the increase was statistically significant (Wilcoxon's signed ranks test, W=1, P=0.05). The fact that one animal slightly lost weight overall accounts for the less marked significance compared to the results at 4°C, where all animals gained weight. On average, the weight gain was 19.9% (maximum weight loss: -8.6%, maximum weight gain 48.9%).

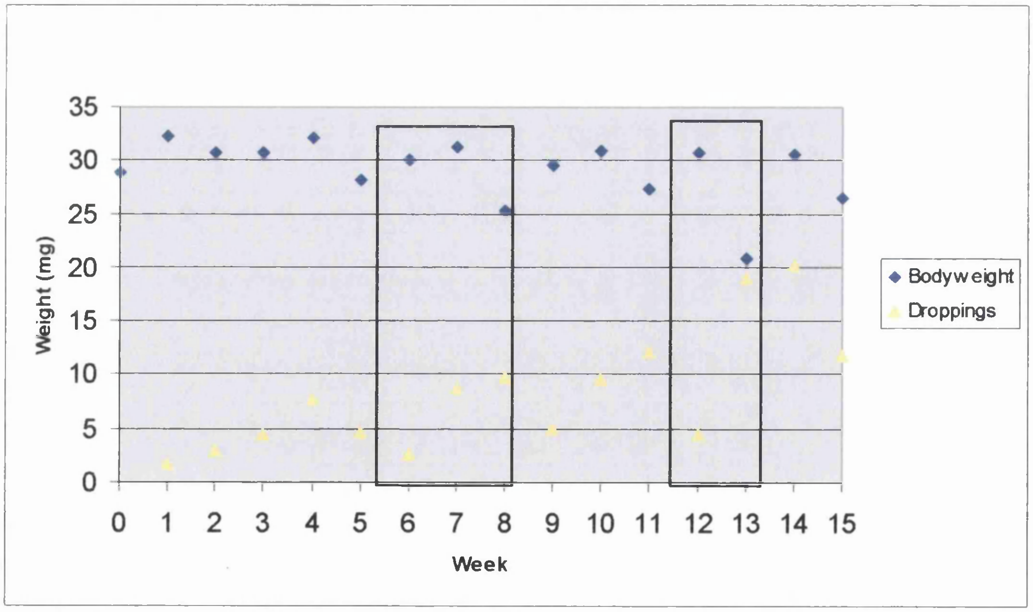


Figure 66 Typical fluctuations in bodyweight and food intake (represented by production of faeces) of *A. dorrieni* (specimen 5) at 13°C. Boxes indicate possible moulting patterns (see discussion).

Next, the following were calculated:

1. Weight of food eaten = weight of food - weight of food not eaten
2. Weight of non-assimilated food = weight of faeces
3. Weight of food assimilated = weight of food eaten - weight of faeces
4. Assimilation rate = Weight of food assimilated * 100 / Weight of food eaten

and the food assimilation rates of *A. dorrieni* were determined. Finally, the Konsumquotient (see section 6.1.3.10, Page 180) was calculated. The results of the above calculations are shown in Table 6-2 (Page172).

6.1.3.4 *Correlations at 13°C*

For each animal, the weekly bodyweight measurements, food intake and faeces produced were examined for correlation.

Food intake and faeces

As expected, in all eight cases there was a strong positive correlation between food intake and production of faeces (Spearman's rank-order correlation r_s between 0.762 and 0.981, $P<0.001$).

Bodyweight and food intake

In six cases, there was no significant correlation between weekly bodyweight values and food intake during the preceding week. In one case, there was a negative correlation significant at the $P<0.05$ level (Animal 5, Spearman's rank-order correlation $r_s=-0.588$) and in one case there was a positive

13°C	Length (mm)	Live weight start (mg)	Live weight end (mg)	Increase in live weight of animal (mg)	Increase in live weight of animal (% of original BW)	Mean weight (mg)	Mean weight of leaf eaten per week (mg)	Amount of leaf eaten as % mean BW	Mean weight of faeces produced per week (mg)	Faeces as % mean BW	Assimilation rate of leaf tissue (%)	Konsumquotient (*KQ*)
Animal no.												
4	4	3.8	5.3	1.5	39.5	7	4.95	70.7	3.9	55.7	22.2	135.2
3	6	9.4	10.8	1.4	14.9	11.8	7.27	61.6	5.3	44.9	27.8	140.3
2	7	8.9	10.3	1.4	15.7	8.6	5.32	61.8	4.3	50	19.4	126.7
8	8	17	19.8	2.8	16.5	16.7	8.55	51.2	6.6	39.5	22.9	130.9
1	9	23	29.8	6.8	29.5	25.9	9.25	35.7	8	30.8	13.6	105.7
6	9	23.3	24	0.7	3	26.4	10.7	40.5	8.4	31.8	21.6	120.8
7	10	22.1	32.9	10.8	48.9	27.8	13.76	49.5	10.7	38.4	22.4	149.9
5	12	28.9	26.4	-2.5	-8.6	29.1	9.08	31.2.	8.3	28.5	8.8	96.0
Mean values	**8.1**	**17.1**	**19.9**	**2.9**	**19.9**	**19.2**	**8.6**	**53.0**	**6.9**	**40.0**	**19.8**	**125.7**

Table 6-2 Weight change, assimilation rates and Konsumquotienten of *A. dorrieni* feeding at 13°C.

correlation significant at the 0.05 level (Animal 3, Spearman's rank-order correlation r_s= 0.543). It may therefore be concluded that the maintenance of bodyweight of *A. dorrieni* is largely independent of food intake.

Bodyweight and faeces

In six cases, there was no significant correlation between bodyweight and faeces produced. In two cases there were positive correlations between these indices (Spearman's rank-order correlation, Animal 3 r_s=0.538, Animal 7 r_s=0.529, both $P<0.05$). This shows that, even when a lot of food has been consumed, there is not always a noticeable effect on bodyweight, confirming the above finding that bodyweight does not strongly parallel food intake and absorption.

6.1.3.5 *20 °C*

Survival to 15 weeks: 100%

At 20°C, all animals fed and regularly produced quantifiable amounts of droppings. As at 13°C, there was considerable fluctuation in bodyweight over time in most individuals, with a clear upward overall trend. When bodyweight on day 0 was compared with day 105, the increase was statistically significant (Wilcoxon's signed ranks test, W=0.025). Again, one animal (also the largest), slightly lost weight overall, but the result is still clearly significant. On average, the weight gain was 56.5% (maximum weight loss: -5.2%, maximum weight gain 155%). The food assimilation rates and Konsumquotienten were calculated as above and are shown in Table 6-3 (Page 176).

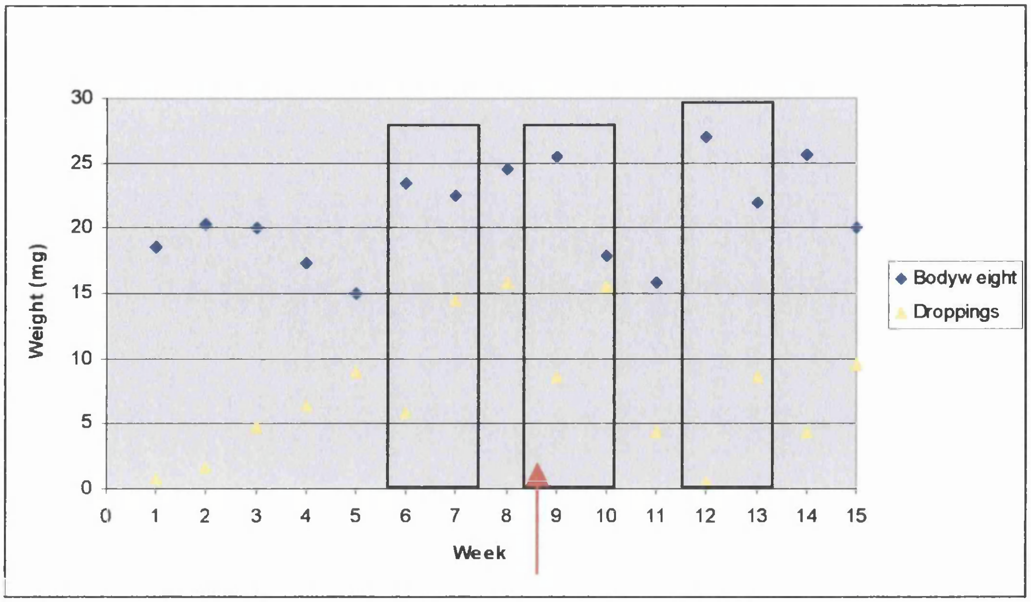


Figure 67 Typical fluctuations in bodyweight and food intake (represented by production of faeces) of *A. dorrieni* (specimen 5) at 20°C. Boxes indicate possible moulting patterns (see discussion).

6.1.3.6 Correlations at 20°C

As with the results from the 13°C series, the weekly bodyweight measurements, food intake and faeces produced were examined for correlations.

Food intake and faeces

Once again there was a strong positive correlation between food intake and production of faeces in all cases (Spearman's rank-order correlation r_s between 0.773 and 0.953, P<0.001).

Bodyweight and Food intake

There were no significant correlations between weekly bodyweight values and weekly food intake. This result further confirms that the maintenance of bodyweight of *A. dorrieni* is largely independent of food intake.

Bodyweight and faeces

There were no significant correlations between weekly bodyweight and faeces produced. This also confirms the above conclusion.

20C	Length (mm)	Live weight start (mg)	Live weight end (mg)	Increase in live weight of animal (mg)	Increase in live weight of animal (% of original BW)	Mean weight (mg)	Mean weight of leaf eaten per week (mg)	Amount of leaf eaten per week as % mean BW	Mean weight of faeces produced per week (mg)	Faeces produced per week as % mean BW	Assimilation rate of leaf tissue (%)	Konsum-quotient (*KQ*)
Animal no.												
3	6	5.1	8.8	3.7	72.5	6.4	5.3	82.8	4.2	65.6	20.4	125.9
4	7	4	10.2	6.2	155	9.3	6.1	65.9	4.8	51.6	20.8	151.8
6	7	9	15	6	66.7	10.6	7	66	5.6	52.8	20.5	138.6
1	8	9	12.1	3.1	34.4	11.9	7.8	65.5	5.7	47.8	26.9	102.3
2	8	18	22.1	4.1	22.8	18.1	8.7	48	7.	38.7	19	146.7
7	9	8.9	17.6	8.7	97.8	11.1	3	27	2.6	23.4	16.2	60.8
5	11	18.5	20	1.5	8.1	21.1	8	38	7.4	35.1	7.8	116.3
8	15	42.5	40.3	-2.2	-5.2	41.6	14.3	34.4	10..7	25.7	24.9	150.5
Mean values	**8.9**	**14.4**	**18.3**	**3.9**	**56.5**	**16.3**	**7.5**	**53.5**	**5.3**	**42.6**	**19.6**	**124.1**

Table 6-3 Weight gain, assimilation rates and Konsumquotienten of *A. dorrieni* at 20°C.

6.1.3.7 *Analysis of differences between the results at 13°C and at 20°C*

Mann-Whitney U tests were utilized to test for differences between the results produced at the two temperature regimes where survival was high. The results which were tested and the relevant P values are summarized in Table 6-4, below.

Results under investigation	**U value**	**P value**
Overall weight gain based on original live bodyweight	18	0.161
Food intake (as % bodyweight)	31	0.959
Assimilation rate of food	27	0.645
Konsumquotienten	26	0.574

Table 6-4 Results of Mann-Whitney U tests testing for differences between two different temperature regimes.

The series of statistical tests detected no significant differences in the results from the two different temperature regimes. Food intake, the assimilation rate of the food and the consumption quotients from the two regimes may all be considered virtually identical. There might be a trend for the overall weight gain to be higher 20°C than at 13°C, but any such difference was marginal.

6.1.3.8 Assimilation rate of leaf tissue

Since the statistical analysis revealed no significant difference between the assimilation rate of leaf tissue at the two viable temperature regimes, the data from both experiments are combined here.

An investigation of the relationship of bodylength and the proportion of the ingested material that is assimilated revealed that the assimilation rate remained virtually constant (averaging 19.7%) throughout the course of a landhopper's life (Figure 68, below).

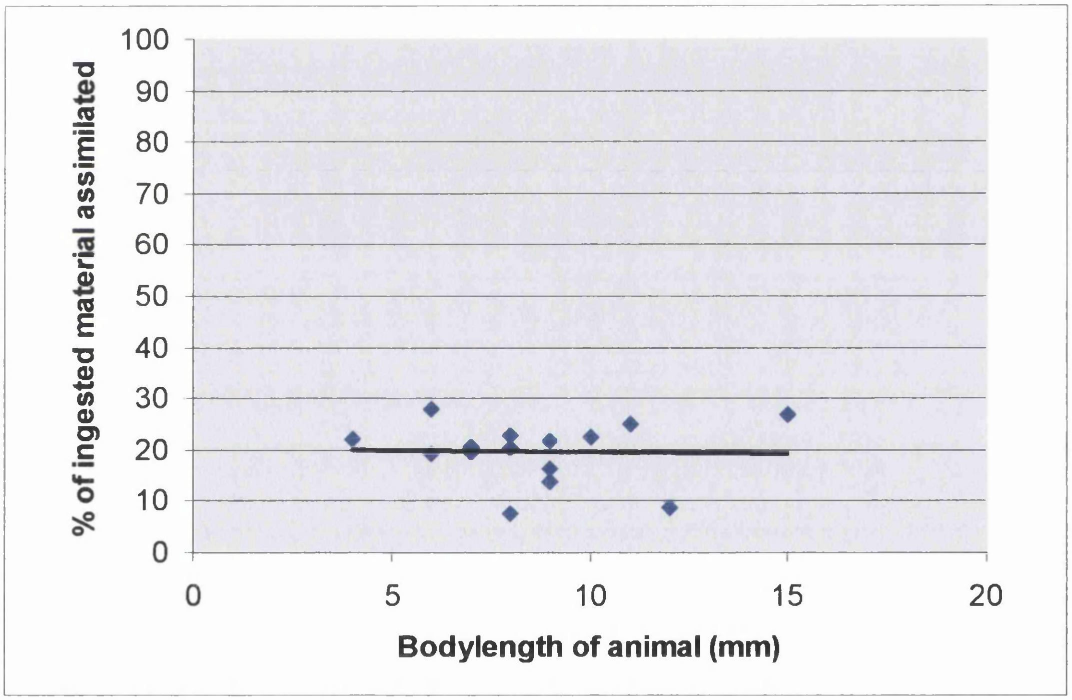


Figure 68 Assimilation rate of Birch leaf tissue ingested by *A. dorrieni* of different sizes.

6.1.3.9 Amount of leaf tissue consumed as proportion of bodyweight in relation to bodylength

As above, the data from both viable temperature regimes are considered together here, as the statistical analysis revealed no significant differences.

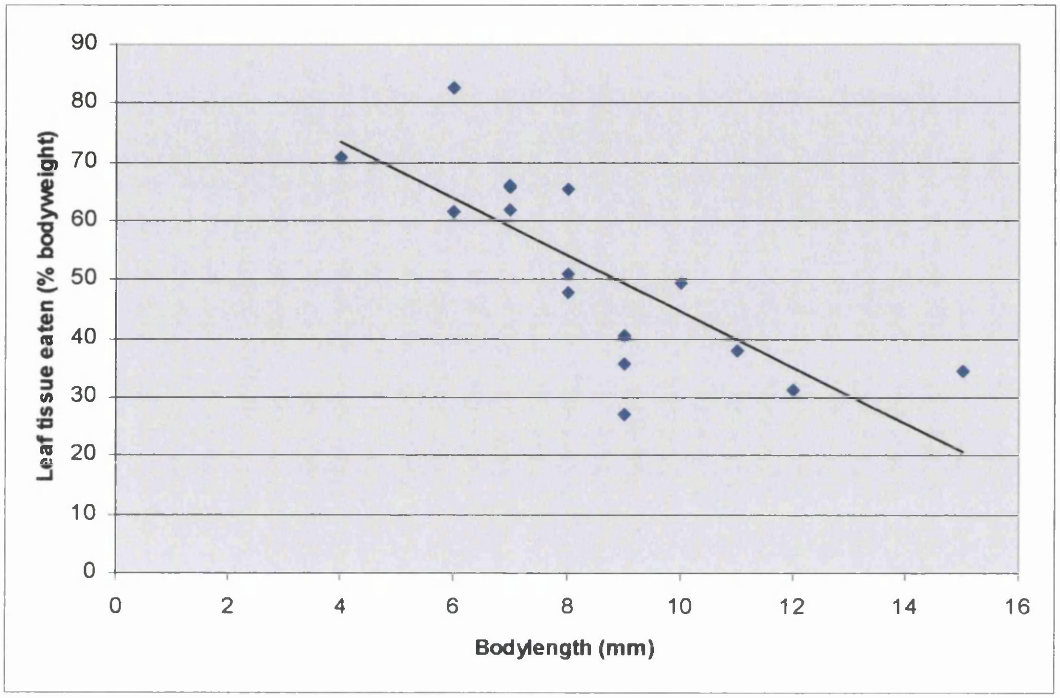


Figure 69 Amount of leaf tissue eaten (as proportion of bodyweight) in relation to bodylength.

The amount of leaf tissue eaten as a proportion of bodyweight falls significantly with an increase in the bodylength of the animal (illustrated in Figure 69, above). Linear Regression analysis resulted in the regression coefficient r^2=0.591 and a significance of P=0.001. Consumption in larger animals is generally considerably less in relation to their bodyweight than that of smaller ones (Dunger, 1958; van der Drift, 1951), and *A. dorrieni* is clearly no exception. This fact, however, can lead to inaccuracies where the food consumption for a certain animal species is to be calculated, e.g. when making comparisons between different species. Next, a method to correct for these inaccuracies is described.

6.1.3.10 Konsumquotienten

It has been generally accepted that food consumption (an approximate measure of metabolic activity) is directly proportional to the surface area ('active surface') of the consumer in different sized adult Diplopoda and Isopoda (Dunger, 1958; Gere, 1956; van der Drift, 1951). The relationship of food consumption to surface area is expressed as: $c/{}^3\sqrt{g^2}$ where *c* = dry weight of food consumed in unit time and ${}^3\sqrt{g^2} \approx$ surface area of the animal, *g* being its live weight. Some authors (Balogh, 1953; Gere, 1956) express *g* in terms of absolute dry weight, and call this expression the 'Van-der-Drift Constant'. This method can easily lead to inconsistencies, as the absolute dry weight of the experimental animals has to be extrapolated from data obtained from other animals of a similar size. Therefore it was decided to follow the approach used by Dunger (1958) and Phillipson (1960) and always use the live weight of the experimental animals for the calculation of the constants. Furthermore, these constants, in keeping with the nomenclature used by the aforementioned authors, are referred to as 'Konsumquotienten' (KQ), and calculated, to obtain more elegant values, as follows:

$$KQ = 100c/{}^3\sqrt{g^2}$$

The KQ is virtually constant when animals of the same species feed on the same substrate under identical environmental conditions for a set amount of time (Dunger, 1958). Therefore this constant can act as a quantitative index of metabolic activity, and comparisons between different species are made possible (Gere, 1956), provided the original observations were made under comparable conditions. Additionally, as mentioned above (section 6.1.3.9), the KQ can be used to correct for differences in food intake in one-species experiments arising from the fact that small animals eat considerably more in relation to their bodyweight than larger ones.

Here, calculation of the Konsumquotienten for the animals feeding on birch leaf tissue at 13°C and 20°C resulted in a mean of 124.9 with a standard deviation of 24.45. Figure 70 (below) illustrates how calculation of the Konsumquotient corrects for the relative decrease in food consumption in larger animals noted previously and in Figure 69 (page 179).

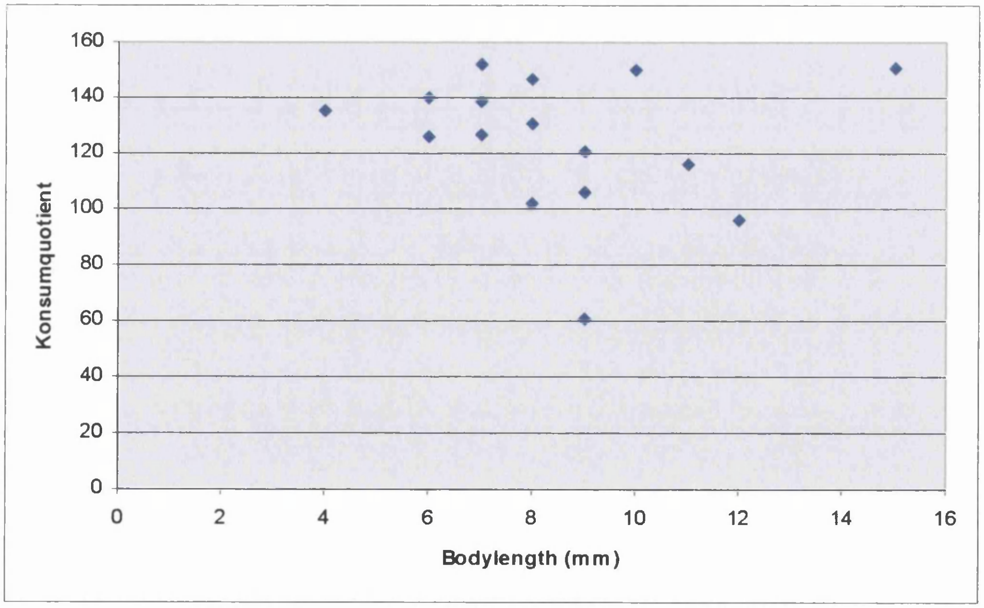


Figure 70 Konsumquotienten of *A. dorrieni* feeding on Birch leaf tissue.

6.1.3.11 *The 'standardized' landhopper*

The data from the experiments at 13 and 20°C were used to compile a picture of the feeding behaviour of a 'standardized' landhopper feeding on Birch litter (Table 6-5, below) This 'typical individual' must be referred to with caution, as it is a result of calculations that do not take variable factors, such as increased feeding of young animals, into account. It does, however, provide a useful indicator of the species' general attributes where a coarse estimate is sufficient, for example when comparing the landhopper with typical British litter-feeding species for which similar data are known.

Length (mm)	Live weight start (mg)	Live weight end (mg)	Increase in live weight of animal (mg)	Increase in live weight of animal (% of original BW)	Mean weight (mg)	Mean weight of leaf eaten per week (mg)	Amount of leaf eaten per week as % mean BW	Mean weight of faeces produced per week (mg)	Faeces produced per week as % mean BW	Assimi -lation rate of leaf tissue (%)	Konsum quotient (KQ)
8.5	15.7	19.1	3.4	38.2	17.7	8.1	53.2	6.1	41.3	19.7	124.9

Table 6-5 Feeding data for a 'standardized' *A. dorrieni.*

6.1.3.12 *Prediction of bodyweight where bodylength is known*

First, the relationship of bodyweight to bodylength was investigated. Since food intake, weight change over time and the *KQ*s were not significantly different at 13 and 20°C, data from the animals of both these temperature regimes were used. A scatter graph with trendline indicates a strong linear relationship (Figure 71, page 183). A linear regression analysis confirms this, returning a strongly significant result (r^2=0.789, P<0.001). Bodylength is therefore a reliable predictor of bodyweight. However, this calculated line of best fit crosses the y axis at -11.047, probably due to an underrepresentation of very small animals in the original data set. Since the bodyweight of an animal cannot fall below 0, in order to act as a reliable predictor, the line of best fit must be corrected to intercept the y axis at 0, which leads to a slight reduction of r^2 from 0.789 to 0.684. The significance of the regression remains at $P<0.001$. The equation by which the bodyweight for any given bodylength may be calculated is that of the line of best fit shown in Figure 71 below, namely:

$$\mathbf{y=2.2241x}$$

where y = bodyweight and x = bodylength

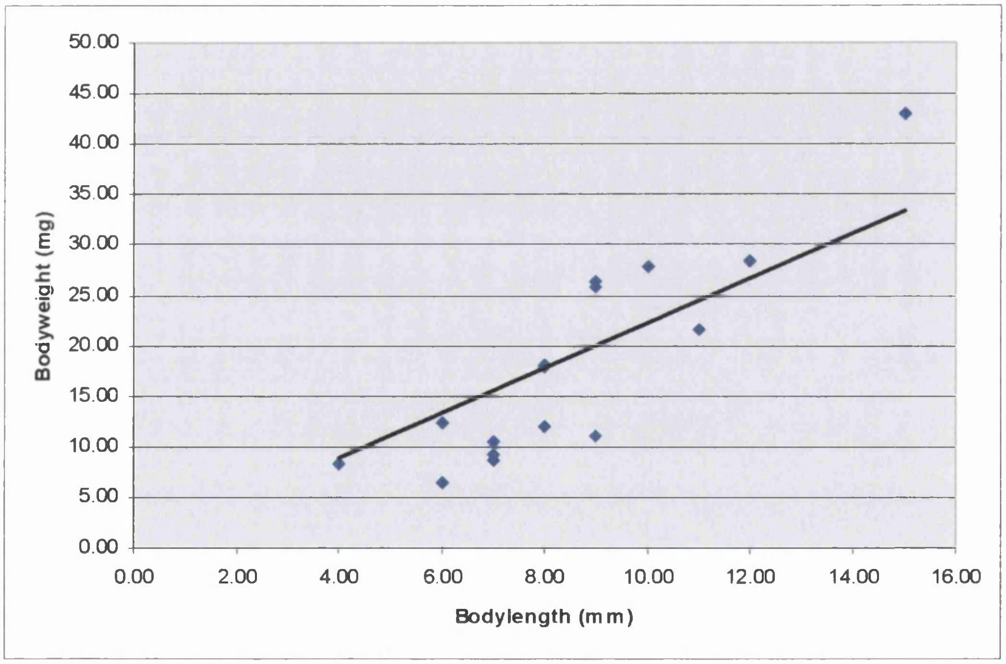


Figure 71 Illustration of the relationship between bodylength and bodyweight in *A. dorrieni*.

6.1.3.13 *Estimation of the biomass of A. dorrieni through the year*

The equation calculated above allows an estimation of the biomass of *A. dorrieni* in a habitat where its population makeup and density is known. A table illustrating the proportions of different size classes as part of the entire population such as Table 3-11 (page 94) and the monthly population totals have to be used in order to obtain the estimate. First, the weight for one animal of each size class is calculated, then multiplied by the expected number of animals in that size class in the month under investigation. Then the weights of all size classes are added up to give a monthly biomass total. The results from these calculations, for Bishop's Wood, Caswell, are summarized in Figure 72 (below).

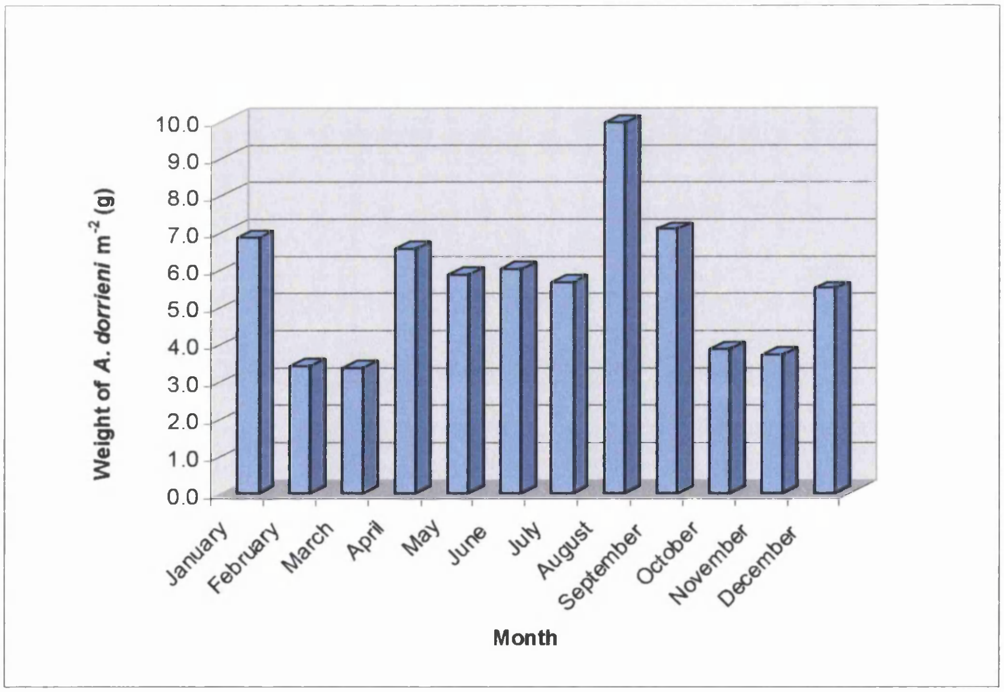


Figure 72 Estimation of the biomass of *A. dorrieni* at Bishop's Wood, Caswell during the course of the year.

6.1.3.14 *Prediction of amount of leaf tissue eaten*

Both bodylength and mean bodyweight were tested for their suitability as predictors for the amount of mean leaf tissue eaten each week. Both values returned significant results, but, as bodyweight was the more strongly significant, it might be assumed to be the better predictor of the amount of leaf tissue eaten (Table 6-6, below).

Predictor variable	**R^2**	**P**	**Equation**
Bodylength	0.481	0.003	$y = 0.795x + 1.307$
Bodyweight	0.784	< 0.001	$y = 0.264x + 3.317$

Table 6-6 Linear regression results and equations for two different predictors of amount of leaf tissue eaten.

Both the above equations were used to produce predictions of leaf tissue eaten on a population scale for Bishop's Wood, Caswell.

First, bodylength was used as a predictor. The amount of leaf tissue eaten per week for an animal of each size class was calculated. Next, this value was multiplied by the expected number of animals of that size class in the month under investigation (similar to the procedure in section 6.1.3.13) and the values for all size classes were added up. Finally, the result was multiplied by four, to give an estimate for leaf tissue eaten per month.

Secondly, bodyweight was used as a predictor. In this case, the expected bodyweight for an animal of each size class had to be determined first. Then the amount of leaf tissue consumed by an animal of each size class based on its expected bodyweight was calculated. Following that, the results for each size class were again multiplied by the number of animals expected for each size class, the size classes added up and the final result multiplied by four to produce monthly results. Table 6-7 (page 187) summarizes the results from all the above calculations. It can be seen that there is little difference between the values received by basing the calculations on bodylength and bodyweight. This difference is not statistically significant (Mann-Whitney U test, U=54, P=0.319). Due to the considerably more complex calculations necessary to receive results based on bodyweight, it is therefore suggested that future predictive calculations are based immediately on bodylength, despite its slightly lower degree of statistical significance as a predictor variable. A further advantage of this method would be that possible inaccuracies created by the prediction of the bodyweight from bodylength will not be amplified further during the calculation of predicted food intake.

Month	Estimated amount of leaf tissue eaten (g) per month per m^2 by the landhopper population at Bishop's Wood, Caswell. Values based on bodylength.	Estimated amount of leaf tissue eaten (g) per month per m^2 by the landhopper population at Bishop's Wood, Caswell. Values based on bodyweight.
January	12	13
February	6	7
March	6	6
April	11	12
May	10	11
June	10	11
July	10	12
August	18	20
September	13	14
October	7	8
November	7	8
December	10	11
Total/year	**121**	**133**

Table 6-7 Predictions of amount of leaf tissue eaten per month (in g) based on bodylength and bodyweight.

These results are likely to be slight overestimates, as less feeding will take place at lower temperatures. The present study reveals that *A. dorrieni* does not feed at (or below) 4°C (section 6.1.3.2), but that substantial feeding takes place at 13°C (section 6.1.3.3), and that there is not much further increase up to 20°C (section 6.1.3.5). Therefore, activation of the feeding response takes place between 4°C and 13°C. Since, under natural conditions, the temperature fluctuates during the day and the substrate may become significantly warmer than the air when exposed to the sun, it is likely that even in cold weather some feeding will take place. In early spring before the trees break into leaf when the air temperatures are still low, temperatures of up to 43°C have been recorded in the leaf litter in full sun in deciduous forests in northern Europe (Firbas, 1927).

An exact prediction of the amount of leaf tissue eaten must take into account that during the cold months, overall less feeding will take place than indicated by the equation. Table 6-8 (below) illustrates the mean temperatures near Bishop's Wood. The results of the present experiments suggest that during January and February, feeding will be significantly reduced. From June to September actual feeding rates will be closest to the values predicted by the equation, since both miniumum and maximum temperatures are close to the values on which the equation is based.

Mean air temperatures (°C)	**min**	**max**	**mean**
January	2.7	7.1	4.9
February	2.0	7.0	4.5
March	3.4	9.2	6.3
April	4.5	11.8	8.2
May	7.5	14.9	11.2
June	10.3	17.9	14.1
July	12.2	19.5	15.9
August	12.3	19.3	15.8
September	10.7	17.2	14.0
October	8.7	14.2	11.5
November	5.2	10.2	7.7
December	3.7	8.2	6.0

Table 6-8 Mean monthly temperatures at Penmaen, Gower (1962-2002).

6.1.4 Discussion – Ingestion, assimilation and egestion under three different temperature regimes

As a result of space and time constraints, only a minimum number of replicates could be performed. Had it been possible to test a greater number of animals, it would have been easier to recognize trends and the calculation of means and equations would have been more accurately representative of the population as a whole. Nevertheless, enough data could be collected to draw some conclusions with a reasonable degree of accuracy.

The bodyweight of most individuals fluctuated widely during the course of the study. This was especially marked in smaller animals. While these fluctuations were apparently random, an investigation of charts displaying the bodyweight and food intake of each animal over time was undertaken in order to look for possible patterns. The food intake was expressed as faeces produced to avoid possible inaccuracies caused by weight loss of the leaf tissue from causes other than hopper feeding activity (see section 6.1.3.1, page 167). This investigation revealed one recurring pattern that is illustrated in Figure 66 and Figure 67 (pages 170 and 174), namely an increase in bodyweight occuring at the same time as a reduction of food intake, followed by a sharp drop in bodyweight accompanied by a rise in food intake. In some individuals this pattern could be observed very clearly and at regular intervals of 3-6 weeks. It is likely that these changes are related to the moult cycle. Unfortunately, moulting generally takes place during the hours of darkness and the exuviae are usually promptly eaten, so that moulting (or an indication of a recent moult by the presence of exuviae) could only be observed very rarely. On both occasions where moults were observed, they occurred at the end of a high bodyweight/low food intake week, elegantly fitting the pattern.

This experiment showed that the activation temperature threshold of *A. dorrieni*, above which feeding takes place, is to be found between 4°C and 13°C. Casual observations showed that feeding resumes in around 50% of individuals at 8°C. Despite the fact that no feeding took place, most individuals were able to withstand a constant temperature of 4°C (i.e. below feeding threshold) for periods of around 1 month, but relatively few animals survived for more than two months. These results are not very different from those obtained for animals which were kept at 20°C and from which food was withheld (section 6.2.3). It is therefore likely that the deaths recorded at the low temperature regime are probably also mainly due to starvation. Individuals kept at lower temperatures might be expected to have lower metabolic rates than those at higher temperatures and thus survive longer without food. The fact that survival rates at the lower temperature regime were no better than those at the higher temperature, suggests that survival at low temperatures puts additional stress on *A. dorrieni*.

Gere (1956) notes changes in feeding rates in Diplopoda kept at a range of temperatures between 16.7 and 21.8°C (expressed as changes in the Van-der-Drift constant). In *A. dorrieni*, food intake, KQs and the assimilation rate of the food were not significantly different between 13°C and 20°C, despite the fact that Spicer and Taylor (1987) noted increases in the oxygen consumption (and thus the metabolic rate) of *A. dorrieni* between 10, 15 and 20°C. While they do not provide exact numerical values, the actual rise in oxygen consumption between 13°C and 20°C taken from their graph is no more than 1µl oxygen/mg dry body weight/hour. This rise may not be sufficiently high to result in a marked change in feeding rate. The optimal temperature at which feeding rates were highest were determined for a number of temperate saprophagous species by van der Drift (1951) and Dunger (1958). Those temperatures were 19°C for *Glomeris marginata* (which was later re-estimated by Gere (1956) as being 'some few grades above 20°C'), and 28°C for both *Armadillidium vulgare* and *P. scaber.* These temperatures, particularly those recorded for the Isopoda, are above those generally found in the animals' natural habitat. It is therefore likely that *A. dorrieni*, as a subtropical species, has optimal temperatures at least equal to or higher than those determined for the temperate species, which would almost certainly be higher than 20°C, and at which considerable changes in food intake and KQs would become apparent. Despite the fact that the temperature under leaf litter can reach surprisingly high levels in direct sunlight (Firbas, 1927), litter temperatures above 20°C are unlikely to occur for prolonged periods in Great Britain, so that estimates of ecological significance will be based here on observations below this value.

The amount of leaf tissue consumed as a percentage of bodyweight was calculated on the basis of leaf tissue dry weight and the values were calculated per week. In order to make comparison with other workers' results possible, the values had to be transformed. Van der Drift (1951) uses leaf tissue of 70% water content and daily values. The results obtained here were adjusted accordingly and the resulting mean percentage of leaf tissue consumed per day by *A. dorrieni* was 21.6% of live bodyweight. Van der Drift (op. cit.) reports mean values of 23% for *Julus scandinavius*, 34% for *C. silvarum* and 26% for *G. marginata* feeding on overwintered broad-leaved litter. These values are very similar to the one calculated here for *A. dorrieni*, indicating that it has similar feeding habits (as regards feeding rates) to a range of European millipedes. O'Hanlon & Bolger (1999) calculated the first comparable value for *A. dorrieni*, estimating that the landhopper consumes around 32 mg *P. contorta* litter per g live weight per day. This value can be adjusted to an estimated food intake of 3.2% bodyweight per day, while the value calculated from the data in this study is 7.6% Coniferous litter is generally more reluctantly accepted by the detritivorous fauna than broad-leaved litter. These data seem to confirm that tendency. However, the *P. contorta* plantation is reported to support a landhopper population independent of external food sources such as broad-leaved litter. It appears, therefore, that *A. dorrieni* is capable of surviving on a food intake of as little as 3.2% of its bodyweight per day. This may be due to the high C/N ratio of *P. contorta* leaf tissue as compared to many deciduous leaf tissues, including *B. pendula* (see section 6.1.3.1). Due to its larger proportion of carbohydrates, the *P. contorta* litter may be more nutritious than that of deciduous trees, thus allowing the animals to survive on a lower rate of food intake.

The assimilation rate of the food consumed (19.7%) was very similar to that calculated for *T. sylvaticus* (21.5%) (Clark, 1954). The assimilation rate was independent not only of temperature, but also of the bodylength (indicative to some degree of the age) of the animal. Many animal species show varying assimilation rates during the course of their lives, generally assimilating food more efficiently during their younger life stages. This may be due to changes in diet, even where these are not immediately apparent, as in *Mitopus morio* (Phalangida), where both adults and juveniles feed on similar prey, but the chelicerae of the younger individuals prevent them from taking in much of the cuticle and other indigestible parts, thus raising their assimilation rate (Phillipson, 1960).

The mean KQ calculated for *A. dorrieni* feeding on Birch leaf tissue, when converted to a value comparable to those used by Dunger (1958) was 17.8. Dunger (op. cit.) reported KQs of 62-40 for Diplopoda and 16-10 for Isopoda. His values were calculated respectively for leaf tissue that decomposes easily and corresponding material that is more resistant to decomposition. In order to determine these values, the experimental animals were kept at 18°C and were fed leaves which had been on the ground for some time (unfortunately not including *B. pendula*). The value calculated here fits in elegantly with Dunger's results, indicating that its role among the woodland decomposers is at least equal to that of the Isopoda.

In order to make comparisons with the Van-der-Drift constants calculated by some other authors, the mean wet weights of all specimens in the 13°C and 20°C were transformed into dry weights using the formula calculated in section 6.1.2. From these, the Van-der-Drift constants were calculated, and both the values calculated from the experimental data and those calculated by the other authors were adjusted to represent daily figures. The Van-der-Drift constant for *A. dorrieni* feeding on *B. pendula* leaf tissue between 13°C and 20°C was 0.4 with a standard deviation of 0.07. Van der Drift (1951) calculated a mean value of 0.77 for *Glomeris marginata* feeding on Oak litter at 18°C and a mean value of 0.23 for *Cylindrojulus silvarum* on Beech litter (no temperature specified). These comparatively modest results for the Diplopoda in relation to *A. dorrieni* as compared to Dunger's (1958) results may be due to the leaf tissue used in Van der Drift's experiments. Both Oak and Beech leaf tissue are known to be distasteful to litter-feeding invertebrates (Lyford, 1943) due to their high tannin content (Dunger, 1958; Lindquist, 1941). Additionally, the temperature in the *C. silvarum* experiment may have been lower than 18°C. Gere (1956) who found temperature-dependent differences in the Van-der-Drift constants of his specimens, which were fed on mixed deciduous litter, reports values of 0.24 and 0.25 for *Chromatojulus sp.* and *Protracheoniscus sp.* respectively, feeding at 21.8°C, and 0.27 for *G. marginata* feeding at 21.1°C. His constants for cooler temperature regimes are somewhat lower. Gere (op. cit.) explains his lower constants for *G. marginata* compared to those calculated by Van der Drift (1951) by the longer period his specimens had spent in captivity (up to 59 days) compared to Van der Drift (up to 5 days) and a resultant decrease in metabolism of the long-term captive animals. A similar phenomenon was observed for *A. dorrieni* in this study (section 6.4.3.2) The comparison of the Van-der-Drift constants calculated by Gere (1956) with the constants calculated from data collected in this study indicates that *A. dorrieni* consumes considerably more than representative species of the Diplopoda and the Isopoda at comparable temperatures. Overall, it appears clear that populations of *A. dorrieni* are likely to play a role in the comminution and decomposition of leaf litter no less important than that of many of the other macroinvertebrate decomposers.

The equations calculated from this experiment allow the creation of reliable estimates of the weights and, together with data from Chapter 3, overall biomass of *A. dorrieni* in a mixed deciduous woodland. In the case of the mixed deciduous woodland investigated here, this value attained a mean of 5.6 g m^{-2}, with a minimum of 3.4 g m^{-2} at the end of winter, and a maximum of 9.9 g m^{-2} at the end of summer. O'Hanlon & Bolger (1997) calculated some similar estimates for *A. dorrieni* populations in woodlands in Ireland, with the difference of using dry weights per m^{-2}. The adjusted values (using the equation calculated in section 6.1.2) were, for a plantation of *P. contorta* between 1.44 (at the end of winter) and 11.1 g m^{-2} (at the end of summer), and for a mixed woodland between 3.7 and 27.7 g m^{-2}. These values are not directly comparable to those calculated from data in this study, as O'Hanlon & Bolger (op. cit.) used animals whose gut had been cleared of all food before determining their dry weight. For example, their adjusted values for the *P. contorta* plantation are very similar to those calculated here for a deciduous woodland. It is known, however, that landhopper population density is considerably higher in the *P. contorta* plantation (O'Hanlon *et al.*, 1997) than in the deciduous woodlands examined here. Had the animals been weighed before emptying their guts, the adjusted biomass values also would have been significantly higher for the plantation than for the deciduous woodland. It is interesting, however, that the values estimated for the mixed woodland are considerably higher than those calculated for the mixed deciduous woodland investigated here, despite the fact that the values do not take the weight of the gut contents into account. This indicates that there are considerably higher population densities in the Irish study. Investigation of O'Hanlon & Bolger's previous work reveals that the population density at the mixed woodland site is indeed up to 17 times greater than at the site studied here (means of maximum density for 2 years of 8679 and 670 m^{-2}, respectively). The lower landhopper densities and lower biomass at the mixed deciduous site compared to the *P. contorta* plantation and the mixed woodland site may be due to the larger proportion of slowly decomposing litter material at the two last-mentioned sites, which results in a more continuous coverage of the forest floor, providing more microhabitat for the landhoppers to colonize and thus allowing more continuous, less patchy and ultimately denser populations to develop.

Estimates of total soil animal biomass in Oak-dominated woods of the mull soil type (as found at the location studied here) are 76.8 g m^{-2}, in similar Beech-dominated woods 70.8 g m^{-2} (Wallwork, 1970). The highest values for individual animal groups following the Lumbricidae were as follows (for Oak-dominated and Beech-dominated location, respectively): Gastropoda 5.3/4.9 g m^{-2}, Diplopoda 4.7/7.5 g m^{-2}, Diptera 3.1/1.5 g m^{-2}. The value for the 'other' crustacean group, the Isopoda, was 0.3/0.1 g m^{-2}. Fitted into this series of estimates, *A. dorrieni* accounts for around 7% of the total biomass, a value similar to that attained by the Gastropoda and Diplopoda, and considerably higher than that of the Isopoda. In order to be comparable to Petersen & Luxton's (1982) biomass estimates for temperate deciduous mull forests, the values calculated here have to be converted to mg dry weight m^{-2}, using the conversion equation in section 6.1.2, resulting in a mean value 2000 mg d wt m^{-2}. The total value given for the total biomass of the 'important soil fauna groups' in Petersen & Luxton (op. cit.) is 8000 mg d wt m^{-2}. Similar to the results above, the top three values following the worms (in this case the Lumbricidae, Enchytraeidae and Nematoda), are those of the Diplopoda (420 mg d wt m^{-2}), the Diptera (330 mg d wt m^{-2}) and the Gastropoda (270 mg d wt m^{-2}). No individual value for the Isopoda is mentioned. Fitted into this series of estimates, *A. dorrieni* could account for as much as 25% of the total biomass, attaining a value almost five times higher than that of the Diplopoda, and higher values still in comparison to the Diptera and Gastropoda. Petersen & Luxton (op. cit.) attempted to use a minimum of five independent biomass estimates to calculate each estimate given in their table, so the latter publication may contain more representative values than the former. Numerically, many of the results from Wallwork's (1970) study agree well with the findings in this study (see Chapter 3). No numerical data were available in Peterson & Luxton (1982). It can, however, be said with some certainty that in temperate deciduous woodlands where *A. dorrieni* has well established populations, it is likely to make up between 7% and 25% of the total biomass.

The equations calculated as a result of this experiment also allow reasonably reliable prediction of the amount of leaf tissue eaten by *A. dorrieni*, based on either bodylength or bodyweight. As will be shown later (section 6.3.4), the results may be slight underestimates, since animals able to choose their own food may come across leaf tissue more attractive than the *B. pendula* litter used here, and may also consume more as a result of a wider range of food choices available (section 6.4.4). In conjunction with the fact that the calculated estimates may be somewhat high due to temperature fluctuations during the year (as explained in section 6.1.3.14), the estimated values appear to represent actual conditions rather accurately. Here, the estimated amount of dry leaf tissue eaten per m^2 by the landhopper population in a mixed deciduous woodland averaged 127g m^{-2} per year.

Dunger (1958) reports a leaf litter production of 150g m^{-2} per year for a mixed deciduous woodland dominated by Ash and Oak at the edge of a wetland in Germany. This value initially appears very low compared to the mean value calculated for Angiosperm and Gymnosperm forests of the temperate zone of 350g m^{-2} (Bray & Gorham, 1964). This difference is explained, however, by the fact that Bray & Gorham (1964) used the entire litter production including that of the ground vegetation and woody tree litter, whereas Dunger (1958) refers to the tree leaf litter only. Hughes (1971) reports a mean tree leaf litter fall (including woody litter) of 277.5 g m^{-2} in an Alder/Birch woodland in the UK. A study of a mixed deciduous woodland in the UK very similar to the woodlands used in this study in both substrate and species composition was reported to have a total annual non-woody litter fall of 363 g m^{-2} (Sykes & Bunce, 1970). According to Hughes (1971), the amount of litter produced by the ground vegetation may make up 80-100% of the tree litter production, depending on the type of woodland, so that the estimate of 363 g m^{-2} does not quite represent the total litter available for decomposition. It appears that mixed deciduous forests with a comparatively wide variety of species such as those investigated here and by Sykes & Bunce (1970), and which include different species of Oak (*Quercus spp.*), some Ash (*F. excelsior*), Sycamore (*A. pseudoplatanus*) and Birch (*B. pendula*) in the canopy with Hazel (*C. avellana*), Hawthorn (*C. monogyna*) and Spindle (*E. europaeus*) dominating the shrub layer and Bramble (*R. fruticosus*) as well as a variety of low-growing ground-covering plants in the herb layer are among the most productive in Europe as regards non-woody litter production.

Assuming a non-woody litter production of at least 363 g m^{-2}, and more probably around 500 g m^{-2} taking the litter from the ground-covering plants into account, *A. dorrieni* may consume between 35% and 25% of the annual litter fall. Values calculated to date regarding proportion of litter fall ingested by landhoppers range from as little as 2.9% for *Mysticotalitrus tasmaniae* (Friend, 1975) to 25% for *A. sylvaticus* (Clark, 1954). These, and the other values calculated for landhopper populations summarized in Friend & Richardson (1986), correlate approximately with the densities of the landhoppers (Friend *et al.*, 1986). The one comparable value calculated for *A. dorrieni* is that of O'Hanlon & Bolger (1999), who estimate that the landhopper population at the *P. contorta* plantation they studied may consume as much as 25% of the annual litter production. The authors report this to be around 500g dry litter weight m^{-2} per year. Since the estimated daily leaf tissue intake of landhoppers feeding on *P. contorta* litter is less than half that of those feeding on deciduous tree litter, a population of more than twice the size of that in deciduous woodlands would be required to clear this very similar proportion of litter. Investigation of the densities calculated here (192-670 m^{-2}) and those calculated by O'Hanlon & Bolger (602-3969 m^{-2}) confirm that this is indeed the case.

A value of consumption of around 25% of the annual litter fall appears to be typical of established *A. dorrieni* populations and those of related species, and may well be representative of many of the woodlands around Britain in which *A. dorrieni* has been able to establish self-sustaining populations.

O'Hanlon & Bolger (1999) summarized several other studies into consumption of annual litter input by the invertebrate fauna and found that most authors estimate that the amount of litter processed by all forest floor detritivores together ranges between 20 and 30% of the annual litter fall, with the maximum value for any one animal group (e.g. Diplopoda and Isopoda) never reaching more than 16%. This maximum value was calculated for all developmental stages of all millipede species inhabiting a forest near Orleans (France). Dunger (1958) estimated that the Diplopoda and Isopoda together may consume around one-third of the annual litter fall and concluded that the amount processed by the entire macrofauna is likely to be somewhat higher than commonly estimated. The values calculated for *A. dorrieni*, both in this study and by O'Hanlon & Bolger (1999) indicate that an established landhopper population may, at least in some locations, consume as much of the annual litter fall as the entire native fauna combined. Furthermore, in woodlands where the landhopper is present, the estimates by other workers (which are based on native fauna only) are much too low and would have to be adjusted considerably to allow for the added influence of these aliens, particularly as, for the most part, most the native fauna does not appear to be significantly impaired by the presence of *A. dorrieni* (Chapter 4).

6.2 Survival of A. dorrieni at 20°C under food deprivation

6.2.1 Introduction

The earlier experiments showed that landhoppers can withstand considerable periods of time without feeding, as long as the ambient temperature remains low. The following experiment was designed to assess whether prolonged survival during periods of food deprivation is also possible at higher temperatures. During passive dispersal, many situations may place *A. dorrieni* in a position where suitable food is absent for periods of time. Ability to assess the landhopper's survival capacity under such circumstances would lead to a better understanding of its potential dispersal capabilites.

6.2.2 Methods

Five individual *A. dorrieni* of similar body length were housed singly in petri dishes as described above (section 6.1.2) but, instead of leaf tissue, only a similarly sized piece of filter paper (as used for lining the petri dish) was used. Feeding on filter paper was observed only rarely and production of faeces was practically nil. The ambient temperature was maintained at 20°C .

6.2.3 Results

The results are summarized in Table 6-9 (page 203). Animal 2 died after only 25 days. The cause of death could not be ascertained. Animal 5 died after 37 days as a result of getting trapped in a water droplet (see section 5.2.2). The remaining three animals all survived a minimum of two months without food, with a maximum survival time of four months. As little as ten days before its death, animal 3 was still observed moving about and jumping vigorously. Two to three weeks before their death, the animals which survived for more than two months began to show a somewhat paler than usual body colouration. The dry weights of the starved animals were significantly lower than predicted (using the equation calculated in 6.1.2) dry weights for non-starved animals of identical live weights (Wilcoxon Signed Ranks test: W=0, P=0.03). This indicated that the starved animals were using up significant proportions of their stored resources, without showing a change in their live weights. The dry weight of the animal that survived for four months was a mere 3.8% of the predicted dry weight of a well-fed individual.

Animal No.	1	2	3	4	5
Length (mm)	7	7	7	8	6
Weight day 1 (mg)	12.5	14	9.4	10.5	4.5
Last recorded live weight	12.2	14.4	9	11	6
Weight change (% original body weight)	-2.4	2.9	4.3	4.8	33
Dry weight (mg)	1.1	3.8	0.1	1.6	0.5
Predicted dry weight (mg) of non-starved animal	3.6	4.2	2.8	3.3	2.1
Survival (days)	**76**	**25**	**121**	**97**	**37**

Table 6-9 Weight change and length of survival and of *A. dorrieni* during food deprivation.

6.2.4 Discussion

Landhoppers show exceptional resilience to food deprivation, a fact which is undoubtedly helpful in their dispersal, since they can potentially survive prolonged transport without the presence of a suitable food source, as long as an adequate level of humidity is maintained. Clark (1954) showed that *T. sylvaticus* is capable of surviving for around three months without food in periods of low ambient humidity, during which it remained burrowed deep in the soil. This time period corresponds with the survival times observed here.

6.3 Palatability of leaf tissue of different origins and degrees of ageing to A. dorrieni

6.3.1 Introduction

Very little is known about food preferences in landhoppers, particularly with respect to preferences regarding the species of origin of the leaf tissue. Morton and Richardson (1984) showed that both *T. vulgaris* and *T. angulosus* are capable of showing distinct preferences for leaves of *Olearia argophylla* over *Eucalyptus obliqua.* No such data have as yet been collected for *A. dorrieni*, despite the fact that, as an invasive alien, its feeding habits are a topic of particular interest.

6.3.2 Methods

Experiments were designed closely resembling the feeding rate experiments above. Landhoppers were housed singly in small petri dishes and fed pieces of leaf tissue which were replaced on a weekly basis. Experiments were continued for five weeks. The plant species used to provide the leaf litter included: Beech (*F. sylvatica*), Pedunculate Oak (Q. *robur)*, Holm Oak (*Q. ilex*), Willow (*Salix sp.*), Rhododendron (*R. ponticum*), Fern (*Dryopteris sp.*), Bamboo (*Sasa sp.*), Geranium (*Geranium sp.*), and Elephant's Ears (*Bergenia sp.*). The deciduous tree species were chosen due to their ubiquitous presence in habitats where landhoppers are plentiful. Rhododendron was chosen because there have been reports of landhopper populations of particularly high densities located in woodlands dominated by a

Rhododendron shrub layer (O'Hanlon *et al.*, 1993). A representative bamboo species was chosen because many bamboos are very successful invasive alien species which are becoming naturalized in many places around Great Britain and provide potentially suitable landhopper habitat among their dense thickets of shoots and rhizomes where humidity remains high, temperature is moderated and their own leaf litter is plentiful. Finally, Fern, *Geranium* and *Bergenia* were chosed because they are common ground covering plants which provide shelter and produce certain amounts of leaf litter which is utilized by litter-dwelling invertebrates such as *A. dorrieni,* in woodlands and parks and gardens, respectively.

For the first series of experiments, all leaf tissue was dead at the time of collection. Where possible, leaf tissue was not collected before it had been on the ground for 12 weeks (to maximize similarity to the previous experiment). With non-deciduous species, only fallen leaves were collected that were clearly brown and where decay was starting to set in, but had not progressed to a stage where manipulation was impossible. As above, the leaf tissue was dried, weighed and offered to the individual landhoppers after rehydration. Once again, control dishes containing only leaf pieces and no landhoppers were set up. Similar to the results obtained in the experiment using birch leaf tissue (section 6.1.3.1), the weight change in the control leaves was very variable both within and between leaf samples and did not allow the calculation of reliable correction factors. The physical properties of the leaves, which would intuitively suggest differences in potential weight loss (tougher types being perhaps less prone to weight loss), appeared to have no effect on the variability of weight loss. There were high and low values of weight loss both among the tough and the soft leaf types. Unfortunately, the C/N ratios of the leaf tissues could not be determined and therefore, Dunger's theory on variable weight loss of leaf tissue (see section 6.1.3.1) could not be tested further. In order to maximize the accuracy of representation of the observed results, the comparison of food intake under the different feeding regimes was based largely on the production of faeces rather than the weight of leaf tissue lost over the course of each week.

In a second series of experiments, the landhopper's ability and readiness to feed on fresh leaf tissue was tested by providing them with a selection of fresh leaves from the same tree species used in the first series, namely Beech, Oak, and Holm Oak. The amount of leaf tissue eaten was calculated by ascertaining the water content of the leaf the experimental piece was cut from and deducting the proportion of water content from the experimental piece at the end of the week. The difference was deemed the portion consumed by the landhopper or lost to other factors such as leaching or bacterial digestion. The mean water contents of the fresh leaves are summarized in Table 6-10 (below). As above, the amount of leaf tissue consumed was based on production of faeces wherever possible.

Leaf type	Beech fresh	Oak fresh	Holm Oak fresh
Mean water content	63%	60%	39%

Table 6-10 Mean water contents of fresh leaves used for feeding experiments.

6.3.3 Results

The results from the feeding experiments are summarized in Table 6-13 to Table 6-18 (pages 217-222). The aspects subsequently under particular investigation include the weight gains of the individual animals over the period of the experiments, the mean amounts of leaf tissue eaten per individual per week [expressed as faeces as proportion of bodyweight, for the reasons explained previously (section 6.3.2)], the assimilation rates of the ingested leaf tissue, the Konsumquotienten, and the possible relationship between the calorific content of the leaf tissue and consumption rates.

6.3.3.1 *Individual weight gain*

The Kruskal-Wallis chi-square test for differences in weight change of individuals (expressed as proportion of initial bodyweight) during the course of the experiment did not reveal significant differences in the different feeding regimes (χ^2=17.405, P=0.096). The difference was even less significant where only those data were compared where dead leaf tissue was used (χ^2=6.434, P=0.599), indicating that much of the variation stems from the data from the fresh leaf tissue experiments. When fed on fresh leaf tissue, three quarters of the experimental animals lost weight (a mean of 0.61%) during the experimental period. The weight changes in the animals fed on fresh leaf tissue were not significantly different from each other (χ^2=2.192, P=0.334). It is interesting to find such comparatively remarkable weight loss, since in earlier experiments the body weight of the experimental animals tended to increase, even where food intake was minimal or absent (section 6.1.3.2 and 6.2.3).

6.3.3.2 *Variations in food intake – dead leaf tissue*

The Kruskal-Wallis chi-square test for variation in food intake (expressed as mean faeces produced as a proportion of mean bodyweight) under the different feeding regimes, and including results from the Birch feeding experiment at 20°C, returned a highly result significant result (χ^2=30.399, P<0.001). By excluding certain treatments, it could be shown that the data may be grouped into two main clusters, within which there are no significant differences. All but two of the treatments belonged to one of the clusters. The first cluster is made up of Holm Oak, Rhododendron and Bamboo, all of which were eaten only very reluctantly (χ^2=2.923, P=0.232). The second cluster encompasses Beech, Oak, Willow, Birch and Fern, which were all eaten to similar degrees (χ^2=5.592, P=0.232). Bergenia was eaten to a significantly larger degree than the plants in cluster 1, but to a significantly lesser degree than those in cluster 2 (χ^2=10.147, P=0.017; χ^2=13.138, P=0.022, respectively). Geranium was eaten to a significantly greater extent than all the other leaf tissues, with a significant difference setting it off from cluster 2 (χ^2=11.126, P=0.049). The varying levels of food intake are illustrated in Figure 73 (page 210).

6.3.3.3 Variations in food intake – fresh leaf tissue

The amount of fresh leaf tissue eaten (expressed as % mean faeces as proportion of mean bodyweight) differed significantly, albeit not strongly, between species of origin of the leaf tissue, with Oak being the most favoured species (χ^2=6.038, P<0.049). Overall, feeding rates on fresh leaf tissue were low, and only marginally higher than those of cluster 1 calculated previously. While both fresh Beech and Oak were eaten in considerably lesser quantities than fallen leaves of the same type, consumption of Holm Oak was greater in its fresh state. The levels of food intake are summarized in Figure 73 (below).

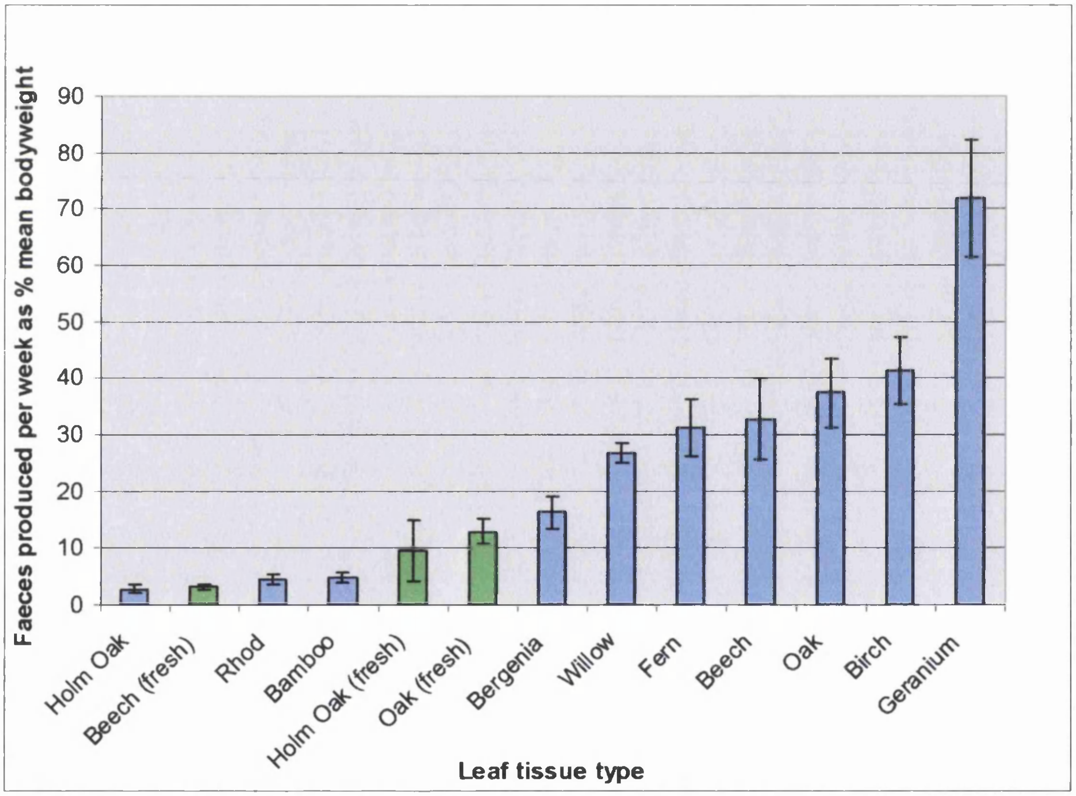


Figure 73 Food intake of *A. dorrieni* feeding at 20°C on leaf tissue of different origins and degrees of ageing (mean +/- SE, N=4 for each leaf tissue type).

6.3.3.4 Assimilation rates

Assimilation rates could not be reliably calculated for the live plant tissue experiments and the dead tissue plant species making up cluster one, due to the minute quantities of litter consumed and faeces produced. For all other leaf tissue types, initially Kruskal-Wallis chi-square tests were performed to ascertain that there are no significant differences in absorption rates within leaf species influenced by the bodylength of the experimental animals. The results are summarized in Table 6-11 (below).

Beech	**Oak**	**Fern**	**Willow**	***Bergenia***	**Geranium**
χ^2=3, P=0.392	χ^2=2.4, P=0.121	χ^2=1.8, P=0.18	χ^2=3, P=0.392	χ^2=0.2, P=0.655	χ^2=0.2, P=0.655

Table 6-11 Results of Kruskal-Wallis chi-square tests for differences in assimilation rates of animals of different bodylength feeding on identical substrates.

Where all six leaf tissue types from this experiment and the results from the Birch feeding experiment (20°C) were compared, significant differences became evident (χ^2=24.442, P<0.001). On exclusion of the birch data, the assimilation rates of which was notably lower than the other leaf tissue types, the difference was still significant, albeit less so (χ^2=11.770, P=0.038). Oak and Willow appeared to have significantly higher assimilation rates than the remaining leaf tissue types. When analysed together, it could be shown that there was indeed no significant difference between the assimilation rates of Oak and Willow (χ^2=0.083, P=0.773), and the remaining four leaf types

Beech, Fern, Bergenia and Geranium (χ^2=2.801, P=0.423). The various mean assimilation rates are illustrated in Figure 74 below.

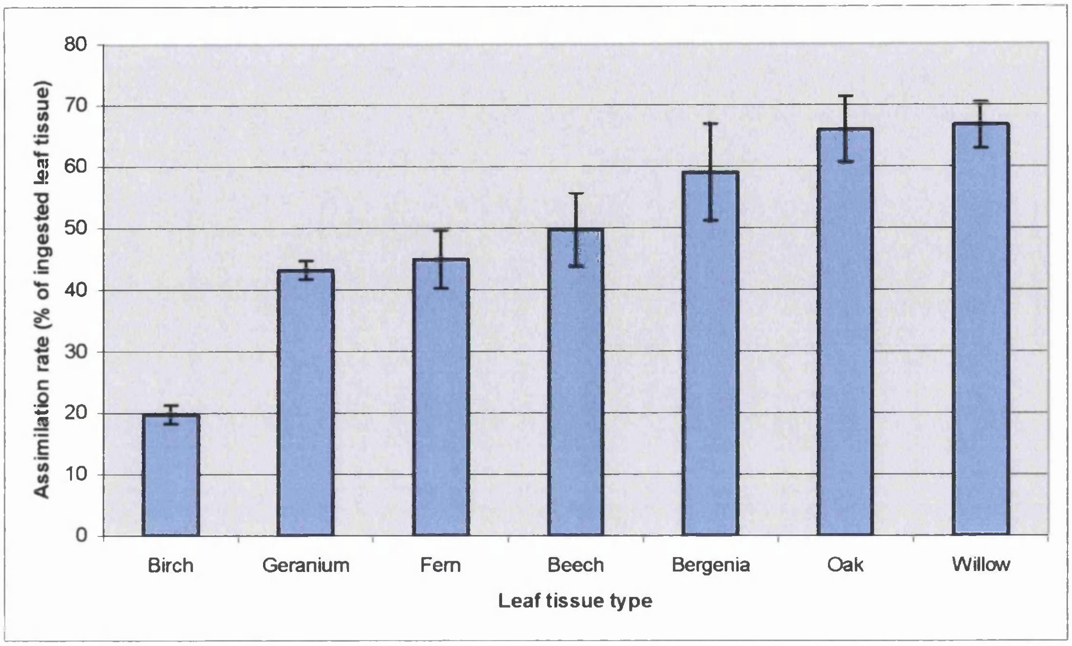


Figure 74 Assimilation rates of *A. dorrieni* feeding on different leaf tissue types (mean +/- SE, n=4 for each leaf tissue type).

The assimilation rates are lower in those types of leaf tissue that were consumed in greater amounts than those that were eaten more reluctantly. Similar results were recorded in *A. vulgare* (Hubbell, 1971; Rushton & Hassall, 1983) The authors showed that *A. vulgare* can increase absorption efficiency by lengthening gut retention time when food is in short supply. It is possible that *A. dorrieni*, when placed under similar conditions, (as above by being offered not small amounts, but instead unfavoured food material only) is also able to utilize to food material taken in more efficiently than where a supply of a favoured food is plentiful.

When assessing assimilation rates in general, it has to be borne in mind that some variation will be due to the weight loss of the leaf tissue due to factors other than the activity of the landhopper. Furthermore, the smaller the amount of leaf tissue consumed and faeces produced, the less accurate the estimation of the assimilation rate will be, so that assimilation rates for more readily consumed leaf tissue types are more reliable than those for less favoured ones.

6.3.3.5 *Konsumquotienten*

The mean KQs calculated for each leaf tissue type are summarized in Figure 75 (page 214). The order of leaf tissue types are identical to those used in Figure 73 (page 210) to allow direct comparison. The feeding data illustrated in Figure 73 are based on production of faeces, which makes it somewhat more reliable than the data on which the KQs calculated below are based (leaf tissue eaten, a value which is subject to some variation, particularly where only small quantities were consumed, see section 6.3.2). Despite this source of inaccuracy, the KQs calculated agree largely with the findings of the quantities of food intake based on the production of faeces. The comparatively high KQs calculated for Holm Oak and Rhododendron (in comparison with actual food intake) are probably due to calculation error as described above rather than being of actual validity as a result of the KQ correcting for differences in bodyweight of experimental animals.

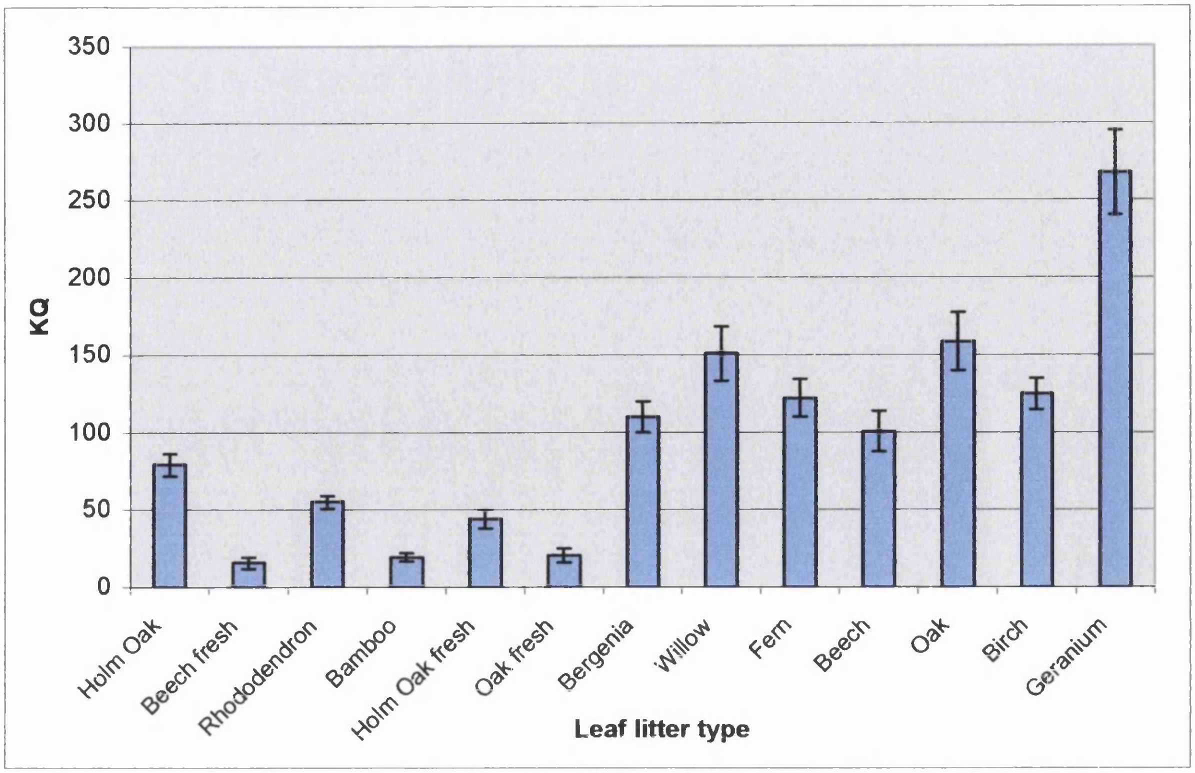


Figure 75 **Konsumquotienten for *A. dorrieni* feeding on different leaf tissue types (mean +/- SE, n=4 for each leaf tissue type).**

6.3.3.6 *Calorific content of the leaf tissue and its effect on feeding rate*

The calorific value of the leaves was determined using a ballistic bomb calorimeter (Gallenkamp CB-370 - Fisons Instruments, Loughborough, UK) Three samples were combusted as per instruction manual for each leaf type. A previous study which determined the calorific value of freshly fallen *B. pendula* leaves reported a value of 5.2 kcal/g dry weight (Hughes, 1971). Since microbial growth on the leaves during their period on the ground is expected to add somewhat to their calorific content, the results obtained here are very accurate. The mean calorific value of each leaf species are illustrated in Table 6-12 (page 215).

Leaf type	Mean calorific value (kcal/g dry weight)
Birch	5.5
Oak	5.1
Oak (fresh)	7.8
Beech	7.2
Beech (fresh)	7.2
Willow	7.7
Holm Oak	7.0
Holm Oak (fresh)	6.2
Rhododendron	6.4
Fern	9.5
Bamboo	3.1
Elephant's ears	7.2
Geranium	7.9

Table 6-12 Mean calorific values of different leaf tissue types.

Intakes of the various types of leaf tissue (again in the order used in Figure 73 and Figure 75) were correlated with the calorific value of the relevant leaf tissue types using Spearman's rank-order correlation. There was no significant correlation between the calorific content of the leaf tissue and its rate of consumption by *A. dorrieni* (r_s=0.204, P=0.503). This indicates that factors other than calorific content of the leaf tissue determine the landhopper's feeding rate, either because not all the calorific value recorded by bomb calorimetry is accessible to the animal or due to other factors affecting the palatability of the leaf tissue in question, such as, for example, tannin content.

Interestingly, freshness of leaf tissue apparently has no effect its calorific content, with fresh Oak containing a lower, fresh Beech an equal and fresh Holm Oak a higher level of calories than the respective dead leaf tissue.

20C	Leaf type	Length (mm)	Live weight start (mg)	Live weight end (mg)	Increase in live weight of animal (mg)	Increase in live weight of animal (% of original BW)	Mean weight (mg)	Mean weight of leaf eaten per week (mg)	Amount of leaf eaten per week as % mean BW	Mean weight of faeces produced per week (mg)	Faeces produced per week as % mean BW	Assimilation rate of leaf tissue (%)	Konsumquotient (*KQ*)
Animal no.													
1B	Beech old	5	4.8	6.5	1.7	35.4	5.4	3.6	66.0	2.4	43.5	67	116.3
2B	Beech old	6	3.9	6.2	2.3	59.0	4.6	3.5	75.0	2.1	45.9	41	125.1
3B	Beech old	9	12.2	14.5	2.3	18.9	12.6	3.6	28.0	2.0	16.3	48	65.8
4B	Beech old	10	19.4	17.1	-2.3	-8.3	17.1	6.4	37.0	4.3	25.1	43	95.8
1O	Oak old	5	4.5	4.4	-0.1	-2.2	4.0	3.9	97.0	1.2	29.5	82	153.2
2O	Oak old	5	4.0	5.5	1.5	37.5	4.7	5.9	126.0	2.6	55.7	64	210.3
3O	Oak old	7	8.3	11.0	2.7	32.5	10.0	6.9	68.8	3.0	30.0	59	148.7
4O	Oak old	7	6.2	8.1	1.9	30.6	7.3	4.6	63.2	2.5	34.1	59	122.2

Table 6-13 Weight gain, assimilation rates and Konsumquotienten of *A. dorrieni* feeding on Beech and Oak litter.

20C	Leaf type	Length (mm)	Live weight start (mg)	Live weight end (mg)	Increase in live weight of animal (mg)	Increase in live weight of animal (% of original BW)	Mean weight (mg)	Mean weight of leaf eaten per week (mg)	Amount of leaf eaten per week as % mean BW	Mean weight of faeces produced per week (mg)	Faeces produced per week as % mean BW	Assimi-lation rate of leaf tissue (%)	Konsum-quotient (KQ)
Animal no.													
1H	Holm Oak old	6	7.1	6.3	-0.8	-11.3	6.7	2.8	41.9	0.08	1.2	n/a	78.8
2H	Holm Oak old	6	6.6	9.8	3.2	48.5	8.6	3.6	41.8	0.42	4.8	n/a	85.8
3H	Holm Oak old	6	7.0	7.7	0.7	10.0	6.4	3.2	50.4	0.18	2.3	n/a	92.8
4H	Holm Oak old	8	15.6	17.2	1.6	10.3	15.0	3.6	26.8	0.44	2.9	n/a	59.2
1W	Willow old	4	1.8	3.9	2.9	116.7	2.5	3.3	132.9	0.72	29.0	73	179.0
2W	Willow old	5	3.5	3.1	-0.4	-11.4	4.9	5.1	104.5	1.5	30.5	67	176.8
3W	Willow old	6	6.9	9.9	3.0	43.5	9.7	6.5	67.8	2.4	25.1	71	142.9
4W	Willow old	7	10	7.6	0.2	24	10.5	5	47.6	2.4	22.5	56	104.3

Table 6-14 Weight gain, assimilation rates and Konsumquotienten of *A. dorrieni* feeding on Holm Oak and Willow litter.

20C	Leaf type	Length (mm)	Live weight start (mg)	Live weight end (mg)	Increase in live weight of animal (mg)	Increase in live weight of animal (% of original BW)	Mean weight (mg)	Mean weight of leaf eaten per week (mg)	Amount of leaf eaten per week as % mean BW	Mean weight of faeces produced per week (mg)	Faeces produced per week as % mean BW	Assimilation rate of leaf tissue (%)	Konsum-quotient (KQ)
Animal no.													
1R	Rhododendron	7	7.6	10.4	2.8	36.8	10.1	2.8	27.5	0.44	4.4	n/a	59.9
2R	Rhododendron	6	9.9	11.7	1.8	18.2	11.0	2.7	24.9	0.46	4.2	n/a	54.6
3R	Rhododendron	5	3.1	5.9	2.8	90.3	5.8	2.0	34.1	0.14	2.4	n/a	62.0
4R	Rhododendron	13	50.2	51.7	1.5	3.0	51.9	6.1	11.8	3.66	7.0	n/a	43.8
1be	Bergenia	7	7.7	8.6	0.9	11.7	7.5	4.1	54.5	1.7	22.6	39	107.0
2be	Bergenia	9	17.0	19.1	2.1	12.4	17.6	5.6	31.2	2.2	12.1	56	82.8
3be	Bergenia	7	11.7	11.9	0.2	1.7	11.2	6.1	54.8	1.2	11.1	77	121.9
4be	Bergenia	7	8.6	11.5	2.9	33.7	10.9	6.3	57.7	2.1	19.1	65	128.2

Table 6-15 Weight gain, assimilation rates and Konsumquotienten of *A. dorrieni* feeding on Rhododendron and Bergenia litter.

20C	Leaf type	Length (mm)	Live weight start (mg)	Live weight end (mg)	Increase in live weight of animal (mg)	Increase in live weight of animal (% of original BW)	Mean weight (mg)	Mean weight of leaf eaten per week (mg)	Amount of leaf eaten per week as % mean BW	Mean weight of faeces produced per week (mg)	Faeces produced per week as % mean BW	Assimilation rate of leaf tissue (%)	Konsumquotient (*KQ*)
Animal no.													
1G	Geranium	9	20.8	21.7	0.9	4.3	20.3	16.3	80.2	8.4	41.2	42.9	219.0
2G	Geranium	8	11.0	15.2	4.2	38.2	11.4	15.6	136.3	10.3	89.7	39.7	308.0
3G	Geranium	8	13.7	16.3	2.6	19.0	16.2	14.2	113.1	8.3	58.8	43.3	221.8
4G	Geranium	8	13.9	20.7	6.8	49.0	17.0	21.3	124.6	12.5	73.5	47	322.2
1F	Fern	7	6.2	7.7	1.5	24.2	8.2	6.3	76.9	3.8	45.8	40.5	154.9
2F	Fern	9	22.0	17.0	-5.0	-21.3	20.0	7.2	36.2	5.1	25.4	34.1	97.7
3F	Fern	7	11.5	11.7	0.2	1.7	11.1	6.2	55.5	3.2	29.1	54.4	124.6
4F	Fern	7	11.4	8.6	-2.8	-24.6	12.7	6.1	47.9	3.1	24.3	50.8	112.1

Table 6-16 Weight gain, assimilation rates and Konsumquotienten of *A. dorrieni* feeding on Geranium and Fern litter.

20C	Leaf type	Length (mm)	Live weight start (mg)	Live weight end (mg)	Increase in live weight of animal (mg)	Increase in live weight of animal (% of original BW)	Mean weight (mg)	Mean weight of leaf eaten per week (mg)	Amount of leaf eaten per week as % mean BW	Mean weight of faeces produced per week (mg)	Faeces produced per week as % mean BW	Assimilation rate of leaf tissue (%)	Konsum-quotient (*KQ*)
Animal no.													
1Bb	Bamboo	7	11.7	8.5	-3.2	-1.8	11.1	0.8	6.8	0.36	3.2	n/a	16.1
2Bb	Bamboo	5	5.3	9.2	3.9	73.6	6.9	1	14.7	0.2	3	n/a	27.6
3Bb	Bamboo	7	9.2	10.8	1.6	17.4	9	0.7	8	0.58	6.4	n/a	16.2
4Bb	Bamboo	5	6.8	7.1	0.3	4.4	5.8	0.6	10.4	0.38	6.6	n/a	18.6
1Bfr	Beech fresh	13	17	15.1	-1.9	-11.2	14.9	0.65	4.4	0.3	2	n/a	9.9
2Bfr	Beech fresh	10	8.7	9.2	0.5	5.8	8.4	0.83	9.9	0.24	2.9	n/a	20.1
3Bfr	Beech fresh	12	11.6	7.6	-4	-34.9	7.4	0.36	4.9	0.32	4.3	n/a	9.5
4Bfr	Beech fresh	10	3.8	4.2	0.4	10.6	3.4	0.54	16	0.12	3.6	n/a	23.9

Table 6-17 Weight gain, assimilation rates and Konsumquotienten of *A. dorrieni* feeding on Bamboo litter and fresh Beech.

20C	Leaf type	Length (mm)	Live weight start (mg)	Live weight end (mg)	Increase in live weight of animal (mg)	Increase in live weight of animal (% of original BW)	Mean weight (mg)	Mean weight of leaf eaten per week (mg)	Amount of leaf eaten per week as % mean BW	Mean weight of faeces produced per week (mg)	Faeces produced per week as % mean BW	Assimi-lation rate of leaf tissue (%)	Konsum-quotient (*KQ*)
Animal no.													
1Ofr	Oak fresh	8	11.8	8.8	-3	-25.4	10.4	0.74	7.1	1.7	16.1	n/a	15.5
2Ofr	Oak fresh	7	8.7	6.4	-2.3	-26.4	8.9	0.44	4.9	1	11.4	n/a	10.2
3Ofr	Oak fresh	7	7.5	6.5	-1	-13.3	8.9	1.07	12	1.5	16.6	n/a	24.9
4Ofr	Oak fresh	8	12.3	12.2	-0.1	-0.8	12.4	1.67	13.5	0.9	7.6	n/a	31.2
1Hofr	Holm Oak fresh	10	24.8	24.3	-0.5	-2	22.6	3.45	15.3	1.1	4.9	n/a	43.2
2Hofr	Holm Oak fresh	7	16	21.7	5.7	35.6	19.3	2.94	15.3	1.1	5.7	n/a	40.9
3Hofr	Holm Oak fresh	7	27.5	27.2	-0.3	-1.1	26.1	2.77	10.6	0.64	2.4	n/a	31.5
4Hofr	Holm Oak fresh	5	17.5	16.7	-0.8	-5.6	16	3.92	24.6	3.98	25	n/a	61.0

Table 6-18 Weight gain, assimilation rates and Konsumquotienten of *A. dorrieni* feeding on fresh Oak and fresh Holm Oak.

6.3.4 Discussion

This series of experiments once again demonstrated that maintenance of the landhopper's bodyweight is largely independent of the quantity or quality of food taken in (see also sections 6.1.3.2 and 6.2). It could be further shown that feeding rates vary significantly depending on the type of leaf tissue provided. Tough leaves such as those of Holm Oak, Rhododendron and Bamboo were only taken reluctantly. A similar reluctance to feed on tough *Eucalyptus obliqua* leaves, with considerably higher feeding rates on softer *Olearia argophylla* leaves, was reported for two *Talitrus* species (Morton *et al.*, 1984). Somewhat softer leaves of deciduous trees and ferns were fed on more readily. *Cerrorchestia hyloraina*, too, was reported to avoid tough leaves and those with thick waxy cuticles (Lindeman, 1991).

Interestingly, there were no significant differences between Beech or Oak leaf tissue, which are generally considered distasteful to litter-feeding invertebrates (see section 6.1.4), and other, comparatively tannin-poor (Zimmer *et al.*, 2000), leaf tissue types. Leaf litter of perennial geraniums elicited the highest feeding rates, which were significantly higher than those for the bulk of the other leaf tissue types offered. Fresh leaf tissue was only reluctantly eaten, to similarly low extents as the tough leaf tissue of Holm Oak, Rhododendron and Bamboo. It may be of note that a large proportion of the animals fed on fresh leaf tissue lost weight over the study period, whereas animals on most of the other feeding regimes, even those that were starved, maintained or even increased their initial bodyweight.

Assimilation rates for the ingested food material are similarly variable in *A. dorrieni* as they are in woodlice. In the latter assimilation rates as high as 70% and as low as 10% have been reported (Sutton, 1980). As explained in section 6.3.3.4, it is possible that *A. dorrieni* possesses an ability similar to that of some Isopoda, whereby it is able to utilize food more efficiently when favourable food is in short supply.

Van der Drift (1951) conducted feeding experiments on Beech and Oak litter (of the F0 layer of his mor-type woodland) at a temperature of 19°C with *Julus scandinavius* and *C. silvarum* as experimental subjects. He reported his data as daily litter consumption in percent live bodyweight, and calculated means of 8% for both Beech and Oak for *J. scandinavius* and 12% and 7% respectively for *C. silvarum.* The mean values for *A. dorrieni* calculated here are very similar: 12.7% for Beech and 7.4% for Oak. Calculations of the KQ of Van der Drift's specimens, which will not be entirely accurate since he provides only mean values, result in values of 9.4 for both Beech and Oak for *J. scandinavius* and 14.1 and 8.2 for *C. silvarum.* Equivalent values for *A. dorrieni* are 14.4 for Beech and 22.7 for Oak. Since the KQ represents a measure for the amount of nutrition required by a certain species feeding on a certain food (Dunger, 1958), it appears that *A. dorrieni* has relatively higher overall food requirements than the millipede species studied by Van der Drift.

Dunger (1958) calculated KQs for a number of Diplopoda and Isopoda feeding at 18°C on Beech or Oak, and, in the case of Oak, used both fresh and overwintered leaf litter. The leaf litter used in this study may be considered an intermediate of these two states, and feeding rates are therefore also likely to be intermediates between the two states. Dunger's (1958) KQ results for overwintered Beech range between 21 and 48.1 for the Diplopoda and 7.8 to 11.2 for the Isopoda. These values are similar to those calculated here, and once again (see section 6.1.4) place *A. dorrieni* below the Diplopoda and above the Isopoda in terms of its nutritional requirements. Dunger's (1958) values for freshly fallen Oak are very low for both Diplopoda and Isopoda, ranging between 1.6 and 3.8. The values for overwintered Oak are considerably higher, namely 18.8 to 46.9 for the Diplopoda and 6.0 to 10.0 for the Isopoda. As before, the value for *A. dorrieni* was higher than that of the Isopoda, and this time even surpassed the minimum recorded value from the Diplopoda.

Many factors are capable of influencing the palatability of a certain type of leaf litter, and ultimately the feeding rate of the detritivorous macro-arthropod upon that litter. Among these factors are the litter's C/N ratio (Dunger, 1958), the concentration of tannins (Lindquist, 1941) and phenolics (Cameron & LaPoint, 1978), the physical strength of the leaf tissue (Zimmer *et al.*, 2000) and a range of other possible factors (Dickinson & Pugh, 1974). Here, the calorific value of different leaf tissues was determined and it could be shown that the preference of *A. dorrieni* for certain leaf tissue types is not influenced by their calorific value, but rather by one or more of the factors mentioned above.

6.4 Direct preference for one leaf type over another

6.4.1 Introduction

A. dorrieni has been shown to take in similar amounts of Oak and Birch leaf tissue when fed exclusively on either leaf tissue type, both when expressed through the amount of faeces produced and through KQs. The assimilation rate of Oak leaf tissue was significantly higher than that of Birch leaf tissue. Oak leaf litter is generally only very reluctantly attacked by the detritivorous macrofauna (Dunger, 1958; Wittich, 1943) due to its high content of tannins (Rushton *et al.*, 1983), lignins and considerable physical strength (Zimmer *et al.*, 2000). All these values are significantly lower in Birch leaf tissue (op. cit.). In this experiment, both animals that had been fed exclusively on Birch litter and freshly caught individuals were given a direct choice of Birch and Oak leaf tissue. The aspects under particular investigation were, whether:

1. one leaf tissue type was preferentially eaten;

2. food intake, KQs and assimilation rates differed between the long-term captive and freshly caught animals; and

3. the overall food consumption , KQs and assimilation rates change when an additional leaf tissue type is offered after fifteen weeks of an exclusive diet of one leaf tissue type.

6.4.2 Methods

In this series of experiments, twelve animals that had been fed on a diet of Birch leaf tissue for 15 weeks (five individuals of the 20°C group and seven individuals of the 13°C group) as well as eight freshly caught animals were given a choice between Birch and Oak leaf tissue of similar degrees of ageing. All twenty animals were maintained at 20°C and the experiment was continued for 6 weeks. Care was taken to supply enough leaf tissue of each type to prevent depletion of either type during the course of the week, which could have resulted in misleading results.

6.4.3 Results

The numerical results are summarized in Table 6-19 (page 230) and Table 6-20 (page 231).

6.4.3.1 Preference for Birch or Oak leaf tissue

Mann-Whitney U tests were conducted for the amounts of Birch and Oak leaf tissue consumed weekly by each animal over the study period. The results are incorporated in the results tables. All of the long-term captive animals ate more Birch leaf tissue than Oak leaf tissue. This difference was clearly significant in three of the twelve cases, and only marginally failed to reach significance (P=0.056) in a further four cases. The results were somewhat less distinct among the recently caught group. Five of the eight animals consumed more Birch leaf tissue, a difference which was clearly significant in three cases, and only marginally insignificant (P=0.056) in the fourth case. Of the remaining three animals (which ate more Oak than Birch leaf tissue) one showed a statistically significant difference between the leaf types. Overall, seventeen out of the twenty animals ate more Birch than Oak leaf tissue, with significant differences in the amounts eaten in six cases, and only marginally insignificant results in a further five. It may therefore be concluded that *A. dorrieni* does show a preference for Birch over Oak leaf tissue, but at the same time regularly consumes considerable quantities of Oak leaf tissue as well, despite Birch material being present.

6.4.3.2 *Food intake, KQs Bodyweight change and Assimilation rates of long-term captive and freshly caught animals*

Mann-Whitney U tests were used to test for differences between the food intakes (expressed as % faeces based on mean bodyweight), the KQs, bodyweight changes and the assimilation rates of long-term captive and freshly caught animals. Both the food intakes and the KQs of the freshly caught animals were significantly higher than those of the long-term captives (U=2, P<0.001 and U=1, P<0.001, respectively). There were no significant difference in the changes in bodyweight in the two groups of individuals (U=33, P=0.27), or in their food assimilation rates (U=47.5, P=0.970).

6.4.3.3 *Changes in Food intakes, KQs and Assimilation rates after simultaneous exposure to two leaf tissue types of animals which had been restricted to feeding on one leaf tissue type for 15 weeks*

Wilcoxon Signed Ranks tests were used to identify changes in food intake, KQ and assimilation rates during the two different feeding regimes. Food intake (again expressed as % faeces based on mean bodyweight) did not change significantly between the two regimes (W=5, P=0.875). The KQs, however, were significantly greater during the two-leaf-tissue-type regime (W=3, P=0.019). The fact that food intake did not significantly increase, while the KQs did, can be explained by the fact that all but one (a very large and possibly senescent individual) of the animals were significantly heavier at the time of the second experiment than at the time of the first (W=1, P=0.006).

Larger animals consume considerably less food in relation to their bodyweight than smaller ones (Dunger, 1958; van der Drift, 1951). Therefore, the fact that there was no significant difference in their food intake (expressed as % faeces based on bodyweight) actually indicates an increase in their food intake between experiments. The KQ corrects for differences in bodyweight of individual animals and is therefore sensitive to the actual increase in feeding which took place in experiment two (employing two leaf tissue types). In addition to the KQs, the assimilation rates were significantly higher during the latter regime (W=4, P=0.028). This may be explained by the higher assimilation rate of the Oak leaf tissue consumed compared to the assimilation rate for Birch leaf tissue (calculated in section 6.3.3.4). The mean assimilation rate for Birch leaf tissue fed alone was 19.30%, that for Oak alone 66.04%, and the mean assimilation rate where both leaf tissue types were offered was 32.67%.

Animal no.	Length (mm)	Live weight start (mg)	Live weight end (mg)	Increase in live weight of animal (% of original BW)	Mean weight (mg)	Mean weight of birch leaf eaten per week	Birch leaf eaten as % mean BW	Mean weight of oak leaf eaten per week	Oak leaf eaten as % mean BW	Total mean weight of leaf tissue eaten per week (mg)	Total amount of leaf eaten per week as % mean BW	Mean weight of faeces pro-duced per week (mg)	Faeces produced per week as % mean BW	Assimi-lation rate of leaf tissue (%)	Mann-Whitney U test results for difference in amount of Oak/Birch eaten	Konsum-quotient (*KQ*)
20-3	6	8.6	14	62.8	11.8	5.5	46.4	1	8.7	6.5	55.1	5.3	44.9	20	0.008**	125.4
20-1	8	12.1	16.7	38	13.4	7	51.9	2.9	21.6	9.9	73.6	4.3	32.4	56	0.548	175.5
20-8	15	41	42.8	4.4	39.2	7	17.9	4.5	11.6	11.6	29.5	9.8	24.9	16	0.016**	100.5
20-5	11	24.8	28.3	14.1	21.1	11.2	52.9	7	33	18.1	85.9	11.6	54.8	36	0.095	237.0
20-6	7	15.3	19.3	26.1	14.8	11	74.1	6.3	42.6	17.3	116.8	7.1	48	59	0.056*	287.0
13-6	9	24	33.8	40.8	32.5	8.7	26.8	4.9	15	13.6	41.8	8.8	27.2	35	0.151	133.5
13-2	7	12.1	15.8	30.6	11.4	3.9	34.1	2.1	18.3	6	52.4	3.7	32.5	38	0.31	118.5
13-5	12	26	35	34.6	32.1	10.5	32.8	7.3	22.6	17.8	55.4	13.6	42.5	23	0.095	176.2
13-8	8	19.8	23.8	20.2	20.8	9.5	45.6	3.3	16.1	12.8	61.7	10	48.2	22	0.016**	169.2
13-1	9	28.4	38	33.8	30.6	14.1	46	4.3	13.9	18.4	59.9	14.5	47.3	21	0.056*	188.1
13-4	4	11.3	15.4	36.3	11.1	7.5	67.9	1.8	15.9	9.3	83.8	5.1	46.3	45	0.056*	186.9
13-7	10	32.9	35.2	7	34	14.4	42.4	4.9	14.3	19.3	56.6	15.2	44.8	21	0.056*	183.9

Table 6-19 Results from the direct choice experiment between Birch and Oak leaf tissue with long-term captive *A. dorrieni*.

Animal no.	Length (mm)	Live weight start (mg)	Live weight end (mg)	Increase in live weight of animal (% of original BW)	Mean weight (mg)	Mean weight of birch leaf eaten per week	Birch leaf eaten as % mean BW	Mean weight of oak leaf eaten per week	Oak leaf eaten as % mean BW	Total mean weight of leaf tissue eaten per week (mg)	Total amount of leaf eaten per week as % mean BW	Mean weight of faeces pro-duced per week (mg)	Faeces produced per week as % mean BW	Assimi-lation rate of leaf tissue (%)	Mann-Whitney U test results for difference in amount of Oak/Birch eaten	Konsum-quotient (*KQ*)
NBO1	15	49.1	50.2	2.2	48.3	20	41.3	69	143	88.9	184	25.8	53.3	71	0.008**	670.3
NBO2	6	8.5	9.8	115.3	8.5	8.9	104.7	6.9	80.5	15.8	185.3	6.2	72.6	61	0.056*	379.4
NBO3	8	11.8	11.5	-2.5	11.6	11.3	97.2	4.9	41.9	16.1	139.1	9.8	84.3	39	0.31	314.2
NBO4	5	4.8	11	129.1	6.2	6.9	110.7	8.3	133.5	15.2	244.2	8.6	138.7	43	0.151	450.4
NBO5	8	10	17.8	78	11.5	16.2	140.7	5.2	45	21.4	185.6	20.2	175.2	6	0.008**	420.0
NBO6	7	9	11	22.2	8.4	5	60.1	5.4	64.2	10.4	124.3	8	95.9	23	0.421	251.7
NBO7	7	11.4	16.9	48.2	13.3	12.9	96.8	3.5	26.1	16.4	123	15.8	118.9	3	0.016**	292.2
NBO8	5	5.2	12.4	138.5	7	12.8	183.6	3	42.6	15.7	226.2	12.8	184.2	19	0.008**	429.0

Table 6-20 Results from the direct choice experiment between Birch and Oak leaf tissue with short-term captive *A. dorrieni*.

6.4.4 Discussion

A. dorrieni showed the expected (see section 6.4.1) preference for Birch leaf tissue over Oak leaf tissue, with more of the animals in group 1 (fed exclusively on Birch for 15 weeks prior to the experiment) showing significant differences between the quantities of Birch and Oak litter consumed than those in group 2 (freshly caught). It is possible that habituation may have played a certain part in the former animal group's food choice, but not to a degree where Oak leaf tissue was rejected. All animals (groups 1 and 2) fed on quantifiable amounts of Oak leaf tissue throughout the experiment despite the continued presence of Birch leaf tissue. Possibly, the Oak litter contains substances beneficial to the landhopper which are absent from Birch litter. In a series of experiments on populations of two species of woodlice fed exclusively on Alder, Birch or Oak litter (each at two different pH values), only one of the 12 cultures became extinct during the study period, and this was one fed exclusively on Birch litter (Zimmer *et al.*, 2000).

Freshly caught animals showed significantly higher food intakes and KQs than those that had been in captivity for 15 weeks prior to the experiment. A similar reduction in metabolism as a result of prolonged captivity has been reported in Diplopoda by Gere (1956). A possible reason for this reduction may be a decrease in activity as a result of continued confinement, but this factor still awaits further investigation.

Lastly, it could be shown that data from feeding experiments where only one leaf tissue type is provided must be used with some caution when estimating feeding rates for a population of landhoppers (unless the population is in a location with only one litter type), as they consume significantly more when more than one leaf tissue type is provided, and probably more still where they are entirely free to choose their own food.

6.5 Live plant material

6.5.1 Introduction

Woodlice feed mostly on dead plant material and sometimes on animal remains and dung where the latter are available. In addition to that, they may derive some nourishment from bacteria and fungi growing on their primary food source (Ing, 1967). However, some (especially the larger species such as *Oniscus asellus* and *Porcellio scaber*) regularly become greenhouse pests as they are prone to attack seedlings (Hopkin, 2003). The same is true for some millipedes (Hopkin, 2004). *A. dorrieni*, given its tendency to occur at very high densities and with feeding habits similar to that of woodlice and millipedes, could also become a potential greenhouse pest. The following experiments were designed in order to assess this threat. In the first, lettuce (*Lactuca sativa*) seedlings were exposed to *A. dorrieni* for a period of seven days, both with and without an alternative food source - in the form of a fallen Birch leaf. In the second, tomato seedlings (*Lycopersicum esculentum*) were used.

6.5.2 Materials and Methods

Approximately 15 seeds were allowed to germinate in glass petri dishes (two containing lettuce and two containing tomato) on filter paper dampened with distilled water. The petri dishes were kept at 20°C under a 12L:12D fluorescent light regime. When roots and a shoot had formed, the number of seedlings was reduced to ten and five landhoppers of <3mm were added to the petri dishes. The seedlings were examined for damage daily. Figure 76 (page 236) and Figure 77 (page 165) show the lettuce dishes on days 0, 3 and 7.

6.5.3 Results

The growth of the seedlings was slow as it was restricted physically by the petri dish and the fact that no nutrients had been added to the water. There was no sign of any physical damage to the seedlings at any stage in the experiment. Both the shoots and even the delicate root system remained untouched by the landhoppers, whether an alternative food source had been provided or not. Where an alternative food source was available, it was readily consumed. A lettuce seedling died naturally on day 5 and a second on day 7 in the arrangement where the alternative food source was present. Both remained undisturbed by the landhoppers for the duration of this study.

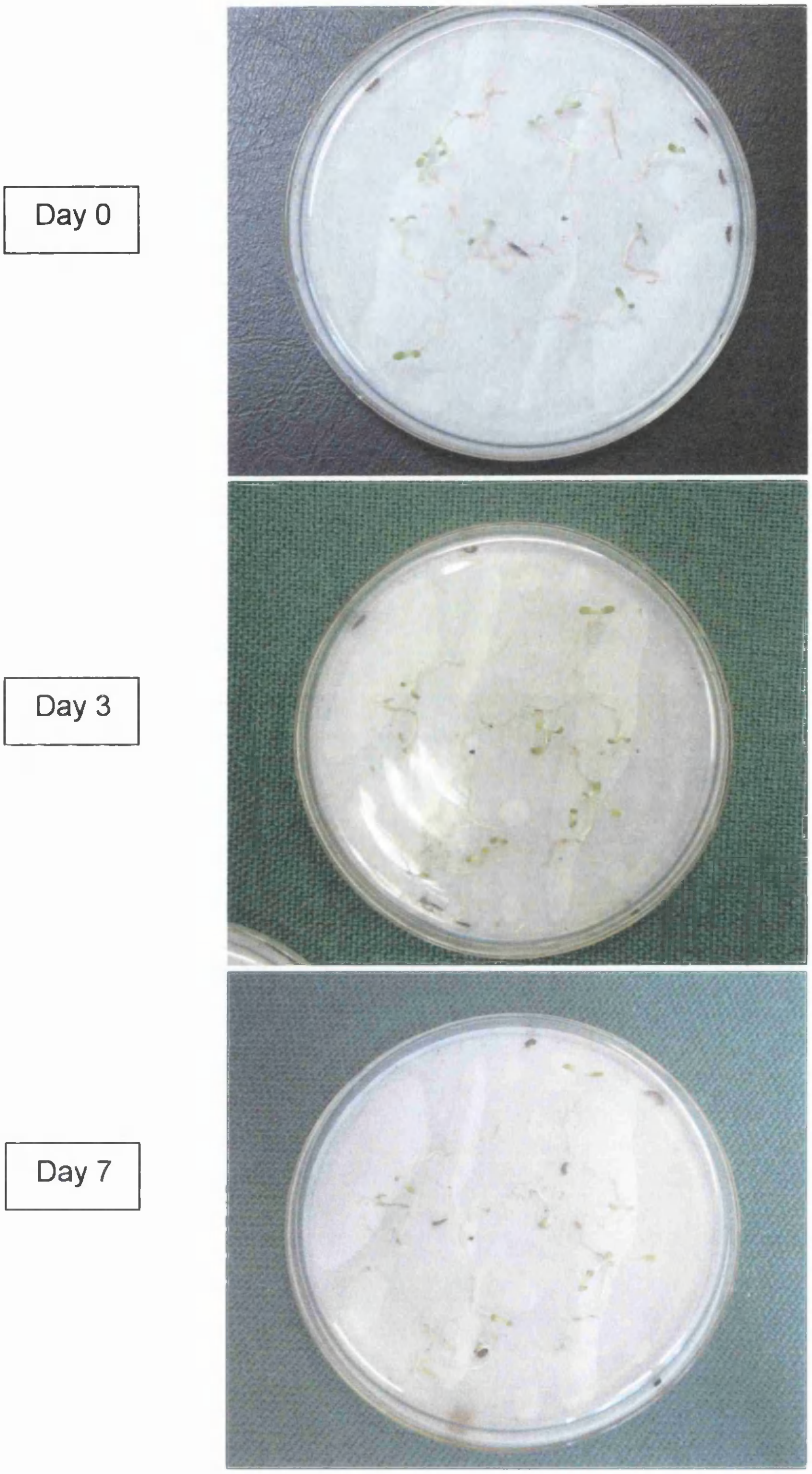


Figure 76 *Lactuca sativa* seedlings exposed to *A. dorrieni* on days 0, 3 and 7 showing lack of damage to seedlings; each petri dish contained 10 plants and 5 animals.

Figure 77 *Lactuca sativa* seedlings exposed to *A. dorrieni* on days 0, 3 and 7 with alternative food source present; each petri dish contained 10 plants, 5 animals and 1 fallen Birch leaf.

6.5.4 Discussion

Both *A. dorrieni's* reluctance to feed on fresh leaf tissue demonstrated earlier (section 6.3.3.3) and the findings of this experiment lead to the conclusion that it is highly unlikely that landhoppers will attack live plants under any circumstances and thus become a greenhouse pest. It would be interesting to investigate whether *A. dorrieni* is physically incapable of ingesting live plant material due to its texture or whether it is unable to digest it due to the fact that live plant tissue will not yet have been colonised by fungi and bacteria. To the gardener, their reluctance to eat fresh plant material makes them even less harmful than the native woodlice and millipedes, which at least occasionally achieve pest status, particularly in greenhouses

6.6 Feeding and food preferences – conclusions and suggestions for further work

In this series of experiments, initial answers to all the questions posed at the beginning of the chapter were found. These are summarized below:

The typical food intake of *A. dorrieni*, and an equation for the prediction of bodyweight from bodylength were determined. These allowed the calculation of estimates of ecological importance such as biomass and proportion of consumption of the annual litter fall. The Konsumquotient (as calculated by Dunger, 1958) can be successfully applied to *A. dorrieni*, and comparisons with other members of the detritivorous macrofauna are possible.

It was found that there is no significant difference in feeding or assimilation rates at temperatures as divergent as 13° and 20°C, and that no feeding takes place at 4°C, placing the activation temperature of *A. dorrieni* between 4°C and 13°C. It could be shown that *A. dorrieni* can survive for considerable periods of time without food, at both high and low temperatures, which greatly increases the species' invasive potential since passive long-distance dispersal is possible even without the presence of a suitable food source.

The species of origin of leaf tissue was shown to greatly influence not only *A. dorrieni's* feeding rate but also the assimilation rate of the food taken in. Fresh leaf tissue of plants whose litter is accepted readily is only eaten in very low quantities, and living plant tissue is not eaten at all.

When exposed to two different types of leaf tissue simultaneously, *A. dorrieni* shows significant preferences, but certain generally unpalatable leaf tissue types are also consumed to a considerable extent, even in the presence of other food material.

This is the first study investigating aspects of the feeding behaviour of *A. dorrieni* in any depth. As a result, there is plenty of scope for future work in this area. Some starting points for future research are suggested in the following paragraphs.

This series of experiments confirms that *A. dorrieni*, like the other species of landhopper studied to date, feeds almost invariably on a diet of a range of decaying plant material (Friend *et al.*, 1986; Lawrence, 1953; Lindeman, 1989; O'Hanlon *et al.*, 1993), and that substrates of a softer texture are generally preferred to tougher ones (Lindeman, 1991; Morton *et al.*, 1984). Its high densities in woodlands where *Rhododendron* dominates the shrub layber recorded by O'Hanlon & Bolger (1997) is probably due to the additional shelter provided by the thick litter layer formed by the slowly decomposing leaves rather than due to *Rhododendron* serving as a primary food source. The main food source in those locations is likely to come from the deciduous trees making up the canopy. Further experiments with *Rhododendron* leaves in a considerably more advanced stage of decay are needed to determine whether these may qualify as a food source.

In casual observations, the terrestrial amphipod *C. hyloraina* has been observed feeding on tissue paper and labels including lettering, but not fruit, bark, insect or mammal flesh or dead individuals of its own species (Lindeman, 1991). Similar observations on *A. dorrieni* during the course of this study reveal very similar results. *A. dorrieni* also refused to eat food of animal origin such as flake and pelleted fish food, fruit and dead conspecifics. Feeding on filter paper was only observed occasionally. Feeding patterns on individual leaves also resembled those reported for *C. hyloraina* (Lindeman, op. cit.), with the animal feeding from the surfaces and the edges, ultimately skeletonising the leaves and only attacking the tougher veins where no alternative food source is available. It would be very interesting to conduct more elaborate studies as to the feeding preferences and feeding patterns of *A. dorrieni*, and compare the results with other landhopper species, possibly detecting differences which may have given *A. dorrieni* an advantage over other landhopper species as regards its invasive potential.

Although the process of decay begins while a leaf is still on the tree (Dickinson *et al.*, 1974), the rapid colonization of the surface of the leaf by fungi and bacteria once on the ground has been shown to be necessary to prime the leaf for attack by macro-arthropods, including amphipods (Friend, 1980; Mackay & Kalff, 1973; Morton *et al.*, 1984; Sutton, 1980). Depending on the study, bacteria or fungi are thought to play the more important role in initial decomposition (Barlocher & Kendrick, 1975; Kaushik & Hynes, 1971), and leaching may also play an important role in making leaf litter palatable to decomposers (Friend, 1980). The importance of each of these factors may vary according to the conditions in which the leaf begins to decompose. While the effects of leaching on the leaf tissue will be mainly the removal of unpalatable compounds such as tannins, colonization by microorganisms such as fungi can alter the composition of the leaf tissue, among other things by increasing its protein content by conversion of plant tissue into microbial tissue and by breaking down plant tissue into sub-units more easily digestible by macro-arthropod grazers (Barlocher *et al.*, 1975). Many litter feeding detritivores particularly favour litter that has been colonized by microorganisms because of the bacterial colonies and fungal hyphae present, which they utilize as a food source directly and some prefer leaf tissue with living microorganisms to identical leaf tissue where these have been killed (Kaushik *et al.*, 1971; Mackay *et al.*, 1973). Morton & Richardson (1984) showed that two species of *Talitrus* do not distinguish between leaf tissue which has been under microbial attack and leaf tissue which has been chemically treated to mimick the hydrolytic effects of microbial colonization. It would be interesting to perform similar studies for *A. dorrieni*, since a low degree of specialization in its food preferences may be a major factor assisting this species in successfully establishing thriving populations among the native fauna.

In this study it could be shown that the calorific content of leaf tissue is not a major influence affecting the feeding rate of *A. dorrieni*. Further work is needed in order to determine which of the other factors suggested as able to influence palatability of leaf tissue to the detritivorous macrofauna (see section 6.3.4) influences feeding rate and food choice in *A. dorrieni*.

During the course of the direct choice experiments, it was observed that freshly caught animals consumed significantly more food than long-term captive individuals. It was suggested that this may be a result of decreased locomotory activity as a consequence of prolonged confinement in the ltc group. A series of actograph experiments similar to those conducted in Chapter 8 would be needed to test this hypothesis.

Optimal feeding temperatures have already been determined for some members of the Diplopoda and the Isopoda (Gere, 1956; van der Drift, 1951), but no similar work has been performed for the terrestrial amphipoda. It could be shown here that *A. dorrieni* does not significantly alter its feeding rates between temperatures of 13 and 20°C, but more detailed investigations over a larger temperature range and at smaller temperature intervals are necessary in order to produce a complete picture. Similar studies are needed to determine *A. dorrieni's* activation temperature (the temperature at which it starts to feed), and whether there is a relationship between feeding rates increasing temperatures.

7 *A. dorrieni* and its potential predators

7.1 General Introduction

Since *A. dorrieni* is a relatively recently introduced species, there are no native predators in Great Britain and Ireland, which specialize in feeding on them. Nutritionally, the calorific value of *A. dorrieni* of 4.6 kcal/g dry weight (determined using bomb calorimetry as described in section 6.3.3.6, $n_{samples}$ = 5), is not much lower than the value of 5.82 kcal/g dry weight determined for 'mixed insects' (Gibb, 1957). Also, the fact that this species has no chemical or physical defenses may add to its attraction as a prey item. Landhoppers share many of the characteristics and habits of woodlice, including their cryptozoic existence and nocturnal habits. Consequently, it may be assumed that predators which already incorporate woodlice in their diets are the most likely potential landhopper predators. The major difference between the alien amphipod and the native isopods as prey items is that the former possesses a vigorous escape response, whereas the latter tend to rely more on their armoured body and occasionally defensive secretions to deter predators. Any potential landhopper predator would have to come to terms with the amphipod's evasive strategy as well as with its cryptic and nocturnal lifestyle in order to utilise it as a major prey item. Since, however, the landhopper's body (contrary to that of woodlice) is neither armour-plated nor chemically-protected, once captured, the actual consumption of the animal will pose few problems. Woodlice are predated by birds, reptiles, amphibians, spiders, harvestmen, centipedes, mites (Cloudsley-Thompson, 1958), carabid beetles, Little Owls (*Athene noctua*) and shrews (Sutton, 1980). Any of these may qualify as potential landhopper predators. In order to become a successful landhopper predator, a potential candidate must have at least one of the following attributes:

- The strength to expose the landhopper from under the substrate and the speed to keep up with its inevitable evasive manoeuvres, after such exposure (e.g. some bird species);
- The ability to follow the landhopper into its habitat i.e. the interstitial spaces in the leaf litter layer and other confined spaces (e.g. centipedes);
- A nocturnal, terrestrial hunting lifestyle which coincides with the landhopper's occasional surface movements (e.g. some spider species).

After applying the above qualities, a few of the woodlouse predators listed previously can be discounted outright, namely:

Reptiles - Among British reptiles, only slowworms would qualify as potential landhopper predators, and those, feeding predominantly on slow-moving fare such as slugs (Smith, 1954), are very unlikely to prey on landhoppers.

The Little Owl - A comparatively slow moving bird which is unlikely to take an interest in landhoppers.

All but perhaps the smallest shrews - As a result of their considerable metabolic needs, these mammals are unlikely to pursue a relatively small and fast moving prey, which may take more energy to obtain that can be gained from it (but see section 7.3.3).

Observing the predation of small, cryptic arthropods such as woodlice and terrestrial amphipods under natural conditions is virtually impossible (Oliver & Meechan, 1993). Consequently, a number of laboratory experiments were designed to assess the potential predation pressure exerted on *A. dorrieni* populations by native predators in the British Isles. Members of all major groups of woodlouse predators not excluded previously were examined for their potential as landhopper predators, and the results are described in the following sections.

7.2 *A. dorrieni* and native invertebrate predators

This section is devoted to an examination of the native litter-dwelling invertebrate predators, and assessments of these for their potential to exert an influence on populations of *A. dorrieni*. Some representative species which were considered most likely to potentially affect *A. dorrieni* were made the focus of experimental investigation.

All collecting of invertebrates was conducted under the guidelines of the Code of Conduct for collecting insects and other invertebrates (JCCBI, 1987).

7.2.1 *A. dorrieni* and members of the Class Insecta

Most of the insects that share the landhopper's habitat also share its feeding habits and thus pose little direct threat to the alien. The similar feeding habits give rise to a possibility for potential competition for food but, due to the ubiquity of potential food material, this is unlikely to be significant factor at any time. At the same time, however, the Class Insecta contains some of the most effective potential predators of *A. dorrieni.* Those are mainly to be found among the beetles (Order Coleoptera).

7.2.1.1 Order Coleoptera

The Order Coleoptera, with its 350,000 described species, represents the largest order of life on Earth (Resh & Carde, 2003). Due to their lifestyles, only comparatively few of those species are likely to come into contact with - and thus be potential predators of - the landhopper in Great Britain. Those species that are likely to pose a threat almost exclusively belong to the Family Carabidae - the ground beetles.

7.2.1.1.1 Family Carabidae

The Family Carabidae has more than 25,000 known species, which makes it one of the largest insect families (Thiele, 1977). Many ground beetles are active and prolific hunters in both their larval and adult stages. Their diet consists mainly of other invertebrates, but carrion and, in some species, plant material is also taken (Forsythe, 1987; Thiele, 1977). Kaczmarek (in Thiele, 1977) found that *Carabus spp.* were more important in terms of energy flow in Pine-Oak and Pine-Oak/Alder forests than 'frogs' or 'birds'. In the case of the Pine-Oak/Alder forest, *Carabus* spp. accounted for more than two thirds of the energy flow into the predatory meso- and macro-fauna of the litter and soil layer.

Most British carabids are flightless and noctumal in their habits and live on the ground among leaf litter and under logs and stones, thus sharing characteristics of *A. dorrieni* and becoming very likely candidates as major predators of this alien amphipod in Britain. There are already species among the Carabidae which are known to feed almost exclusively on amphipods. *Nebria complanata*, for example, feeds mainly on *Talitrus saltator* and *Talorchestia brito*, both of which are present in large numbers in the beetle's natural habitat (the strandline of south and west European beaches) (Rudolph, 1970). Its choice of food is in no way predetermined, as the beetle has been shown to accept a wide range of other food items under laboratory conditions (op.cit.). Instead, it seems to take primarily amphipods because they are ubiquitous in its habitat (op.cit.). Another species incorporating amphipods into its diet is *Bembidion laterale*, which has been recorded as feeding on *Corophium volutator* and *T. saltator* under natural conditions, as well as on larvae of the Dolichopodidae (Diptera) (Green, 1956). These observations confirm that the supralittoral amphipods' generally very efficient escape mechanisms and cryptic lifestyle, which are very similar to those of *A. dorrieni*, do not entirely protect them from predation by carabids, and they further strengthen the assumption that *A. dorrieni* could be subject to a similar fate in its terrestrial habitat.

For this present study, three carabid species, which had been found regularly and in some numbers in habitat suitable for the landhopper, were chosen for closer investigation. All beetles were collected under logs in a woodland where *A. dorrieni* was known to be present. They were placed in 90mm petri dishes with a sheet of damp filter paper (Whatman No.1) in the larger (bottom) halves of the dishes. Airholes had been made in the larger half of the dishes using a soldering iron. The beetles were kept unfed in the petri dishes for 2 days before experiments were commenced.

7.2.1.1.1.1 Pterostichus madidus

P. madidus is a large (length 15-20mm) ground beetle which is widespread and very common across a variety of habitats, including gardens (Anderson & McFerran, 2001). This distribution as well as its numbers make this species very likely to come into contact with *A. dorrieni.*

Acceptance of *A. dorrieni* as a prey item

Five landhoppers ranging in size from 3 to 8 mm were placed with each beetle overnight. All three beetles predated at least one landhopper by the next morning. It was therefore concluded that *P. madidus* accepts *A. dorrieni* as a prey item.

Investigation of the preference of *P. madidus* for the introduced landhopper or the native woodlice

The prey species used were *Porcellio scaber* and *Philoscia muscorum* measuring no more than 9 mm (the length of the largest *A. dorrieni* used). Three criteria were taken into consideration in the selection of these particular species in order to achieve maximum practical applicability in the subsequent preference experiments:

1. their abundance and tendency to occur at high densities, which has to resemble that of the landhopper;

2. their preferred habitats, which are to be very similar to those favoured by the landhopper;

3. their escape mechanisms, which should as similar as possible to those shown by *A. dorrieni*.

Both species show adequate suitability and great similarity in criteria one and two. As regards the escape mechanisms, *P. muscorum* is adapted for fast running when attacked whereas *P. scaber* tends to drop off into the undergrowth where possible and feigns death, moving off at a reasonably fast pace only when disturbed further (Oliver *et al.*, 1993; Sutton, 1980). This mixture of escape mechanisms resembles those shown by the landhopper, particularly where the landhopper is prevented from jumping as in a petri dish, under logs and stones or in deep leaf litter. Neither *P. scaber* nor *P. muscorum* are thought to have particularly effective chemical defences

(Sutton, 1980). *Philoscia spp.* have been described as producing a gum-like substance from their uropods following continued harrassment, but this is apparently only 'distasteful' to spiders rather than an effective repellent (op. cit.).

For five consecutive nights, five woodlice and five amphipods were placed with each beetle every night and the number of animals eaten was recorded the following day. The results are displayed in Table 7-1 (Page 252). All three *P. madidus* fed on both woodlice and landhoppers, but the number of landhoppers taken was considerably higher than that of woodlice. This preference was statistically significant in two out of three individuals (Mann-Whitney U Tests: U=1, P=0.016; U=4.5, P=0.095; U=2.5, P=0.032; respectively).

	Subject 1		Subject 2		Subject 3	
Night	Isopoda	Amphipoda	Isopoda	Amphipoda	Isopoda	Amphipoda
1	0	3	1	3	0	2
2	0	2	0	1	0	3
3	1	2	1	2	2	2
4	1	1	2	1	1	1
5	0	2	0	3	0	3
Total	**2**	**10**	**4**	**10**	**3**	**11**

Table 7-1 Number of woodlice and landhoppers eaten by three *P. madidus* over five consecutive nights.

Landhoppers were predated so readily that feeding even took place during the daylight hours, making photographic documentation possible (Figure 78, below). These data show that *P. madidus* may be an efficient predator of *A. dorrieni* under natural conditions and may well turn out to exert an influence over existing or establishing landhopper populations.

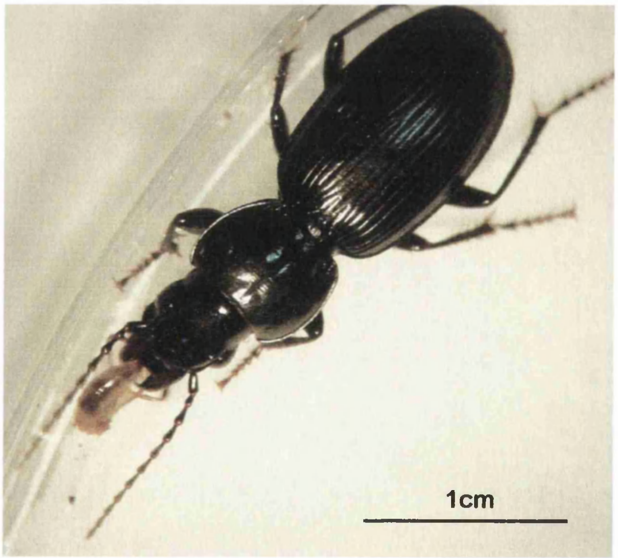


Figure 78 *Pterostichus madidus* feeding on *A. dorrieni*.

7.2.1.1.1.2 Abax parallelepipedus

A. parallelepipedus (syn. *A. ater*) is a large (length 18-22mm) ground beetle (Anderson *et al.*, 2001), which is known to readily feed on slugs and snails (Symondson & Liddell, 1993) and has been the focus of studies investigating its potential use as a biocontrol agent (Symondson, 1994). It is also known to feed freely on carrion, including dead invertebrates (Thiele, 1977).

<u>Acceptance of *A. dorrieni* as a prey item</u>

Five landhoppers ranging in size from 3 to 8 mm were placed overnight with each beetle. In all three cases, at least one landhopper had been predated by the following morning. It was therefore concluded that *A. parallelepipedus* accepts *A. dorrieni* as a prey item.

<u>Investigation of the preference of *A. parallelepipedus* for the introduced landhopper or the native woodlouse</u>

The same choice offered to *P. madidus* (section 7.2.1.1.1.1) was used here. The results are displayed in Table 7-2 (below). All three *A. parallelepipedus* consistently refused to feed on woodlice ('Isopoda') but predated landhoppers ('Amphipoda') virtually every night.

	Subject 1		Subject 2		Subject 3	
Night	Isopoda	Amphipoda	Isopoda	Amphipoda	Isopoda	Amphipoda
1	0	1	0	1	0	2
2	0	1	0	2	0	1
3	0	1	0	1	0	2
4	0	1	0	2	0	0
5	0	1	0	1	0	1
Total	**0**	**5**	**0**	**7**	**0**	**6**

Table 7-2 Number of woodlice and landhoppers eaten by three *A. parallelepipedus* over five consecutive nights.

While the number of landhoppers taken would probably not be enough to sustain growth and reproduction in *A. parallelepipedus* [most carabids have to eat at least their own bodyweight every day (Scherney, 1959)], it shows they will be eaten in the absence of more suitable (e.g. molluscan) prey, and in preference to native terrestrial crustaceans. This preference was statistically significant in all three subjects (Mann-Whitney U tests: U=0, P=0.008; U=0, P=0.008; U=2.5, P=0.032; respectively).

7.2.1.1.1.3 ***Harpalus rufipes***

H. rufipes is a medium sized (length 10-17mm) ground beetle (Anderson *et al.*, 2001). It is one of the oligophagous members of the Carabidae, regularly incorporating plant seeds and other vegetable matter into its diet (Forsythe, 1987; Thiele, 1977), which otherwise consists of small insects (including ants, aphids, lepidopteran larvae and other Coleoptera) and arachnids (Skuhravy, 1959). This beetle is known for being particularly active during wet weather, and fairly inactive during dry spells (Dempster, 1975). This habit predisposes this beetle species to encounter *A. dorrieni* during hunting. None of the animals used here measured more than 14mm.

Acceptance of *A. dorrieni* as a prey item

Once again, five landhoppers ranging in size from 3 to 8 mm were placed with each beetle overnight. In all three cases, at least one landhopper was predated by the following morning. It was therefore concluded that *H. rufipes* accepts *A. dorrieni* as a prey item.

Investigation of the preference of *H. rufipes* for the introduced landhopper or the native woodlice

The same choice between amphipods and isopods used previously (sections 7.2.1.1.1.1 and 7.2.1.1.1.2), was given. The results are displayed in Table 7-3 (below). All three *H. rufipes* consistently refused to feed on woodlice but predated landhoppers every night. Given *H. rufipes'* smaller size, the quantity of landhoppers taken was considerably higher than that recorded for *A. parallelepipedus*, and may be close to its food intake under natural conditions. The beetles' preference for the landhopper was statistically significant in all three subjects (Mann-Whitney U tests: U=0, P=0.008 for all three animals).

	Subject 1		Subject 2		Subject 3	
Night	Isopoda	Amphipoda	Isopoda	Amphipoda	Isopoda	Amphipoda
1	0	2	0	1	0	3
2	0	1	0	2	0	2
3	0	3	0	2	0	1
4	0	2	0	1	0	2
5	0	1	0	1	0	2
Total	**0**	**9**	**0**	**7**	**0**	**10**

Table 7-3 Number of woodlice and landhoppers eaten by three *H. rufipes* over five consecutive nights.

7.2.2 *A. dorrieni* and members of the Class Chilopoda

In 1958, J. L. Cloudsley-Thompson wrote:

> *"Centipedes always live in damp, dark and obscure places under stones, fallen leaves, logs, under bark and in crevices of the soil, from which, like woodlice and millipedes, they issue forth at night."*

Centipedes thus share both the habitat and the nocturnal lifestyle typical of *A. dorrieni.* Three of the five orders within the Chilopoda are represented in Britain. These are the orders Geophilomorpha, Scolopendromorpha, and Lithobiomorpha. Most British members of the order Geophilomorpha are subterranean, pale-coloured, long-bodied, short-legged and fairly slow moving animals, which feed on various soil-dwelling invertebrates and some plant material (Cloudsley-Thompson, 1958). Due to their habitat and slow movement they are very unlikely to be potential predators of *A. dorrieni* and were not considered in this study.

7.2.2.1 Order Scolopendromorpha

7.2.2.1.1 Family Cryptopsidae

The order Scolopendromorpha is represented in Britain by only one Family, the Cryptopsidae. There are only three British species, all within the Genus *Cryptops* (Wheater *et al.*, 1996). *Cryptops spp.* resemble the more common centipedes of the order Lithobiomorpha, but they have 21 pairs of legs instead of 15. They are fairly small (length around 25mm) and of a light orange colour (Cloudsley-Thompson & Sankey, 1968). Like the Lithobiomorpha, they are active nocturnal hunters, but, due to their small size and comparatively small poison claws, are limited to prey which is small and soft-skinned (Cloudsley-Thompson, 1958).

7.2.2.1.1.1 Cryptops hortensis

C. hortensis is the most commonly encountered *Cryptops* species in Britain. Two specimens were obtained from habitat where landhoppers were known to be present. As with the spiders and carabid beetles described previously , they were housed in petri dishes lined with damp filter paper. Food was withheld for two days prior to the experiment.

Acceptance of *A. dorrieni* as a prey item

Five landhoppers ranging in size from 3 to 8 mm were placed with each centipede overnight. Both specimens predated at least two landhoppers by the next morning. However, no landhoppers over 6mm in length were taken. It was therefore concluded that *C. hortensis* accepts *A. dorrieni* as a prey item, but may be reluctant, if not actually unable, to attack larger individuals.

Cryptops spp. are rare in Britain, and even the relatively common *C. hortensis* occurs only at low densities (Cloudsley-Thompson *et al.*, 1968). Thus, while *Cryptops* spp. will probably utilise small landhoppers as a food source where the opportunity arises, they are not in a position to exert much of an influence over landhopper populations.

7.2.2.2 Order Lithobiomorpha

7.2.2.2.1 Family Lithobiidae

Most of the commonly encountered centipedes belong to the order Lithobiomorpha. They are active and powerful predators which are capable of very fast movement (Wheater *et al.*, 1996). The two most widespread species are *Lithobius forficatus* and *Lithobius variegatus*. They are also the largest British Lithobiomorpha, reaching lengths of 32 and 23 mm respectively (Cloudsley-Thompson *et al.*, 1968). *L. forficatus* has been observed feeding on woodlice under natural conditions, and will take a variety of insects and even slugs and worms in the laboratory (Cloudsley-Thompson, 1958). Cannibalism has also been recorded under crowded conditions (Cloudsley-Thompson, op. cit.). A very detailed study of the environmental preferences of *L. forficatus* revealed that it preferred high humidities and ground temperatures of about 12°C (Bauer, 1955), conditions very similar to those favoured by *A. dorrieni.*

7.2.2.2.1.1 ***Lithobius forficatus***

Acceptance of *A. dorrieni* as a prey item

Six *L. forficatus* were collected from habitat where landhoppers were known to be present. They were housed singly in petri dishes, as described for *C.*

hortensis (Section 7.2.2.1.1.1). Five landhoppers ranging in size from 3 to 8 mm were placed with each centipede. This elicited an almost immediate feeding response, which made photographic documentation possible (Figure 79, page 262). During the following night, a minimum of two more, but on two occasions as many as all four remaining landhoppers, were predated. It was therefore concluded that *L. forficatus* very readily accepts *A. dorrieni* as a prey item. Following the feeding on landhoppers, the centipedes' droppings took on a distinctive orange colour (Figure 80, below).

Figure 79 *Lithobius forficatus* feeding on *A. dorrieni*.

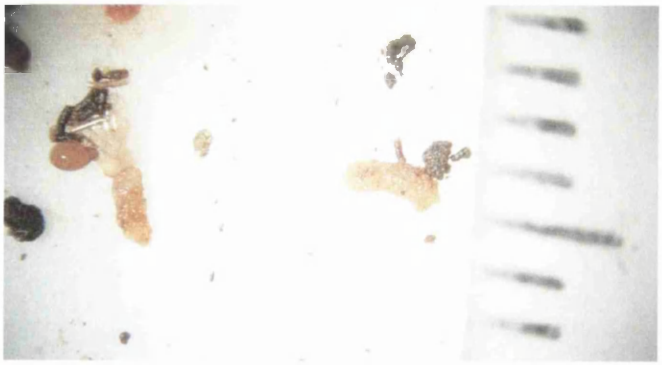


Figure 80 Droppings of *L. forficatus* after feeding on *A. dorrieni*, scale in 1mm increments.

Investigation of the preference of *L. forficatus* for the introduced landhopper or the native woodlice

The choice employed for the Coleoptera (sections 7.2.1.1.1.1 to 7.2.1.1.1.3) was also used here. The results are displayed in Table 7-4 below. All five *L. forficatus* fed on both woodlice and landhoppers. The Mann-Whitney U test was used to test for statistical significance of preference and the following U and P values were obtained: U=5, P=0.151; U=2, P=0.032; U=9, P=0.548; U=0, P=0.008; U=5, P=0.151; U=1.5, P=0.016; respectively. Three of the six animals (subjects 2, 4 and 6) showed a statistically significant preference for landhoppers. Two animals (subjects 1 and 5) showed some preference, however, this was not strong enough be statistically significant at the 0.05 level. Only one animal (subject 3) did not show any preference.

	Subject 1		Subject 2		Subject 3	
Night	Isopoda	Amphipoda	Isopoda	Amphipoda	Isopoda	Amphipoda
1	1	5	2	3	1	2
2	1	2	0	3	2	1
3	1	5	0	3	1	1
4	1	0	0	1	1	2
5	1	3	1	2	2	4
Total	**5**	**15**	**3**	**12**	**7**	**10**

	Subject 4		Subject 5		Subject 6	
Night	Isopoda	Amphipoda	Isopoda	Amphipoda	Isopoda	Amphipoda
1	0	2	0	4	1	2
2	0	1	2	1	0	2
3	0	2	1	5	0	2
4	0	2	2	2	0	3
5	0	2	1	2	2	4
Total	**0**	**9**	**6**	**14**	**3**	**13**

Table 7-4 Numbers of woodlice and landhoppers eaten by six *L. forficatus* over five consecutive nights.

It may be concluded that *L. forficatus* will feed readily on *A. dorrieni*, and even prefers landhoppers to woodlice, at least in conditions where the former are relatively easy to capture, although there is some individual variation.

7.2.2.2.1.2 Lithobius variegatus

L. variegatus is similar in appearance and habits to *L. forficatus*, but is usually considered more 'rural' in its distribution (Cloudsley-Thompson, 1958). It is certainly more common in broad-leaved woodlands (where it can occur at considerable densities) than in gardens (pers. obs.).

Acceptance of *A. dorrieni* as a prey item

Five *L. variegatus* were collected from habitat where landhoppers were known to be present. They were housed singly in petri dishes, as *L. forficatus* (above). Five landhoppers ranging in size from 3 to 8 mm were placed with each centipede. As in *L. forficatus*, this elicited an almost immediate feeding response, and once again photographic documentation was possible (Figure 81, page 262).

Again, during the following night, several more landhoppers, were predated by each centipede. *L. variegatus* thus very readily accepts *A. dorrieni* as a prey item.

Figure 81 ***Lithobius variegatus*** **feeding on** ***A. dorrieni.***

Investigation of the preference of *L. forficatus* for the introduced landhopper or the native woodlice

The choice between amphipods and isopods used for *L. forficatus* (section 7.2.2.2.1.1) was also here. The results are displayed in Table 7-5 (page 263). The observed preference for the landhopper as a prey item was tested statistically with Mann-Whitney U tests. The following U and P values were obtained: U=2, P=0.032; U=1, P=0.016; U=0, P=0.008; U= 4, P=0.095 (U=0, P=0.029), U= 1, P=0.016.

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	Subject 1		Subject 2		Subject 3	
Night	Isopoda	Amphipoda	Isopoda	Amphipoda	Isopoda	Amphipoda
1	2	3	1	2	0	2
2	1	3	0	3	0	2
3	1	2	0	2	0	1
4	2	2	1	1	0	4
5	1	3	0	2	0	3
Total	**7**	**13**	**2**	**10**	**0**	**12**
	Subject 4		Subject 5			
Night	Isopoda	Amphipoda	Isopoda	Amphipoda		
1	0	3	0	3		
2	0	0	0	3		
3	1	2	1	1		
4	1	3	0	2		
5	1	2	1	2		
Total	**3**	**10**	**3**	**10**		

Table 7-5 Numbers of woodlice and landhoppers eaten by five *L. variegatus* over five consecutive nights.

All animals showed a significant preference for the landhopper over the native woodlice. Subject 4 initially.showed a non-significant P value due to the fact that a nonparametric 'rank' test was used, which was falsified by the fact that the individual had not fed on either prey during night 2. When night 2 is removed from the analysis, a significant P value of 0.029 is obtained.

7.2.3 *A. dorrieni* and members of the Class Arachnida

Members of the Class Arachnida commonly found in Britain in habitats favoured by the landhopper include spiders (Order Araneae), harvestmen (Order Opiliones), mites (Order Acari) and pseudoscorpions (Order Pseudoscorpiones). The mites and pseudoscorpions found in British woodlands are too small to pose a threat to any but the very smallest landhopper and will not be further discussed.

A number of harvestman species share the landhopper's habitat due to their common humidity requirements (Wheater *et al.*, 1996) and, since they are classed as nocturnal, carnivorous feeders (Sankey & Savory, 1974) incorporating other harvestmen, snails, earthworms, millipedes, woodlice, spiders, earwigs, flies, mites, springtails, aphids, leaf-hoppers and 'other small invertebrates' into their diet (Bristowe, 1939; Sankey, 1948), there is some potential that they may become predators of *A. dorrieni.* Most harvestmen, however, are fairly slow and unwieldy in their movements, and their typical way of hunting is to imprison their prey in a palisade of their eight legs and dropping down upon it (Roters, 1944), a technique which would be singularly unsuccessful with the landhopper, which will burrow into the substrate where possible and jump frantically otherwise. Therefore it is unlikely that landhoppers would make up a large part of the harvestmen's diet under natural conditions.

In order to examine this hypothesis, three harvestmen (*Oligolophus* spp.) collected from landhopper habitat were housed singly in the confines of petri dishes for one week. Five small landhoppers were added to each, and, as expected, none of the harvestmen showed any evidence of predatory activity directed towards them.

A considerable number of ground-living spiders are potentially both large and fast enough to hunt down and kill landhoppers. Since many of those spiders are well known for their wide-ranging diet [including even earthworms (Nyffeler, Moor & Foelix, 2001) and gastropod molluscs (Nyffeler & Symondson, 2001) it was decided to focus on this order of the Arachnida in this investigation.

7.2.3.1 *Order Aranae*

Spiders are, with few exceptions, predatory animals. They are probably best known for their ability to hunt using silken webs, which can be very elaborate structures. As a result, the fact that a large proportion of spiders (particularly ground-living species) use webs only for shelter rather than for hunting (or even not at all) is often overlooked. Spiders from both the web spinning and actively hunting groups were examined here.

Spiders under closer investigation here include members of the Families Agelenidae (*Tegenaria sp.*), Gnaphosidae (*Haplodrassus sp.*) and Dysderidae (*Dysdera sp.*). Spiders of the genera chosen occur in some numbers in habitat suitable for the landhopper, and would therefore have the greatest potential for influencing newly forming as well as established populations. Since spiders are known to feed predominantly on prey no longer than their own bodylength (Nyffeler, Sterling & Dean, 1994), only landhoppers smaller or equal to the bodylength of the spider were offered as potential prey items.

7.2.3.1.1 Family Agelenidae

Tegenaria sp.

There are eleven species of *Tegenaria* in northern Europe. While some of the species hunt using large sheet webs, many live at ground level and build much reduced webs among rocks and dead wood (Roberts, 1996), potentially bringing them into contact with landhoppers. Five adult specimens of *Tegenaria sp.* were collected from crevices in bark and under logs in habitat where *A. dorrieni* was known to be present. They were transferred to clear plastic cups (85mm diameter at the rim, no. 10, A. W. Gregory, London SE4) with small airholes in the flexible lids, and left to acclimatise and construct a web. They were regularly supplied with water by gentle misting but were not fed for 5 days prior to each experiment.

Acceptance of *A. dorrieni* as a prey item

All five individuals immediately accepted a live specimen of *A. dorrieni* placed into their webs (Figure 82, page 267) and were even capable of subduing individuals the same length as their own bodies. In one case, where a very large landhopper was introduced, the animal was only partially eaten.

In general, however, nothing but a small ball of cuticle remained of the landhopper after two hours.

Figure 82 ***Tegenaria sp.*** **feeding on** ***A. dorrieni.***

Acceptance of native woodlice as prey items

The prey species used here were *Porcellio scaber* and *Philoscia muscorum* measuring no more than 9 mm (the length of the largest *A. dorrieni* used and also the body length of the spiders). All five spiders immediately accepted a live woodlouse placed into their webs and were capable of subduing it. In three cases, however, this required multiple bites, presumably due to the prey's strong cuticle. Single bites to the ventral surface and to the head respectively resulted in almost immediate paralysis. In one case, the dead woodlouse was dropped and fell to the bottom of the container, where it was actively sought out and eaten. Much larger portions of cuticle were left after feeding on this prey was completed (after a maximum of 2 hours). This often still resembled the intact woodlouse, thus confirming the strength and relative indigestibility of the woodlouse's body armour.

Investigation of the preference of *Tegenaria sp.* for the introduced landhopper or native woodlice

A landhopper and a woodlouse of similar size and weight were introduced into the web together and the reaction of the spider observed. The experiment was repeated twice with each spider, with a week between tests. In seven cases, the spiders attacked the landhopper first and in three cases the woodlouse. It was always, however, the prey animal which started to move first that initiated attack. The order of attack is consequently more likely to be due to the fact that landhoppers showed the more vigorous evasive activity, and started such activity sooner following introduction into the web, rather than there being an actual preference by the spider. Generally (in eight cases) the second prey animal was also killed as soon as it started moving. In the remaining two cases, the second prey item fell to the bottom of the web and was ignored during the initial feeding bout. In both cases, however, it was found dead and partially digested in the web 24 hours later. Where feeding was interrupted to kill the second prey item, the spider went back to its original prey immediately in two cases (in both cases the original prey was a landhopper). In four of the remaining six cases, the spider went back to the first prey item after feeding on the second for a period of time (5 +/-2 mins) and twice went on to feed on both prey items alternately, once even arranging the two side by side, alternating between them several times over a 20 minute period.

Due to the fact that *Tegenaria sp.* were so responsive to movement on the web, statistical analysis was deemed unsuitable for the data produced in this experiment. *Tegenaria spp.* are ambush hunters. It is thus evolutionarily beneficial to the spider to have a wide-ranging prey spectrum so it can benefit from most prey animals that happen to become caught in its web. Since both landhoppers and woodlice were observed to be killed and eaten readily by *Tegenaria sp.*, it may be concluded that the spider accepts both prey items equally.

7.2.3.1.2 Family Gnaphosidae

Haplodrassus signifer are described as 'quite fierce nocturnal hunters' which spend the day in a silken retreat (Roberts, 1996). They live under stones, in moss and leaf litter and at the base of grass tussocks, and they have been recorded from wet and even boggy sites, where they inhabit drier raised microhabitats (op.cit.).

Two adult female *H. signifer* were collected under logs in a woodland where *A. dorrieni* was known to be present. They were placed in 90mm petri dishes with a sheets of damp filter paper (Whatman No.1) in the larger (bottom) halves of the dishes. Airholes had been made in the larger half of the dishes using a soldering iron. The spiders were acclimatised for 5 days before experiments were commenced, during which time they were not fed.

Acceptance of *A. dorrieni* and native woodlice as prey items

H. signifer almost immediately accepted both *A. dorrieni* and a native woodlouse (*P. scaber*) as prey items (Figure 83, below).

Figure 83 ***Haplodrassus signifer*** **feeding on** ***A. dorrieni.***

Investigation of the preference of *Haplodrassus signifer* for the introduced landhopper or the native woodlice

As in the *Tegenaria sp.* experiments, prey species used here were *P. scaber* and *P. muscorum* measuring no more than 9 mm (the length of the largest *A. dorrieni* used and also the body length of the spiders). For five consecutive nights, five woodlice and five amphipods were placed with the spiders every night and the number of animals eaten was recorded the following day.

The results are displayed in Table 7-6 (below). Both individuals fed on isopods and amphipods readily, and to very similar extents. Neither animal showed a preference for either prey type (Mann-Whitney U Tests: U=11.5, P=0.841; U=10.5, P=0.690, respectively).

	Subject 1		Subject 2	
Night	Isopoda	Amphipoda	Isopoda	Amphipoda
1	1	2	0	2
2	0	2	1	1
3	2	1	1	0
4	3	2	2	1
5	2	2	1	2
Total	**8**	**9**	**5**	**6**

Table 7-6 Number of woodlice and landhoppers eaten by two *H. signifer* over five consecutive nights.

7.2.3.1.3 Family Dysderidae

The Genus *Dysdera* is of particular interest as *Dysdera spp.* are are often considered specialized woodlouse predators (Chinery, 1993; Cloudsley-Thompson, 1958; Pollard *et al.*, 1995; Roberts, 1996) and may therefore be particularly predisposed to incorporating another crustacean into their diets. These spiders are noctumal wandering predators which hunt exclusively at ground level (Roberts, 1996), habits which make them particularly prone to encounter *A. dorrieni.*

Three specimens of *Dysdera sp.*, two females and one male, were collected under logs in a woodland where *A. dorrieni* was known to be present. As with the Gnaphosidae, the spiders were placed singly into petri dishes lined with damp filter paper and acclimatised for 5 days prior to the experiments, during which time they were not fed.

Acceptance of *A. dorrieni* and native woodlice as prey items

All individuals immediately accepted both *A. dorrieni* and a native woodlouse (*P. scaber*) as a prey items.

Investigation of the preference of *Dysdera sp.* for the introduced landhopper or the native woodlice

Once again, the prey species used were *P. scaber* and *P. muscorum* measuring no more than 9 mm (the length of the largest *A. dorrieni* used and also the body length of the two larger spiders). The prey items placed with the small female spider (body length = 6mm) were chosen to be no longer than the body length of the animal. For five consecutive nights, five woodlice and five amphipods were placed with each spider every night and the number of animals eaten was recorded the following day. The results are displayed in Table 7-7 (below). All animals fed on isopods as well as amphipods, but there was an obvious preference for the native woodlice. This preference is, however, not strong enough to be statistically significant (Mann-Whitney U tests: U=5, P=0.151; U=7, P=0.31; U=7, P=0.31; respectively).

	Subject 1 (male)		Subject 2 (large female)		Subject 3 (small female)	
Night	Isopoda	Amphipoda	Isopoda	Amphipoda	Isopoda	Amphipoda
1	5	0	5	2	2	0
2	3	0	5	0	0	1
3	3	5	1	0	0	0
4	2	0	1	4	1	0
5	3	2	3	2	1	0
Total	**16**	**7**	**15**	**8**	**4**	**1**

Table 7-7 Number of woodlice and landhoppers eaten by three *Dysdera sp.* over five consecutive nights.

7.2.4 Summary – Invertebrates

Table 7-8 (Page 274) lists arthropod predators which were caught in the same localities as *A. dorrieni,* and shows whether or not they were found to accept the amphipod as food under laboratory conditions. The list includes the species described previously.

Where prey acceptance was not determined during the course of the above experiments, the procedure used for determination was as follows: The predators were housed singly in petri dishes of 90mm diameter lined with damp filter paper. Five *A. dorrieni* of a variety of sizes (3-8mm) were added to each petri dish. The petri dishes were examined daily for signs of predation, and those predators that had eaten were marked as 'accepting *A. dorrieni* as food'. Where no landhopper had been predated after one week, the predators were marked as 'not accepting *A. dorrieni* as food'. With the exception of *Zora sp.,* a minimum of two predators per species were examined.

Genus/Species	Order	Accepts *A. dorrieni* as food
Cryptops hortensis	Scolopendromorpha	yes
Lithobius forficatus	Lithobiomorpha	yes
Lithobius variegatus	Lithobiomorpha	yes
Carabus violaceus (a)	Coleptera	no
Notiophilus biguttatus (b)	Coleptera	no
Nebria brevicollis (c)	Coleptera	no
Abax parallelopipedus	Coleptera	yes
Badister sp. (d)	Coleptera	yes (small only)
Harpalus rufipes	Coleptera	yes
Pterostichus nigrita (e)	Coleptera	yes
Pterostichus madidus	Coleptera	yes
Dysdera sp.	Aranae	yes
Haplodrassus signifer	Aranae	yes
Tegenaria sp.	Aranae	yes
Zora sp. (f)	Aranae	no

Table 7-8 Selected arthropod predators sharing *A. dorrieni* habitat and their acceptance of the amphipod as a prey item.

(a)

Carabus violaceus is a large (length 20-30mm) ground beetle, which, like the other *Carabus spp.*, is said to consume '*almost every kind of insect within reach, adult or larva*' , as well as carrion, both of vertebrate and invertebrate origin (Thiele, 1977). It has been reported to be particularly partial to earthworms and slugs (Forsythe, 1987; Thiele, 1977). It was therefore particularly interesting to observe that the *C. violaceus* specimens in this study showed little interest in *A. dorrieni*, even where those were within easy reach. It appeared as if the beetles were unable to detect landhoppers that were not in direct contact with their mouthparts. Furthermore, they made no attempt to pursue those landhoppers that they touched accidentally on their travels around the petri dish, and which moved away as a result. It may therefore be concluded that it is unlikely that *C. violaceus*, and probably other *Carabus spp.*, will turn out to be successful predators of *A. dorrieni* under natural conditions. In such locations the landhopper will be considerably more difficult to encounter and to catch than under laboratory conditions.

(b)

Notiophilus biguttatus is known for its fast reflexes which make it a perfectly adapted and very successful predator of springtails (Anderson, 1972; Bauer & Voellenkle, 1976; Forsythe, 1987; Thiele, 1977). While there are reports that it may be a specialist feeder upon the Collembola (Schaller, 1950), more recent crop content analysis has shown that mites and Diptera and other arthropods can make up as much as 78% of its diet (Anderson, 1972). As a result, *N. biguttatus* would be an ideal candidate for the predation of landhoppers, which show an escape response very similar to Collembolans.

It was therefore surprising to find that the specimens under investigation refused to feed on even the smallest landhoppers in the laboratory. There is a possibility that the confinement in a petri dish could have stressed the animals, which, as a visual predator have particularly keen eyesight (Thiele, 1977), and thus prevented a predatory response. On the other hand, it is also possible that *A. dorrieni* would not be considered as a prey item even under satisfactory conditions due to its novelty or other - as yet unknown - factors. A larger sample size and replication in different experimental arrangements would be needed to elucidate this point further. While a possible predator-prey interaction between *N. biguttatus* and *A. dorrieni* would be very interesing to observe, it is unlikely that *N. biguttatus* would be able to influence landhopper populations to a noticeable extent due to its small size (5-6mm) (Anderson *et al.*, 2001), enabling it to take only very young individuals, and also due to its mainly diurnal habits (Thiele, 1977), reducing the likelihood of it getting in contact with its potential prey, which restricts most of its activity to the hours of darkness.

(c)

Nebria brevicollis, a medium sized (length 10-14mm) ground beetle (Anderson *et al.*, 2001), is considered a strictly carnivorous species and has been known to aggregate in groups of up to 70 individuals, a behaviour which is very unusual among ground beetles (Forsythe, 1987). It can be very common in typical landhopper habitat. During the experiments, however, it showed no inclination towards accepting *A. dorrieni* as prey. It has been suggested that *N. brevicollis* may only feed for 2-3 weeks after emergence in early summer and then enter a period of diapause lasting until the beginning of the breeding season in the shorter days of late summer (Penny, 1966). It is possible, that this experiment, which was conducted in mid-July, may have coincided with the period of diapause during which no food is taken. Replication at an earlier time of year is needed before it can be stated with certainty that *N. brevicollis* does not accept *A. dorrieni* as prey.

(d)

Badister sp. are small (length 5-6mm) ground beetles, many of which show a preference for humid habitats (Anderson *et al.*, 2001). *B. bipustulatus*, one of the most common and the most easily identifyable *Badister* species, is known to feed on freshly dead immature woodlice and snails and is therefore sometimes considered as more of a scavenger than an active predator (Forsythe, 1987). The individuals tested here fed readily on *A. dorrieni.* Only individuals of <4mm were predated, however, probably due to the small body size of the beetles.

(e)

Pterostichus nigrita is very similar to *P. madidus* (see section 7.2.1.1.1.1, page 249) in its appearance and habits, but is somewhat more hygrophilous (Anderson *et al.*, 2001), which may lead to it having an even more likely association with *A. dorrieni. P. nigrita* fed on landhoppers readily and freely.

(f)

Seven similar *Zora spp.* are found across Britain and Northern Europe, but these resemble each other closely in appearance and habits and can only be distinguished by examination of the epigynes and male palps under high magnification (Roberts, 1996). They are known to hunt actively during the day at ground level and in low growing vegetation but are also found in leaf-litter, under stones and similar habitats (Roberts, op. cit.). This hunting behaviour is likely to bring them into close contact with landhoppers, particularly during the early morning when the latter are most active (see section 8.3). It was therefore interesting that, in this study, *Zora sp.* consistently refused to feed on the provided landhoppers. Further experiments would be needed to elucidate the reasons for this, taking into account factors such as the novelty of the landhoppers as prey items, unsuitable maintenance habitat and possible specialization on particular type of prey.

7.2.5 Discussion - Invertebrates

This is the first study dealing with the potential predators of *A. dorrieni* and their actual acceptance of the landhopper as a food item (albeit under controlled conditions). The only other reference to possible predation can be found in a study based on the feeding ecology of *T. sylvaticus* in Australia where a predatory mollusc, a land planarian, a lycosid spider and a centipede 'were placed separately in small containers of soil with known numbers of *T. sylvaticus'*, and only the land planarian captured and ate amphipods under these conditions (Clark, 1954). No reference is made to the numbers of predators used, the size of the containers, the type and texture of the 'soil' or the period of exposure. Landhoppers often stay hidden under leaf litter or in the top layer of the soil for prolonged periods of time, especially when conditions are not favourable, and would be expected to do so when confined in a small container in the presence of a potential predator, especially where the latter is unable to follow them into the substrate. Alternatively, the predators could have been prevented from showing their natural behaviours. In both cases, the experimenter would have obtained false negative results in the experiments. Under natural conditions, the landhoppers might well be predated while active on the surface during the night, or the predator might well be able to follow them into the loose leaf litter they generally inhabit.

This study showed that *Tegenaria sp.* readily accept woodlice as prey items, contradicting a report stating that house spiders of this genus ignore woodlice placed on their sheet web (Hopkin, 2003). It is possible that, perhaps, the spiders in Hopkin's (2003) study had not been starved prior to the experiment. Recent experiments indicate that *Dysdera* may not actually prefer woodlice as prey, but rather be forced to specialize in them as a food source by restrictions imposed by its habitat and habits (Pollard *et al.*, 1995). The observations in this study indicate, however, that they show a clear preference for woodlice, at least when given the choice between woodlice and amphipods.

Overall, it could be shown that *A. dorrieni* clearly faces considerable predation pressure by many carnivorous members of the native invertebrate fauna. Further research is needed before it can be said with any certainty whether this predation pressure is, or could eventually become (by increases in numbers of successful landhopper predators), strong enough to affect already established or newly establishing *A. dorrieni* populations. At this point in time, however, predation by native invertebrate predators does not appear to have a controlling influence on landhopper populations, nor do landhopper populations appear to significantly increase native predator numbers (see Chapter 4).

7.3 A. dorrieni and native vertebrate predators

This section provides an overview of *A. dorrieni's* potential vertebrate predators. Those species which were considered most likely to potentially influence *A. dorrieni* populations by their predation of the alien amphipod were made the focus of experiments. Due to the considerable complexity of the topic and the lack of prior investigations in this area, this study can only hope to provide an initial glimpse of the actual predator-prey relationships under natural conditions.

7.3.1 Amphibians

The collection, handling and maintenance of the amphibians used in this study followed the Guidelines for use of live amphibians and reptiles in Field Research (ASIH, HL & SSAR, 2001).

7.3.1.1 Newts (Order Caudata)

Newts are described as feeding on a wide variety of prey items (namely worms, slugs, snails and insects while on land, and aquatic insect larvae, small crustacea, molluscs, frog spawn and tadpoles of frogs and newts while in water) (Smith, 1954). It is therefore possible that they would accept *A. dorrieni* as prey where it is available. Due to the newts' small size, however, they are unlikely to be able to visually follow a landhopper's jumping escape response once it has been triggered. Furthermore, they are not sufficiently fast-moving to catch a jumping landhopper. Where the newts are in a position to catch the amphipod by surprise and/or among leaf litter hampering its vigorous jumping, however, it is likely to be predated. Overall, landhoppers are probably occasionaly incorporated into the diets of the newts which occur in habitat colonized by *A. dorrieni*, but predation by newts is unlikely to become a common enough occurrence to exert control over the landhopper's invasive potential.

7.3.1.2 *Frogs and Toads (Order Anura)*

7.3.1.2.1 Introduction

Attempts to maintain Common Frogs (*Rana temporaria*) in the laboratory in order to perform similar experiments had to be aborted, as the frogs did not settle in the enclosures provided and refused all food, and their notoriously vigorous escape response (Smith, 1954) made them vulnerable to injury. Common Frogs generally take active, fast moving prey in preference to slow, sluggish species (Thiele, 1977), and large predatory prey such as carabid beetles make up the bulk of the diet of forest-dwelling frogs (Zimka, 1966), so that an impact on *A. dorrieni* populations through predation by frogs is highly unlikely.

Common Toads (*Bufo bufo*) are well known for their catholic diets and their large appetites. As early as 1869, the food of the toad was described as "*seeming to consist of all living animals that are susceptible of being swallowed*" (Smith, 1954). Of this considerably wide prey spectrum, ants, beetles and isopods appear to be particular favourites, but ultimate prey choice depends greatly on the locality (op. cit.). In this study, experiments were designed to assess the acceptance of *A. dorrieni* as a prey item and investigate whether this alien terrestrial crustacean is preferred to the native species.

7.3.1.2.2 Experiments

Toads were collected during June and July, after the breeding season. For the initial simple acceptance and preference experiments, the toads were placed in white plastic buckets with some damp tissue paper to maintain humidity and acting as a hide, and 5 woodlice and 5 landhoppers were added. This was followed by 15 minutes of observation during which the prey items eaten were recorded. At the end of this time period, the enclosures were covered with perforated lids and the animals left undisturbed for 3 hours, after which time the number of prey animals predated was recorded once again. The results are summarized in Table 7-9 (below). The numbers of woodlice and the numbers of landhoppers taken were compared for the 15 minutes and the 3 hours stages, and were found not to be significantly different from each other (Mann-Whitney U test: U=37.5, P=0.133, for both stages).

Specimen	Number wl taken after 15 mins	Number lh taken after 15 mins	Number wl taken after 3 hours	Number lh taken after 3 hours
1	0	0	5	0
2	0	0	4	3
3	1	0	5	3
4	0	0	5	0
5	1	0	4	2
6	0	0	0	3
7	4	0	5	5
8	1	1	3	3
9	0	0	2	0
10	1	0	3	4
11	1	1	0	0

Table 7-9 Numbers of woodlice (wl) and landhoppers (lh) taken by toads offered five prey items of each type, after 15 minutes and after 3 hours.

The observations showed that the toads reacted strongly to movement, and that woodlice, which were generally active once introduced into the experimental enclosure, were watched and struck at more frequently than the generally inactive landhoppers. Furthermore, landhoppers were considerably more prone to shelter under the provided tissue paper than woodlice, and to remain there, inactive, presumably until darkness. This further reduced their probabililty of being predated, and explains why only eight out of the eleven individuals tested preyed on landhoppers. This experiment showed, however, that landhoppers are not in any way inpalatable to toads and are preyed upon readily where they are available, and sufficiently mobile.

Next, an attempt was made to re-create more natural conditions in order to assess the toads' ability to capture the landhopper in the wild. Initially, 50 landhoppers and 50 woodlice were placed into a depth of 2.5 cm of leaf litter in opaque boxes of 50x30x20 cm with a water bowl, and a toad was introduced and left to feed for 72 hours. It was found, however, that, probably due to the depth of the leaf litter, the toad was apparently unable to access the prey animals, which remained deep within the litter (as observed in section 8.2), and the original numbers (minus two which had drowned in the water bowl) were recovered at the end of the experiment.

In order to encourage the prey animals to emerge from the substrate, three small vivaria with a layer of soil and only a few pieces of leaf material on the surface, as well as a water bowl, a hiding place and a petri dish into which food items were placed, were constructed (Figure 84, page 284).

Figure 84 Short-term maintenance arrangement for *B. bufo.*

These vivaria were place in a constant temperature room at 20 °C with a 12L:12D light regime and a toad placed in each. When the animals started accepting food in their novel environment (maggots and earthworms were used to assess readiness for experimentation), 10 woodlice, 10 landhoppers and 5 litter-dwelling earthworms were placed into their vivaria, and the remaining prey animals counted after 24 and 48 hours. The results are summarized in Table 7-10, below.

Specimen	No. wl taken after 24 hrs	No. lh taken after 24 hrs	No. ew taken after 24 hrs	No. wl taken after 48 hrs	No. lh taken after 48 hrs	No. ew taken after 48 hrs
1	7	8	2	10	10	5
2	3	3	1	3	3	1
3	1	0	2	1	0	2

Table 7-10 Numbers of woodlice (wl), landhoppers (lh) and earthworms (ew) taken by *B. bufo* housed to represent semi-natural conditions, after 24 and 48 hours.

This experiment, although it investigated the behaviour of only three individuals, one of which was exceptionally reluctant to feed, showed that toads are capable of successfully predating landhoppers, even under conditions where these are provided with hiding places and space to conduct their evasive manoeuvres. It further showed that the toads will do so even in the presence of native prey species. It is highly likely that the toads stalk the landhoppers without drawing attention to their presence before striking so quickly that no escape response is elicited, rather than actively pursuing fleeing individuals. Further investigation with night-vision equipment would be of great interest to confirm this view.

7.3.1.2.3 Discussion - Amphibians

It has been shown here that toads readily feed on *A. dorrieni*, and that they are in all probability capable of doing so successfully under natural conditions. It is therefore likely that *A. dorrieni* will turn out to make up part of the diet of toads resident in areas colonized by the landhopper. Due to their large appetites and the fact that they are relatively common compared to most other British amphibians, it is possible that toads may have some effect on landhopper population densities and population expansion.

7.3.2 Birds

Many birds are extremely fast and accurate predators of invertebrates, and intertidal amphipods make up a large part of the diet of many shorebirds (Reid, 1947). Due to most landhoppers' tendency to occur at high densities and preferentially inhabit loose leaf litter, they are potentially within the range of many litter-feeding birds. There are no published reports of northern hemisphere birds feeding on a terrestrial amphipod, and only a few published reports of southern hemisphere birds doing so. This is probably to a large part due to the difficulty of accurately observing the predation of small, cryptic invertebrates under natural conditions (Oliver *et al.*, 1993). Nevertheless, many birds, particularly those resident in wet eucalypt forests, are believed to regularly incorporate amphipods into their diets (Friend *et al.*, 1986). Those birds reported as feeding on terrestrial amphipods include the Pink robin (*Petroica rodinogaster*) (Friend, 1975), the Lyrebird (*Menura superba*) (Searle, 1928) and the Noisy scrub-bird (*Atrichornis clamosus*) (Smith & Calver, 1984).

Among northern hemisphere birds, the thrushes are probably the most likely candidates for becoming important landhopper predators, as they already feed on a variety of cryptic litter-dwelling invertebrates, and habitually turn over leaf litter in the search for their quarry. Additionally, there have been reports of a North American thrush species (*Ixoreus naevius*), which has very similar feeding habits to British thrushes, readily feeding on semi-terrestrial amphipods where the sandhoppers' beach habitat meets the birds' less exposed woodland/scrub territories (Egger, 1979). Smaller birds such as

Robins (*Erithacus rubecula*), Dunnocks (*Prunella modularis*) and perhaps Wrens (*Troglodytes troglodytes*) forage in similar habitats and have been known to feed on members of the leaf-litter fauna (Witherby *et al.*, 1938). These species are, however, less prone to create the large-scale litter movements typical of foraging thrushes [particularly Blackbirds (*Turdus merula*) and Song Thrushes (*Turdus ericetorum*)], vigorous enough to uncover landhoppers.

7.3.2.1 *Blackbirds*

The Blackbird is without doubt the most widespread, and probably numerous, large avian leaf-litter feeder throughout most of the British Isles. It incorporates a wide variety of invertebrates and fruit into its diet (Witherby *et al.*, 1938) and is potentially both strong enough to expose the landhoppers from under their protective litter layer and fast enough to keep track of and catch them during their evasive manoeuvres. Blackbirds are often seen foraging in leaf litter containing native amphipods in Tasmania (A. Richardson, pers. comm.), similar to the Lyre bird (*Menura novaehollandiae)*, which has been reported to incorporate landhoppers in its diet (Searle, 1928). Blackbirds were also regularly seen foraging in landhopper habitat in Britain, however it was not possible to accurately identify the prey items taken, which is why direct observation is usually considered not a reliable method for mobile birds (Moreby & Stoate, 2000). Studying nestling food would have not proved fruitful either, since blackbirds feed their young predominantly on earthworms rather than arthropods. Therefore, a flock of captive sub-adult Blackbirds was utilised for this study.

Initially, the birds were trained to collect their daily ration of live insects (maggots and beetle larvae) from two white plastic trays, first without and later with the addition of some leaf litter, with an observer present in close proximity (Figure 85, page 290). During this time, the dominance hierarchy among the birds was established. This is illustrated in Figure 86 (page 290). After 1 week, when the birds had become used to this procedure, both trays were filled with equal amounts of previously frozen leaf litter and 50 landhoppers placed in each. As usual, the birds appeared in order of their dominance, and readily fed on the new prey item, often pursuing jumping hoppers into the surrounding grass and eventually successfully capturing them.

On subsequent three days, 50 woodlice were placed in one tray and 50 landhoppers in the other. The time spent feeding in each tray, particularly by the dominant bird, was recorded, with an emphasis on the first feeding bout, which tended to result in much of the leaf litter being scattered out of the tray. Additionally, any defence of either tray against other birds was watched for. The dominant bird always arrived first, scanned both trays for a few seconds, and, on all three days, went on to feed in the tray containing landhoppers. This first feeding bout lasted a mean of 155 seconds. At the end of this period the tray was typically 80% devoid of leaves. The bird then moved on to the woodlouse tray and foraged there for a mean 72 seconds until this, too, was largely empty. During this time, the subordinate birds remained around the perimeter and foraged in the scattered leaves. When they eventually moved into the trays, typically after the dominant bird had finished its first bout in each tray and started to move from one to the other in shorter bouts of circa 30 seconds, they did not show any preference as to which tray they foraged in first. By this time, the invertebrates had probably already spread out of the scattered leaf litter into the surrounding grass and were not concentrated in any one area. Due to the periods of time spent pursuing escaping prey and foraging in the grass between in-tray feeding bouts, the results could not be presented in table format or analyzed statistically. The experiment showed, however, that the landhopper is without a doubt a potential, and perhaps even favoured, prey item of the blackbird, and that the bird is fully capable of uncovering, pursuing and capturing this extremely agile prey.

Compared to the other potential landhopper predators examined thus far, the Blackbird is the most likely to exert a strong influence on landhopper populations due to its size and agility. It may even be able to limit the alien's invasive potential by utilising it as a food source in those habitats where it is forced to gather in limited patches of cover which can be systematically searched, such as in gardens.

Figure 85 Blackbirds (cinnamon [left] and silver [right] phases) foraging in trays containing landhoppers and woodlice.

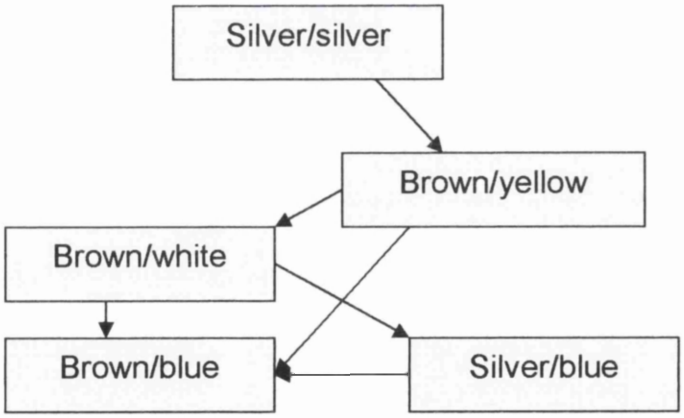

Figure 86 Dominance hierarchy of flock of captive sub-adult *T. merula*. First colour indicates body colour, second colour indicates leg ring colour. Silver/silver (also the oldest individual) was dominant over all other birds.

7.3.2.2 Other thrushes

The only other thrush species which could be examined for acceptance of *A. dorrieni* as a prey item was the Fieldfare (*T. pilaris*). It could be shown that captive Fieldfares took *A. dorrieni* readily and captured it without difficulty, but this species is unlikely to exert an effect on current landhopper populations due to their more northerly distribution (generally only bringing them to the British Isles as winter visitors) and its less pronounced ground-feeding habits in woodland compared to blackbirds and song thrushes (*T. ericetorum*) (Witherby *et al.*, 1938).

7.3.3 Mammals

As described in the Introduction to this section, there are not many potential mammalian amphipod predators in the UK. There has, however, been one report of cuticular remains of *A. dorrieni* being found in the stomachs of Pygmy shrews (*Sorex minutus*) accidentally caught in pitfall traps filled with formalin (O'Hanlon & Bolger, 1997).

Further, non-destructive research into the feeding behaviour of this shrew in landhopper-colonized habitat would be very interesting, but unfortunately fraught with major problems. Observation of shrews in the wild is a very difficult undertaking, and a reliable determination of the nature of the prey items taken would be more difficult still. Laboratory observations require a special license, and are notoriously unreliable, as captive shrews will feed on many prey items they would not naturally pursue (P. Llewellyn, pers. comm.). However, even if *A. dorrieni* were utilized regularly as a food source in the locations it has populated, shrews are unlikely to have a controlling effect on landhopper populations due to the low densities at which they occur (Churchfield, 1986).

7.4 General Discussion

This series of laboratory experiments has shown that *A. dorrieni* probably faces considerable predation pressure by representatives of most native predators of invertebrates under natural conditions. It is thus even more surprising that this alien has been able to establish such thriving populations, and spread as widely across the country as it has, in probably no more than a century.

The results from this study have only been able to provide a first glimpse of the complex predator-prey relationships between native predators and the landhopper. There is much scope for further research in this area, and possible upward changes in densities of predators in areas which are well colonized by *A. dorrieni* compared to those which are still free from the alien should receive particular attention.

8 Activity and dispersal of *A. dorrieni* under laboratory conditions

8.1 General Introduction

This section consists of three parts, all of which are aimed at providing a first insight into *A. dorrieni's* dispersal capabilities, by investigating its surface activity levels, activity rhythms, and its potential ability and inclination to cross leaf-litter free areas. A better understanding of these aspects of landhopper biology will make it easier to predict potential future spread, including the speed of any such colonizations.

Due to restrictions with regard to both time and resources, many of the experiments could only be replicated the minimal number of times, which means that the results only allow the formation of an initial, 'baseline' representation of the landhopper's behaviour under natural conditions. Thus, there is much scope for further research. Areas of research pressingly needing further investigation are highlighted in the discussions.

8.2 Nocturnal surface activity of A. dorrieni under laboratory conditions

8.2.1 Introduction

Although landhoppers are described as cryptozoic (Hurley, 1968), they have been known to move freely on the surface of the litter, particularly at night (Friend, 1980). Reports of landhoppers that normally dwell in leaf litter being caught in traps positioned on tree trunks (Moeed & Meads, 1983), found inside houses (Mallis, 1954), and even in the rainforest canopy (Friend *et al.*, 1986) are further evidence of this behaviour.

This experiment was designed to investigate whether, and to what extent, *A. dorrieni* emerges from the leaf litter during the hours of darkness. Information on this aspect of behaviour is essential in order to assess the animal's ability to disperse over open ground, as well as its potential exposure to predators.

8.2.2 Materials and Methods

In order to approximate to natural conditions, leaf litter containing *A. dorrieni* was collected the day before the experiments. The leaf litter was taken from suburban gardens where landhopper densities were known to be high. The same sample was used on two consecutive nights and kept at room temperature with a natural photoperiod during the day. The entire procedure was repeated at weekly intervals for one month.

The litter was placed in a white plastic bowl to a depth of approximately 6 cm. A 50 cm long transparent plastic tube of equal diameter had been attached to the bowl in order to provide natural light intensity while preventing the escape of subjects. Recording equipment consisted of a VHS camera (Panasonic, Bracknall, UK) fitted on a stand to point vertically downwards and connected to a VHS video recorder (Panasonic, Bracknall, UK) capable of *Long Play*, which was used for this experiment. In order to record the animals' activity, a flash of light of 12 s duration was produced every hour using a desk lamp with a 60W bulb and a specially constructed timer (Figure 87, page 296). Figure 88 (page 296) shows the complete arrangement.

Relative humidity just above the surface of the substrate was maintained at 80%. Recording was started between 18:45 and 19:00h except on night 3 when recording had to be delayed until 21:00h. Times of the first flash were 19:24, 19:30, 21:19 and 19:31h, respectively.

Figure 87 Electronic timer constructed to produce one 12s on-phase per hour.

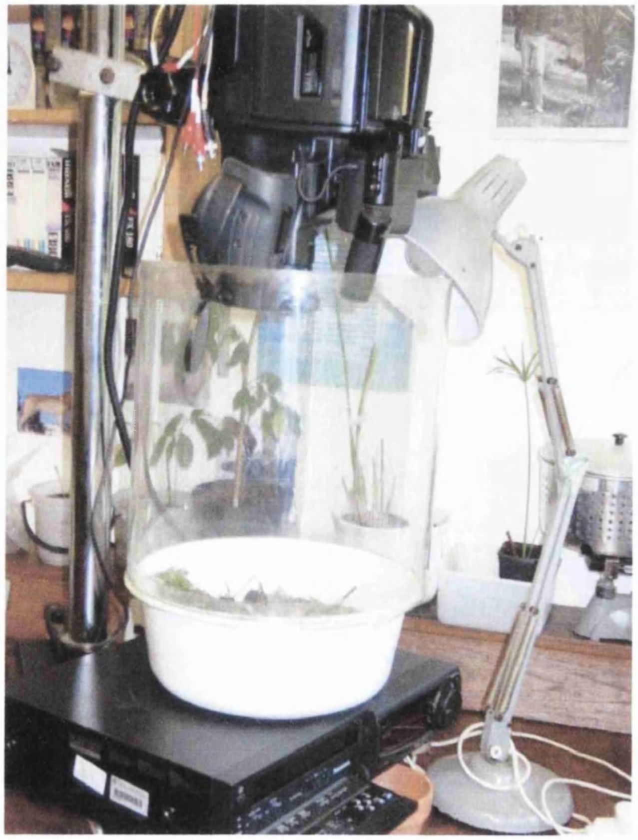

Figure 88 Arrangement for recording nocturnal surface activity of *A. dorrieni.*

8.2.3 Results

The results are summarized in Table 8-1 (below). Landhoppers were observed on the surface during 5 of the 24 recorded flashes. Generally, only one individual was seen. On one occasion, however, as many as eight were observed on the surface simultaneously. The only other animals observed on the surface of the litter during this experiment were isopods, which were also seen on 5 of the 24 occasions, but never in large numbers.

Flash	Night 1	Night 2	Night 3	Night 4
1	no activity	1 wl walking	no activity	no activity
2	no activity	no activity	1 lh jumping	8 lh jumping and scuttling
3	no activity	no activity	no activity	3 lh scuttling, 1 wl walking
4	no activity	2 wl walking	no activity	1 lh walking
5	1 lh walking	no activity	no activity	1 wl walking
6	no activity	no activity	1 wl walking	no activity

Table 8-1 Observations of surface activity during the hourly light flashes (lh...landhopper, wl...woodlouse).

8.2.4 Discussion

It appears that landhoppers remain buried in the substrate for most of the hours of darkness as well as during the day. The frantic surface activity recorded on one occasion indicates either that conditions were particularly 'suitable' for surface activity, or the animals had been brought to the surface by a different factor (such as a hunting centipede deeper in the litter).

It is not possible to say at this point what constitutes, or indeed if there are, particularly 'suitable' conditions predisposing landhoppers to become active on the surface. It would be very interesting to record environmental variables, such as changes in air pressure before impending rain, in relation to landhopper surface activity. Ambient humidity and temperature, however, do not seem to be crucial factors. Humidity at the surface was kept at 80% on all four nights and all four experiments were conducted in the same location where the temperature was kept constant. Availability of food may play a role, but the large amount of leaf litter present suggests that this is unlikely to have contributed in a major way to the sudden increase in activity. Activity also subsequently declined after its peak early in the night, which is unlikely to happen in case of a food shortage.

Results from section 8.3 indicate that, had it been possible to continue the experiments until the morning, a marked increase in landhopper surface activity may have been recorded from just before to just after dawn (as they are most active at this time). It appears, however, that landhoppers, as well as woodlice, are rather prone to remain hidden within a litter layer, where this provides adequate levels of shelter, food and humidity, rather than venturing onto the surface. Nevertheless, the experiment showed that emerging onto the surface of potentially adequate litter habitat during the hours of darkness is a natural, if not frequent, behaviour of *A. dorrieni*. This would facilitate potential dispersal, since the animals emerging onto the surface in the context of this behaviour are probably well fed and hydrated, as opposed to those individuals that may be active on the surface only as a result of adverse conditions in their original habitats.

At least occasionally, nocturnal surface activity has to be of a considerably large scale, in terms of active landhopper numbers, duration of activity and distance covered, since there has been a reliable report of more than two dozen individuals sheltering under the topmost bag of a stack of four sacks of building sand, which had only been in position (on a concrete surface) for 48 hours prior to the discovery of the animals (F. Harper, pers. comm.). There had been some rain during at least one of the previous two nights, which may have been the main factor encouraging the landhoppers to become active on the surface.

There is much scope for further research into the surface activity of *A. dorrieni*, particularly since it is an important factor in the landhopper's dispersal potential. If, for example, it is discovered that landhoppers only emerge from the leaf litter when forced to do so in order to survive, they may be much less likely to successfully cross litter-free spaces such as roads or fields, and arrive on the other side in sufficient numbers to form new colonies, than if they are found to venture out from their hiding places on a regular basis.

Investigations under natural conditions in landhopper-colonized areas should be undertaken as soon as possible, and with the aid of night-vision equipment. These investigations should incorporate observations under different weather conditions and in different habitat types.

These should include at least two directly opposite habitat types, namely:

a) habitats where there is more or less continuous litter cover providing shelter and food, such as in a level area of deciduous woodland, and

b) habitats where shelter and food are very patchily distributed and landhoppers have to congregate in restricted spaces during the day, such as in gardens).

While data should be collected for all hours of darkness, the results produced in section 8.3.3 suggest that the main focus should be the hours around dawn, when the landhopper activity appears to be at its peak.

8.3 Activity recording

8.3.1 Introduction

With increasing distance from the intertidal zone, crustaceans usually exhibit a predominant activity pattern based on light and dark intervals, rather than changes in water level (Barnwell, 1968; Palmer, 1973). Many terrestrial crustaceans, as well as millipedes and other myriapods whose cuticles lack a waxy outer layer and therefore render the animals very prone to desiccation, are nocturnal or crepuscular, taking advantage of lower temperatures and increased ground moisture in the evening, at night or at dawn in order to feed and disperse on the surface (Cloudsley-Thompson, 1958; Powers *et al.*, 1983).

Many studies of decapods focus on, or at least touch on, activity rhythms (e.g. (Bliss, 1979; Bliss *et al.*, 1978; Henning, 1975; Henning & Klaassen, 1973; Linsenmair, 1967). Activity rhythms in amphipods are less commonly studied, but there have still been a few investigations on the subject (e.g. Kennedy, Naylor & Jaramillo, 2000; Scapini *et al.*, 1992; Williams, 1983). A comprehensive list of the earlier studies up to 1980 is provided in DeCoursey (1983). All research to date, however, has focussed on aquatic or semi-terrestrial amphipod species, and no attempt has as yet been made to investigate the activity rhythms of landhoppers. The aim of this section was to design an effective experimental technique for examining landhopper activity rhythms in the laboratory, and the production of a set of baseline data which may be used to build on in future studies.

8.3.2 Materials and Methods

The experiments were conducted in a windowless room at an ambient temperature between 15 and 18°C. The photoperiods were 9L:15D (regime 'a'), and 15L:9D (regime 'b') respectively. These corresponded with the natural photoperiod at the time of the collection of the experimental animals. The animals were kept in translucent open-topped plastic containers (20x20x10cm) with leaf litter under this light regime for up to a week until they were used in the experiment. The light was provided by a 30 Watt neon tube mounted 40 cm above the experimental setup, giving an approximate light intensity of 10 µmole photons m^{-2} s^{-1} in the experimental arena. The level of activity was measured automatically using a custom built system loosely based on an arrangement used for freshwater amphipods (Kusano & Kusano, 1991), and adjusted for use with landhoppers. In this arrangement, the animal moving in a petri dish interrupted an infra-red beam (projected approximately 2 mm above the bottom) and each interruption was recorded as a pulse on an event recorder (arrangement illustrated in

Figure 89, page 304 and Figure 90, page 304).

The animal to be examined was placed in a medium sized petri dish (5.5 cm diameter), which was mounted inside the metal ring holding the infra-red light source and photo cell. This arrangement had the added advantage that it allowed light into the petri dish only from above. Two small holes in the sides of the petri dish allowed for interference-free passage of the the infra-red beam across the experimental arena. It was also found to be necessary to line the sides of the petri dish on the inside with black insulation tape with pinholes over the holes in the petri dish to properly focus the beam. The petri dish was lined with two sheets of damp filter paper (cut to size to exactly fit inside the dish). The filter papers were moistened with distilled water to saturation point. Very smalll amounts of water were added each day around the middle of the light phase in order to make up for humidity lost through evaporation.

Attempts were also made to keep the filter papers constantly moist by means of a cotton wool thread running through a plastic sleeve and connecting the filter papers to a small flask of distilled water. However, this arrangement led to an accumulation of water in the petri dish and proved unsuitable. The petri dish lid was connected to the metal ring by a ridge of 'Blu-tack' (Bostik Ltd., Leicester, UK) in order to provide a tight seal and thus minimize evaporation. On one side of the petri dish, a selection of small pieces of leaf litter of various species of trees was provided, which acted as food and shelter for the animal under examination. These leaf pieces were replaced by small pieces of artificial sponge, filter paper and thin latex where the effect of food deprivation on the activity level was being examined. The filter papers and food were changed each time a new animal was introduced into the experimental arrangement to ensure that it would not be affected by substances (such as pheromones) possibly left behind by the previous subject.

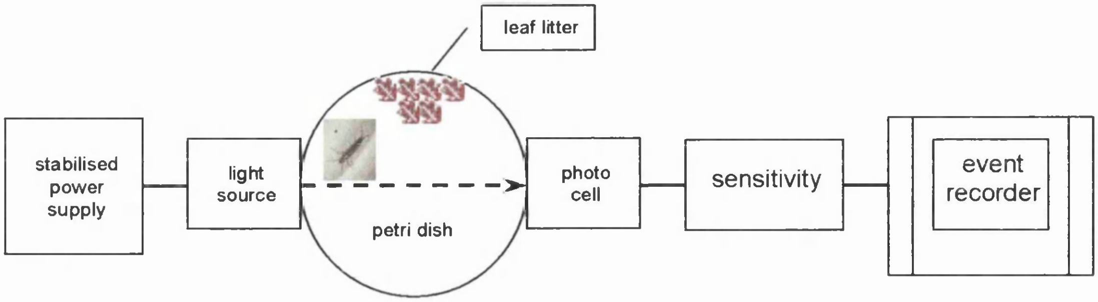

Figure 89 Diagram of the system used for monitoring the activity of *A. dorrieni.*

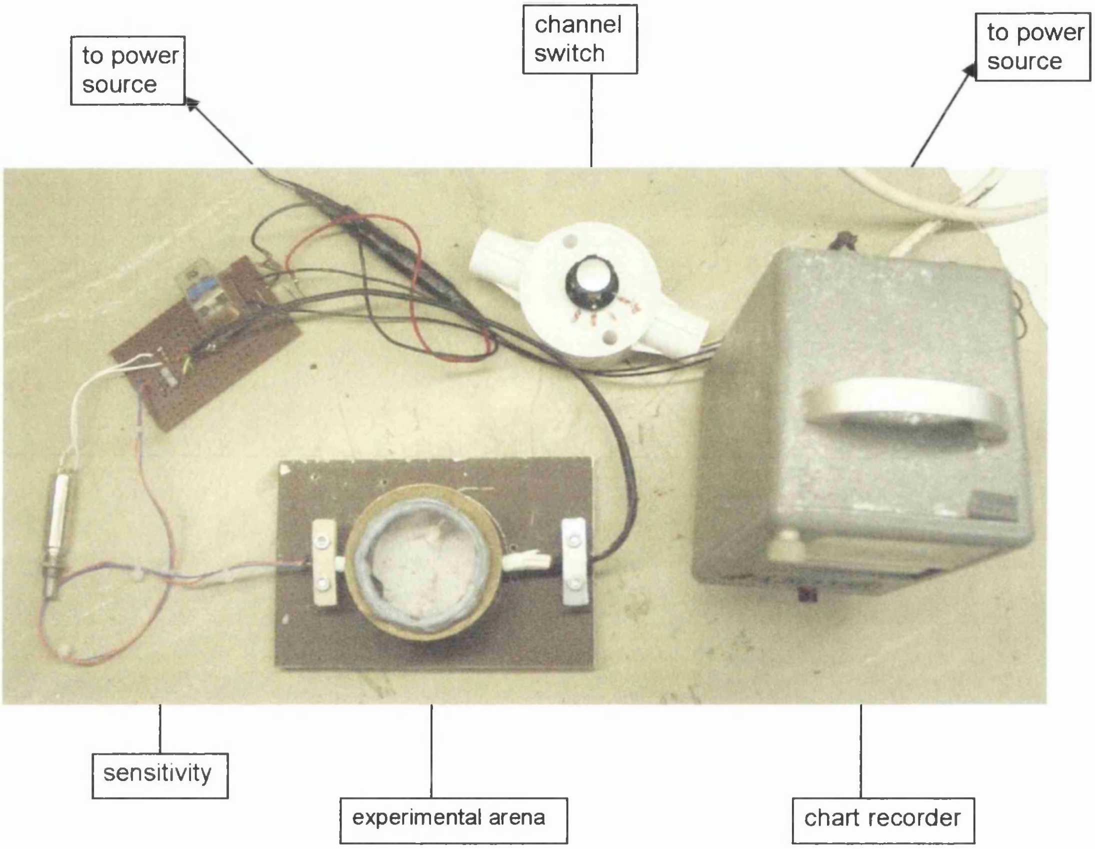

Figure 90 Photograph of the main components in the arrangement used for monitoring the activity of *A. dorrieni.*

The individual animals were introduced during the light period. The first 24 hours were considered an acclimatisation period and the results were not included in the analysis. The following three 24 hour periods were used to establish mean activity levels. In both light regimes, 10 animals (5 of each sex) were tested. In order to assess the effect of food deprivation on activity levels, a further 5 individuals were tested at the 9L:15D regime, and one further female carrying eggs was tested under this regime, in order to receive results from 3 gravid and 3 non-gravid individuals for comparison. The animals' activity was assessed by numbers of interruptions of the infra-red beam per hour, as recorded on the chart recorder. At the end of the four days, the animals were removed, anaesthetised with CO_2 (as described in section 5.3) and their breeding condition determined. Subsequently, they were allowed to recover and then released. The marks on the chart recorder trace were counted and recorded. It was found necessary to adjust the speed of the chart recorder to 5.08 cm/hour (standard setting 2.54 cm/hour) to produce sufficient accuracy.

Three problems were regularly encountered during data collection, namely:

- Inactivity due to an imminent moult - data collected from those animals were not included in the analysis.
- Inactivity due to disease (presumed to be Whitey disease, see section 5.4). This could generally be avoided by only choosing animals that did not show the typical bleached body colour. On two occasions, however, the first visible signs of the disease, along with the inactivity, developed during the four-day period of the experiment. Data from these diseased animals were also excluded from the analysis.

- Relocation of leaf fragments into the path of the beam. Where this occurred, the data for that particular 24-hour period were excluded from the analysis and an additional 24-hour period conducted. One individual, however, seemed to have such a penchant for this activity (she moved the leaf litter into the path of the beam on five consecutive nights), that she had to be released without any data having been collected.

8.3.3 Results

The mean number of interruptions per hour was calculated for the three 24-hour periods for each animal. Then, the means calculated for each animal were used to calculate means for a typical:

1. 'male'
2. 'female'
3. 'individual (either sex)'

These 'baseline' data are represented in Figures 96-101 (pages 326-328). It can be seen that under both light regimes, activity levels declined very quickly once the light was turned on, and reduced to very low levels or even ceased entirely within a maximum of two hours after 'dawn'. Activity levels started to rise immediately after the lights were turned off, but did not reach maximum levels until 9 -10 hours after 'dusk'. This time period applied to both light regimes, meaning that the peak in activity occurred earlier during the dark period in regime a) than in regime b). In the latter peak activity was reached just before 'dawn'. Peak activity levels were higher in regime b) (maximum reached by females with 63 intercepts/h) than in regime a) (maximum reached by males with 45 intercepts/h). Overall activity, however, was significantly higher in regime a) (Mann-Whitney U test: U=183.5, P=0.031).

There were no statistically significant differences between male and female activity levels under either light regime (Mann-Whitney U test: U=264.5, P=0.633 and U=232, P=0.245, for regimes 'a' and 'b' respectively).

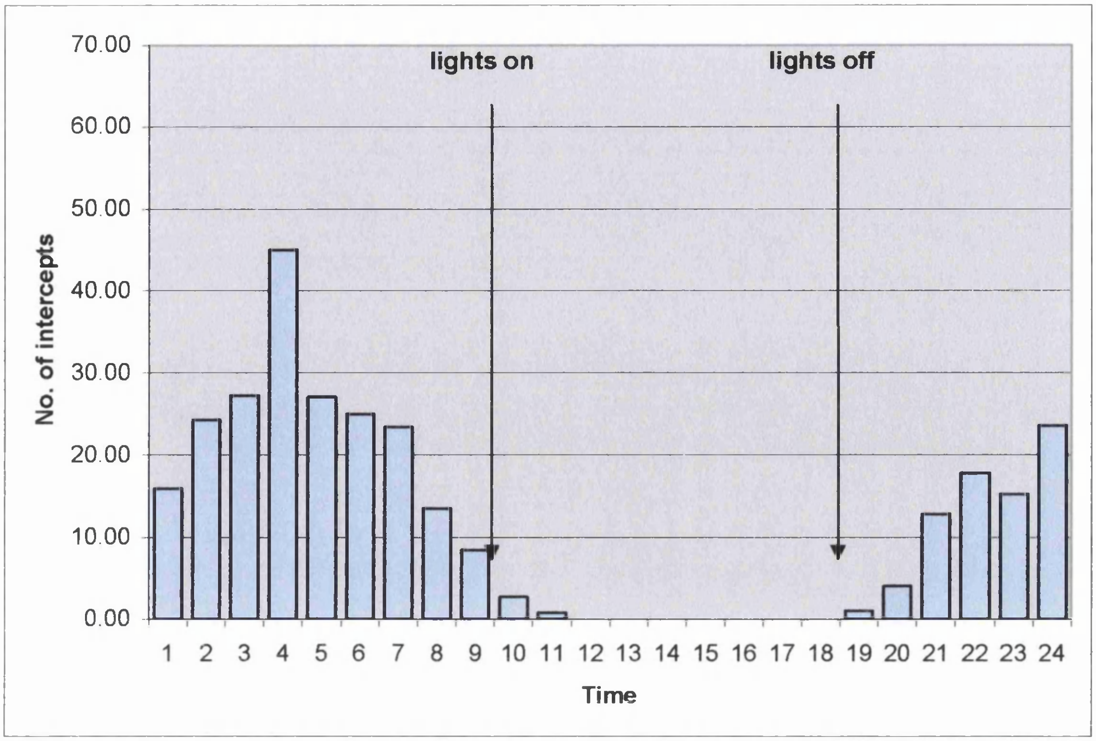

Figure 91 Diel change in the activity level of male *A. dorrieni* during the 9L:15D regime.

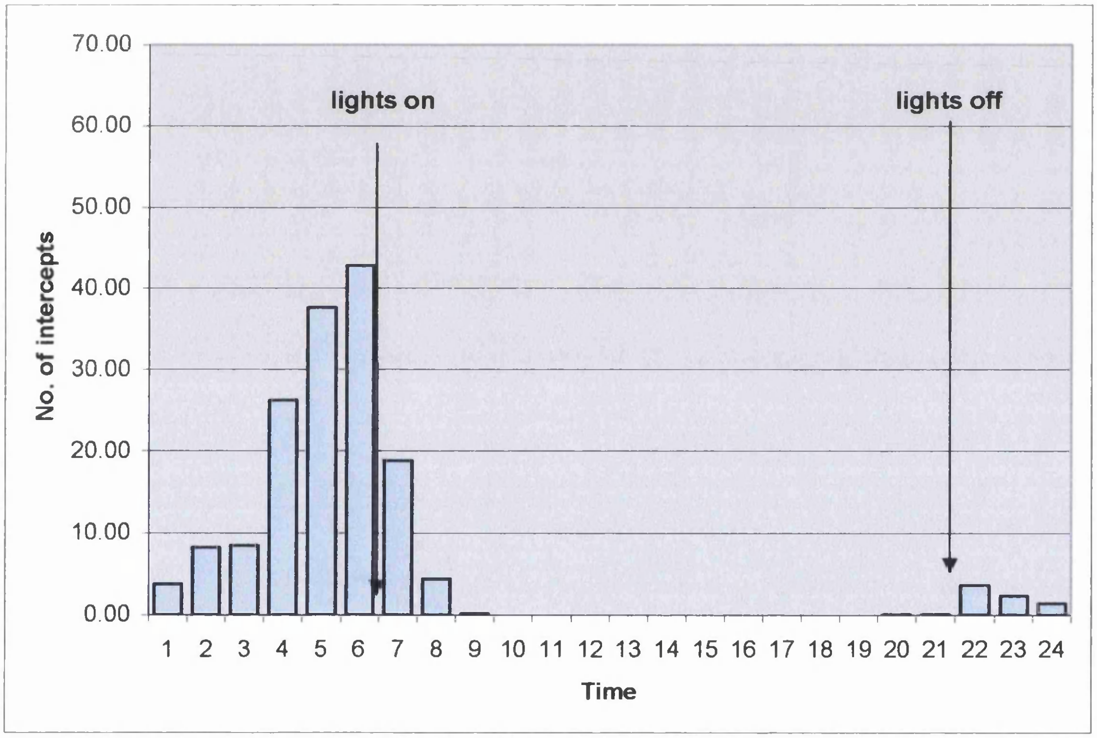

Figure 92 Diel change in the activity levels of male *A. dorrieni* during the 15L:9D regime.

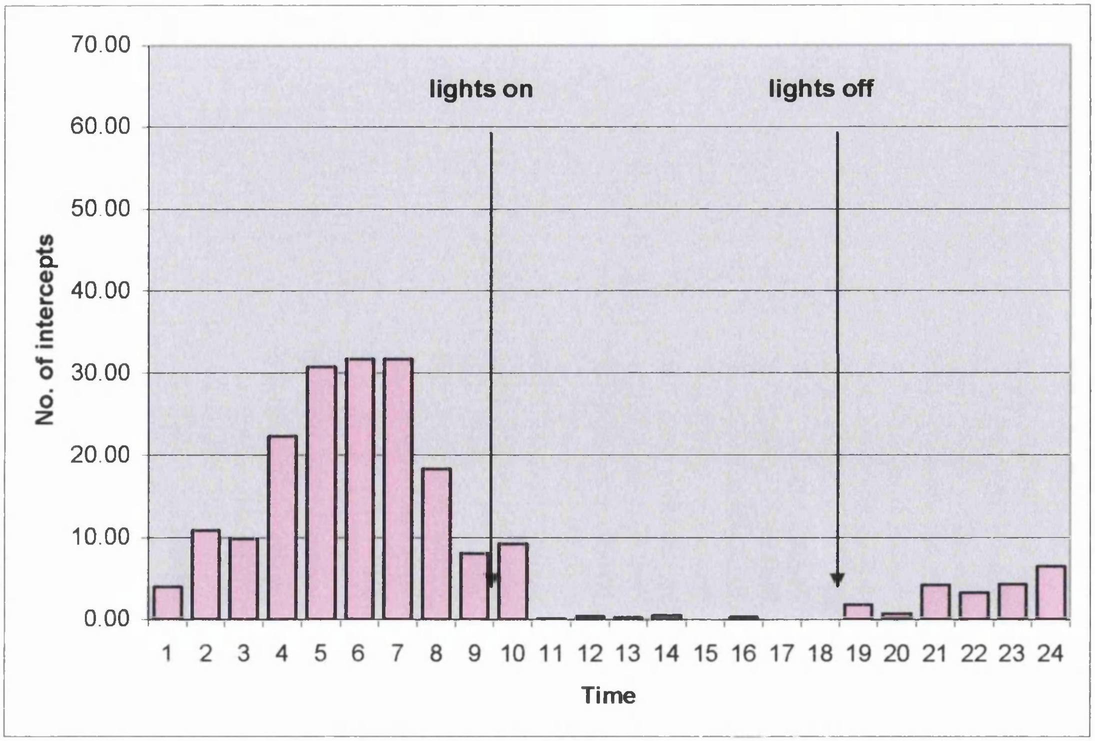

Figure 93 Diel change in the activity level of female *A. dorrieni* during the 9L:15D regime.

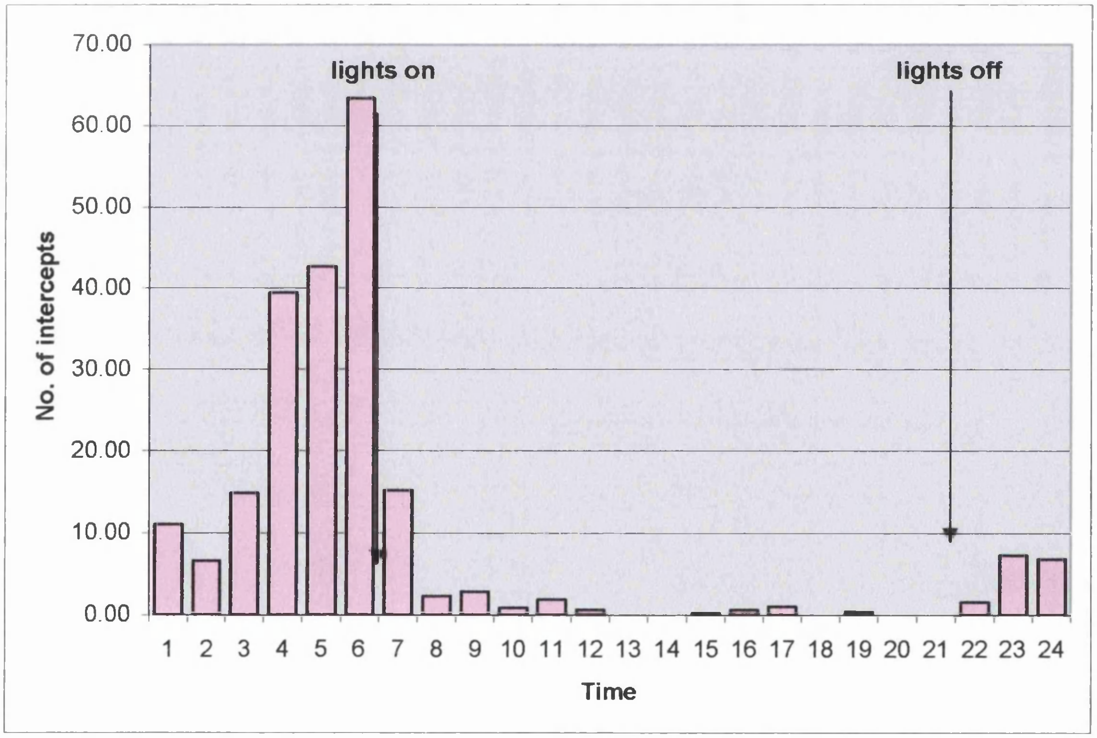

Figure 94 Diel change in the activity levels of female *A. dorrieni* during the 15L:9D regime.

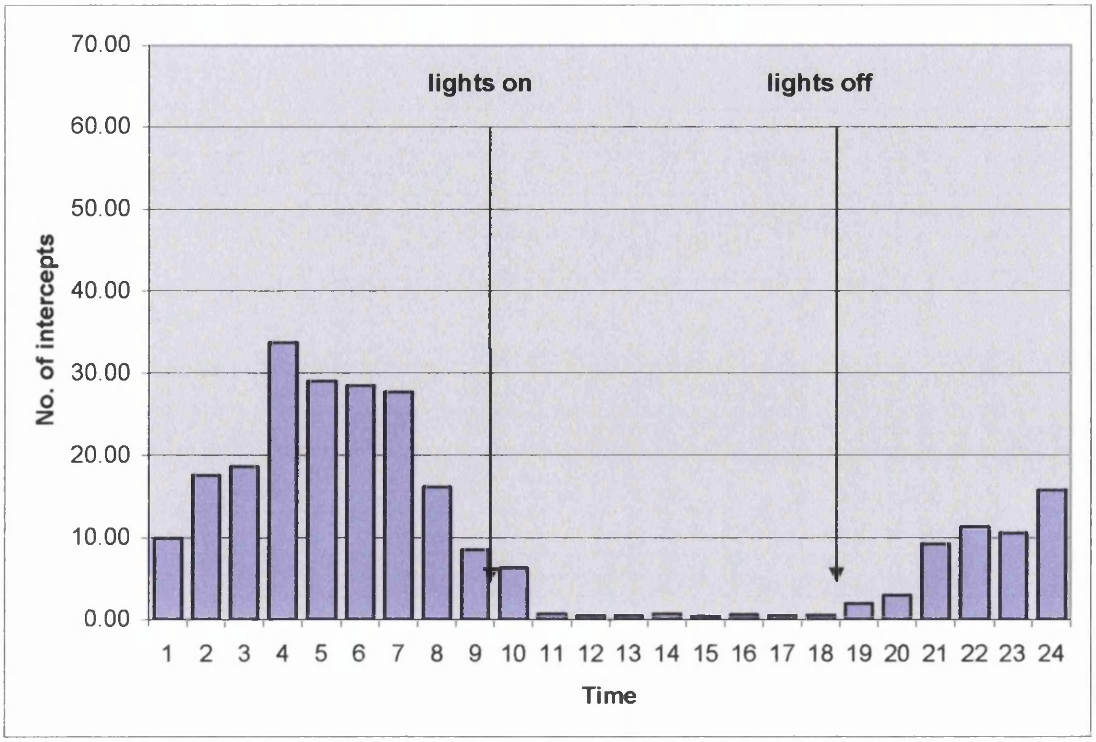

Figure 95 Diel change in the activity levels of *A. dorrieni* (both sexes) during the 9L:15D regime.

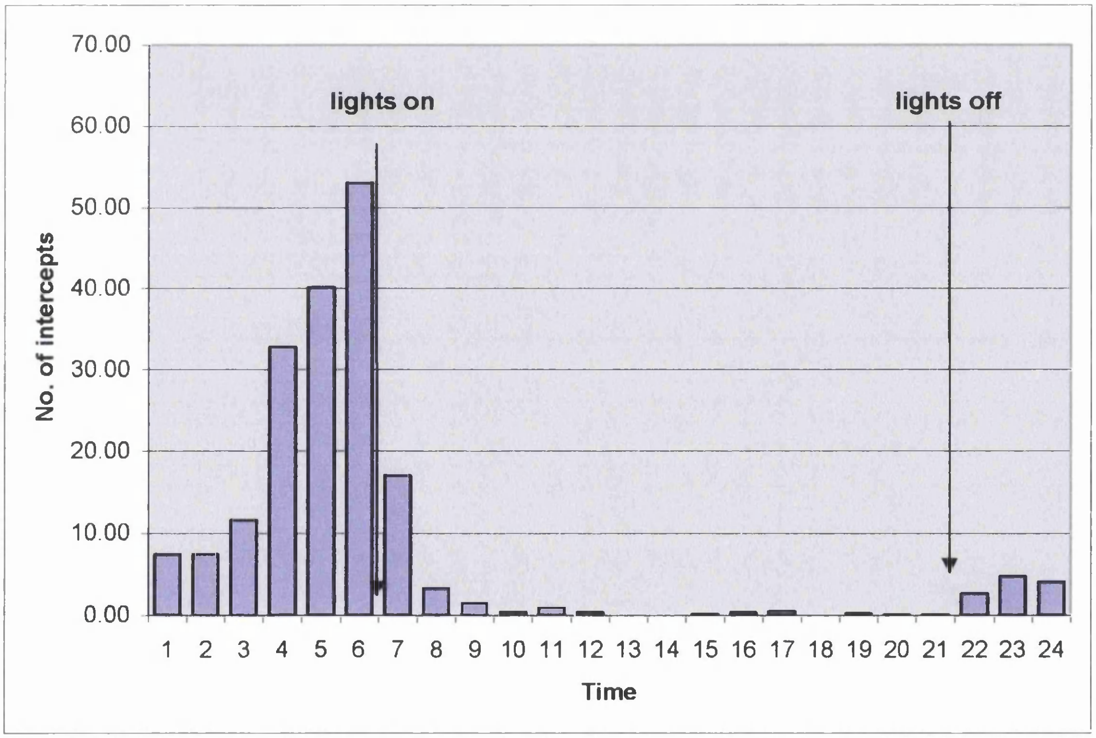

Figure 96 Diel change in the activity levels of *A. dorrieni (*both sexes) during the 15L:9D regime.

The animals which were tested under conditions of food deprivation showed significantly lower activity levels than those individuals with access to food (Mann-Whitney U test, U=189.5, P=0.042). The activity levels for this group are illustrated in Figure 102 (below).

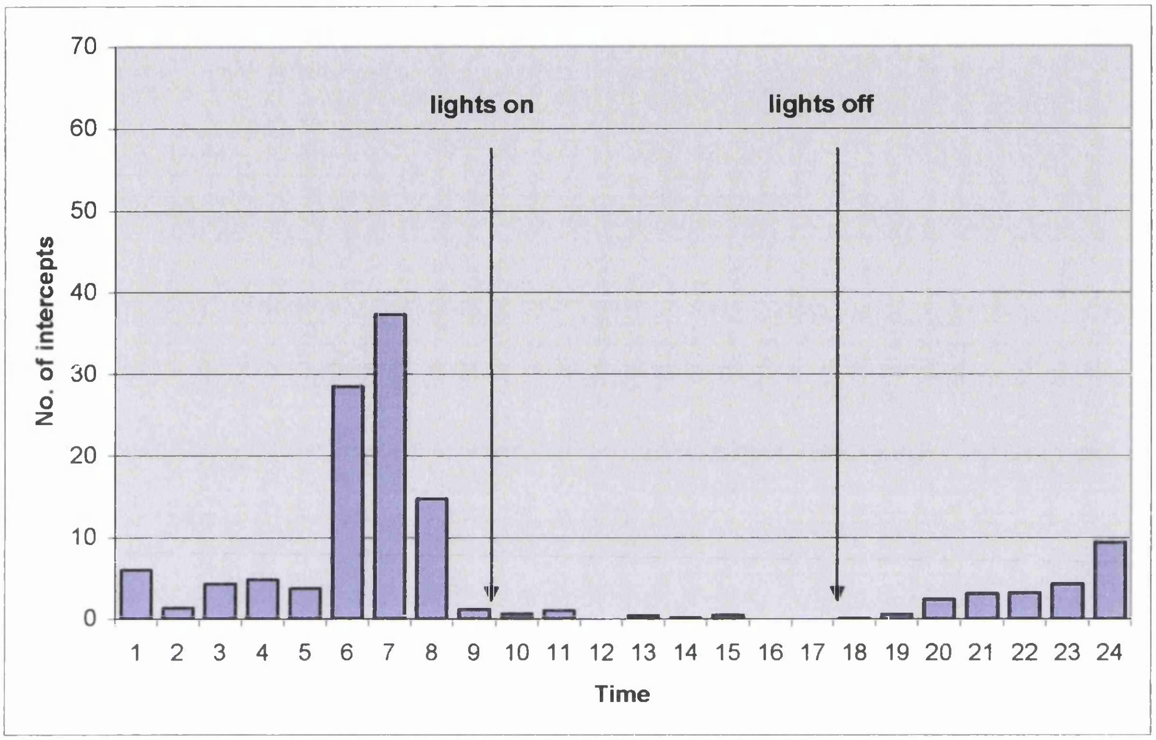

Figure 97 Diel change in the activity levels of *A. dorrieni* (both sexes) during the 9L:15D regime when food was withheld.

Finally, the activity levels of females with eggs in the brood pouch and those not carrying eggs were compared (Figure 103, page 330). There was a noticeable difference, with females carrying eggs being less active than those without eggs. This difference, however, was not quite statistically significant (Mann-Whitney U test, U=203.5, P=0.082).

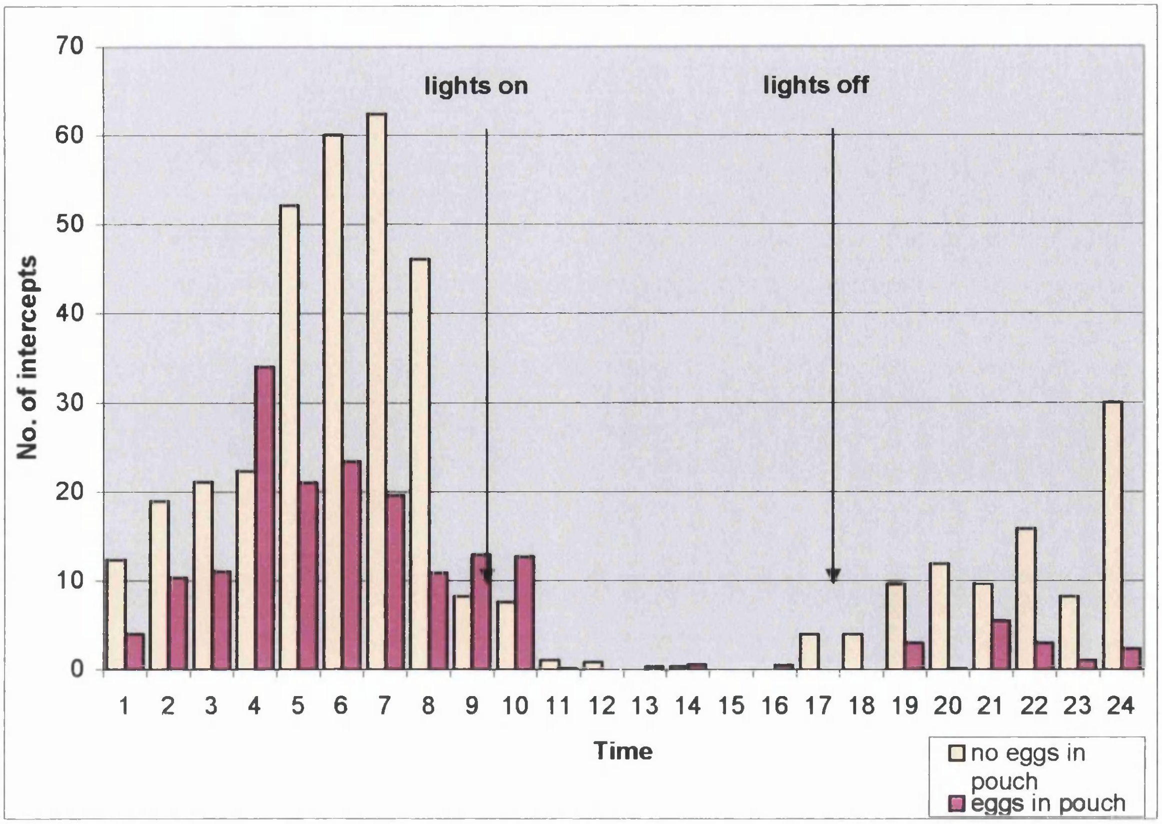

Figure 98 Diel change in the activity levels of female gravid and non-gravid *A. dorrieni* during the 9L:15D regime.

8.3.4 Discussion

It could be shown that *A. dorrieni* possesses a marked diel activity rhythm, with over 90% of all activity occurring during the hours of darkness. Maximum activity levels are reached 9-10 hours after the onset of darkness, independent of the length of the preceding light phase. This leads to a peak in activity during the early hours of the night in the short-day regime, whereas it results in a peak just before ‘dawn’ in the long-day regime. The data collected for the short-day regime may not be entirely representative of the activity under natural conditions, as the ambient temperature during the tests was higher than it would have been at the time of comparable light – dark rhythm outdoors. The data collected for the long-day regime, on the other hand, probably represents activity levels under natural conditions quite accurately, indicating that a peak in activity around dawn may be typical for *A. dorrieni.* Peaks in activity, both during the early hours of the night and again around dawn have been observed in some populations of the semi-terrestrial amphipod *T. saltator* (Geppetti & Tongiorgi, 1967; Scapini *et al.*, 1992), whereas in other populations such peaks were not apparent (Bregazzi & Naylor, 1972).

The continuation of activity into the first one or two hours of the light phase is most likely a result of the unnatural sudden change in light levels created by the artificial lighting in the laboratory. Ideally, dusk and dawn should have been imitated in the laboratory for this experiment. Unfortunately, however, the necessary equipment was not available. Had there been a gradual change in light intensity, it is very likely that activity levels would have reduced gradually in line with the changing light levels and reached their minimum daytime levels when light levels would have reached full intensity.

Interestingly, there was no noticeable difference in the activity levels of male and female *A. dorrieni.* Initial results from pitfall trapping (section 9.1) indicated that males may be more active than females, as they were caught more frequently. On the other hand, the activity levels recorded here do not indicate the animals' propensity to disperse. It is thus possible that females are just as active within the leaf litter as males, but that the males devote some of their activity to surface dispersal.

When food was withheld, activity levels were significantly lower than under identical conditions where food was provided. Intuitively, activity levels would have been expected to rise in the absence of food, as animals might be expected to search for a food source. Repeated experiments over longer periods of time are needed to determine whether, perhaps, activity increases with the length of time that food has been withheld (during the three nights of this experiment, the individuals may have engaged in coprophagy, which may have reduced their urge to find alternative food).

A decrease in activity in females carrying eggs in the marsupium compared to non-ovigerous individuals could be observed. This decrease would probably have been statistically significant had sample size been larger. In *A. dorrieni*, eggs are easily lost from the marsupium during vigorous movement, so minimizing activity levels and thus potential exposure to predators or inhospitable conditions which may make vigorous movements necessary would be a very useful adaptation to ensure maximal survival of the brood.

Much additional research is needed in order to build up a complete picture of landhopper activity rhythms. In particular, investigation is required into whether:

- the observed rhythms are endogenous [as they are in *T. saltator* (Bregazzi *et al.*, 1972)] or defined by external sources;
- there may be remnants of tidal rhythms [these may be present especially in landhopper species other than *A.dorrieni* which are confined to locations close to the shoreline by their high sodium requirements (Friend, 1987; Richardson *et al.*, 1991)];
- activity patterns vary with changes in environmental factors (particularly humidiy and temperature).

8.4 Dispersal capabilities of A. dorrieni under laboratory conditions

8.4.1 Introduction

One characteristic that all successful invasive species have in common is their ability to disperse swiftly and effectively from their point of introduction. Dispersal is effected in many different ways by different species. It may be active or passive, although there are rare examples of combinations of the two. For example, in certain Coleoptera (such as members of the Genus *Meloe*) the larvae actively seek out an adult member of a different species in order to passively 'hitch a ride' to their destination, and some small flying insects (such as members of the Homoptera) actively fly to a certain height in order to then passively drift on the wind for long distances.

There are examples of dispersal taking place at virtually any stage of the life cycle in one species or another. For example, plant seeds (the major stage of dispersal in most higher plants) may be carried by air and water currents as well as by animals. Eggs of aquatic animals may be carried over long distances by the current. Larval and juvenile stages may also be carried by water currents (as in many crustaceans) or air currents (as in certain arachnids), or disperse by their own agency (as in many fish species). The adult stage - in animals often the largest, most resistant and most mobile stage in the life cycle - generally contributes most to a species' dispersal by flying, swimming or walking. Many species have developed ingenious adaptations to maximise their dispersal efficiency.

At first sight, one would not predict that *A. dorrieni* would be able to disperse effectively. Its physiological adaptability and resistance to changing environmental conditions is very limited throughout its juvenile and adult stages (Cowling *et al.*, 2003; Cowling *et al.*, 2004; Morritt, 1987). The egg stage is dependent on incubation in the female's brood pouch, and the animal, once hatched, is incapable of flight (a major factor in dispersal success in many similar sized terrestrial animals) or rapid locomotion over distances. Despite these limitations, it has been claimed that the landhopper is capable of covering 40 m in a single night (Duncan, in Hurley 1968). The original publication by Duncan could be located, but the means by which this observation was obtained are not described. Attempts to contact the author failed to elicit any clarification.

The fact that *A. dorrieni* has become very widespread in some parts of the UK suggests that it must be capable of reasonably efficient dispersal, despite the indications that this should be otherwise. There are, currently, no studies on the dispersal capabilities of *A. dorrieni*, either in the laboratory or in the field. The following series of experiments was designed to provide some insight into the landhopper's inherent dispersal capabilities and limitations. The results from two pilot experiments were used to obtain the baseline information necessary to produce a set of effective replicated experiments and are included here to aid future experimental design.

8.4.2 Pilot experiment 1

8.4.2.1 Materials and Methods

The experimental arena consisted of a metal tray (90 x 50 x 5cm) into which five roughly circular piles (15cm in diameter and 2cm thick) of compost were placed, one in the centre and one near each corner. The pile in the centre was connected to one of the corner piles by a bridge of compost (8cm wide and 1cm thick). All compost, with the exception of the central pile, contained 60% water (a level previously determined as being suitable for survival of *A. dorrieni,* and achieved by mixing the relevant amounts of distilled water and dried compost). This proportion of water was maintained as close to its original level as possible during the course of the experiment by spraying with distilled water once every 24 hours. The central pile contained only 40% water and was not moistened during the course of the experiment.

Pieces of fallen birch leaf were placed at regular intervals across the surface of the compost to serve as food sources, with two pieces of circa $1cm^2$ on each corner pile and the bridge, respectively. No food was placed on the centre pile. On day 1, twenty *A. dorrieni* of >3mm were placed on the central pile (illustrated in Figure 99, page 319). The arrangement was covered with a thin transparent plastic sheet to maintain a relative air humidity of around 70%.

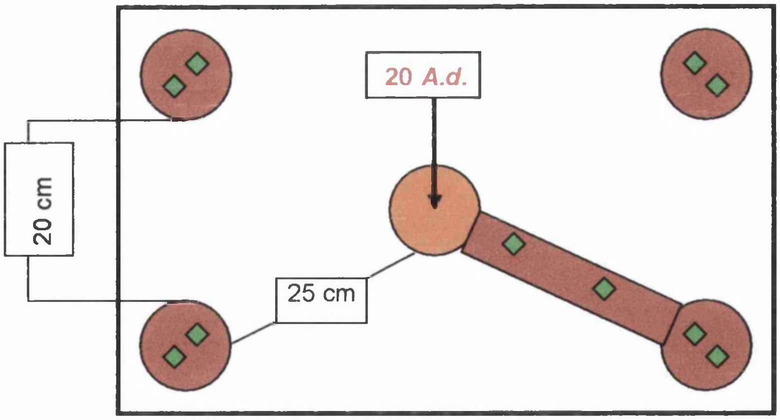

Figure 99 Experimental arena day 1 immediately after introduction of animals;
◆ ... leaf fragment, 🟧 ... drying compost, 🟫 ... humid compost.

8.4.2.2 Results

After 24 hours, 13 animals had moved from the drying central pile. More than half of those had moved along the 'bridge'. However, 5 had crossed open space (illustrated in Figure 100, below).

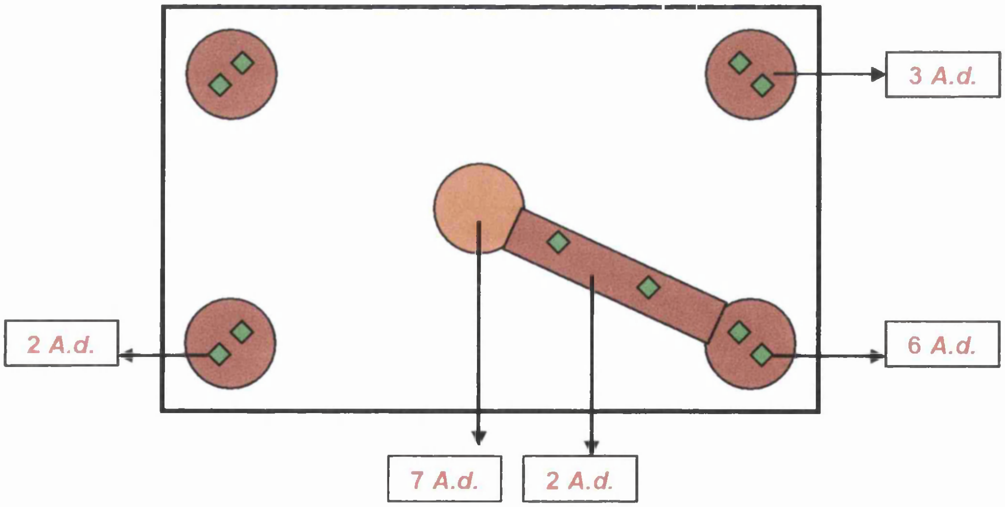

Figure 100 Experimental arena day 2, showing dispersal of animals after 24 hours;
◆ ... leaf fragment, 🟧 ... drying compost, 🟫 ... humid compost.

After 48 hours, all twenty *A. dorrieni* had moved from the drying central pile. Five were found dead, one in each corner pile and one in the 'bridge'. Ten live *A. dorrieni* were located in the corner pile connected to the centre pile by the 'bridge'. The corner pile which contained 2 individuals after 24 hours still contained 2 after 48 hours, in addition to the dead individual. The corner pile containing three *A. dorrieni* after 24 hours now contained only 2 live individuals and the 1 dead counterpart. The third pile that did not contain any *A. dorrieni* after 24 hours contained 1 live and 1 dead individual (illustrated in Figure 101, below).

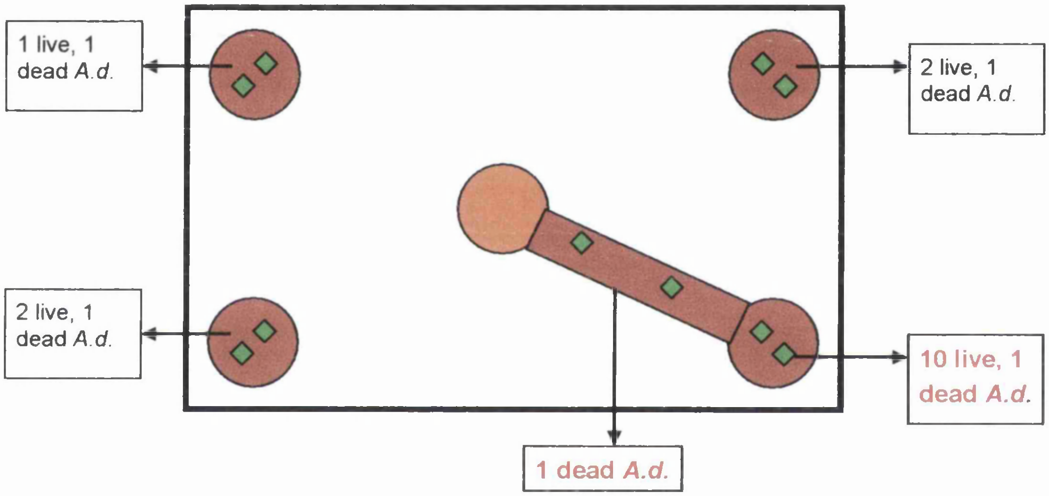

Figure 101 **Experimental arena day 3, showing dispersal of animals after 48 hours; ◆ ... leaf fragment, 🟧 ... drying compost, 🟥 ... humid compost.**

8.4.2.3 ***Discussion***

This preliminary experiment demonstrated that *A. dorrieni* is capable of escaping unfavourable conditions such as low substrate humidity so long as the distances are relatively short. The fact that more than half of the animals followed the 'bridge' and accumulated in the nearest corner pile leads to the conclusion that the animals are influenced by any one, or a combination of, the following factors:

1. ability to follow a substrate humidity gradient
2. aversion to crossing open spaces
3. reluctance to move further than absolutely necessary

Since the individuals present in the corner piles after 24 hours were not marked, it cannot be proved that these are the same individuals present in the corner piles after 48 hours. As, however, there was no obvious reason for them to leave (food and shelter being provided and the humidity adequate) and the number of animal after 48 hours was equal to or larger than that after 24 hours, it is not unreasonable to assume that a large proportion of the individuals present in the corner piles would be those that had arrived there after 24 hours. Since those individuals are unlikely to die spontaneously, at least some of the individuals found dead after 48 hours are likely to be those arriving from the central pile (with one incongruity in top right corner pile). It seems that the individuals that waited too long before leaving the central pile being already somewhat dehydrated when leaving, did not survive the move as well as those that left while they were still well hydrated.

8.4.3 Pilot experiment 2

8.4.3.1 Introduction

Pilot experiment 1 showed that *A. dorrieni* is capable of travelling short distances (a minimum of 25 cm), both under cover and over open ground in order to reach more favourable habitats. This distance appears to pose no problem to *A. dorrieni*, since three out of four individuals survived, with the likelihood of the survival rate being even higher if individuals had started their move well hydrated. In order to determine *A. dorrieni's* potential as a successful invader, the maximum distance which can be covered by a good proportion of the initial population must be determined. Since the survival rate in Pilot experiment 1 was relatively high where cover in the form of a compost bridge was provided, Pilot experiment 2 was designed to focus on longer-distance dispersal over open ground.

8.4.3.2 Materials and Methods

The same metal tray as in Pilot experiment 1 was used (90 x 50 x 5cm). This time, however, only two piles of compost were placed in the tray (15cm in diameter and 2cm in thickness), one at each end of the tray. One pile contained 60% and the other only 40% water. Once again, the 60% pile was moistened during the experiment whereas the other pile was allowed to dry out. The distance between the two piles was 60cm. The temperature was 13°C. Food was provided on the moist pile in the form of pieces of fallen birch leaf. On day 1, twenty *A. dorrieni* of >3mm were placed on the 40% pile. The arrangement was covered with a thin transparent plastic sheet to maintain a relative humidity of around 70%.

8.4.3.3 Results

After 24 hours, 15 *A. dorrieni* had moved from the dry pile. 11 had reached the moist pile successfully, two were found dead near the moist pile, one was found dead near the dry pile and one had climbed out of the tray and was found dead outside (Figure 102, below).

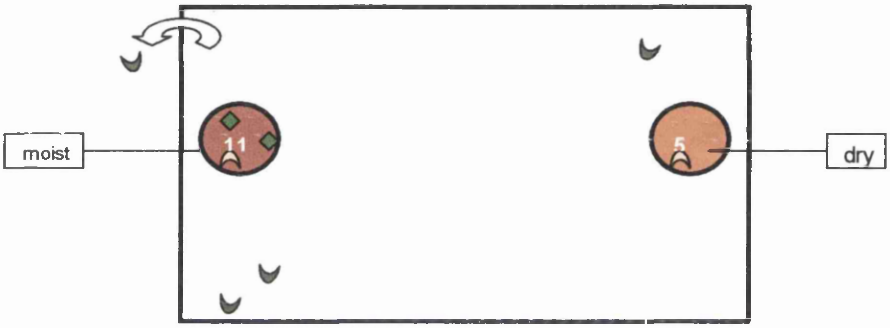

Figure 102 Experimental arena after 24 hours; ◆... leaf fragment, 🟧 ... drying compost, 🟫 ... humid compost, ◡ ... dead *A. dorrieni*, ◠ ... live *A. dorrieni*.

After 48 hours, all individuals had left the dry pile. However, only one had reached the moist pile alive, all others were found dead near and very near to the dry pile (Figure 103, below).

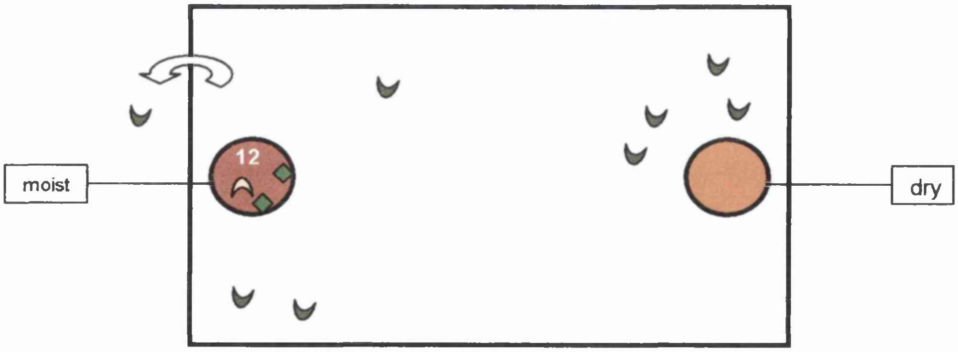

Figure 103 Experimental arena after 48 hours; ◆... leaf fragment, 🟧 ... drying compost, 🟫 ... humid compost, ◡ ... dead *A. dorrieni*, ◠ ... live *A. dorrieni*.

8.4.3.4 Discussion

Pilot experiment 2 showed that *A. dorrieni* can quite easily cross stretches of open ground of at least 60cm. It is unlikely that all the animals took a direct route. It is more likely that most travelled along the walls of the tray thus covering rather longer distances. More than 50% of individuals succeeded in locating the moist pile within 24 hours. As discussed in Pilot experiment 1, it can be assumed that a large proportion of the animals found dead after 48 hours were those individuals that had not left the dry pile within the first 24 hours. Thus, most of those that remained in the dry pile for over 24 hours once again failed to survive the move to the moist pile. This seems to confirm the earlier assumption that merely overcoming distance is not as much of a problem for *A. dorrieni* as trying to overcome distance when already somewhat dehydrated. A remarkable finding was the fact that one individual managed to climb 5cm of vertical metal. It is unlikely that the animal escaped by jumping, as it would have been virtually impossible for it to find its way through the narrow gap between the tray and the plastic sheet.

8.4.4 Experiment 1

8.4.4.1 Introduction

As discussed earlier, in order to determine *A. dorrieni's* potential as a successful invader, the maximum distance that can be successfully covered by a good proportion of the initial population must be determined. As the survival rate in Pilot experiment 2 was still very high, even though no cover in the form of a compost bridge was provided, It was decided to increase the size of the experimental arena for Experiment 1.

8.4.4.2 <u>Materials and Methods</u>

Two very long fibreglass tanks were obtained (Internal measurements: 270 x 47 x 22cm). They were mounted on bricks to ensure that they were perfectly level so that the animals would not be influenced by any physical gradient. The tanks were covered by transparent plastic sheets to maintain a humidity of about 70% at a temperature of around 15°C. Unless otherwise stated, food in the form of fallen birch leaf pieces was provided on the damp compost. Several trials with different layouts were performed. Each trial has its own short Introduction, Results and Discussion section in order to illustrate the reasons for and aims of each subsequent trial. This is followed by a Discussion section encompassing the entire series of Layouts.

8.4.4.2.1 Layout A – Introduction

Layout A (Figure 104, below) was designed to resemble Pilot experiment 2 above as closely as possible, only on a larger scale.

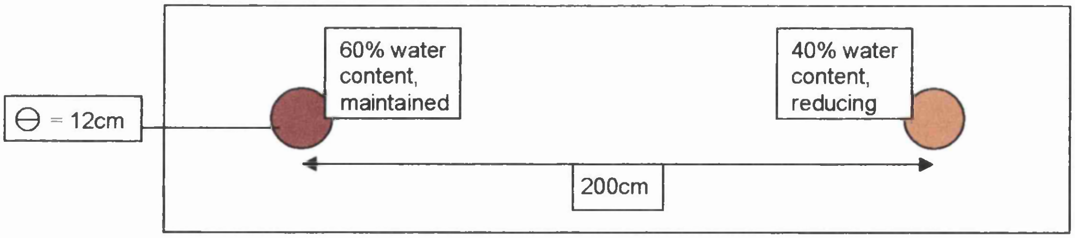

Figure 104 **Experimental arrangement in 'Layout A'.**

Twenty randomly selected *A. dorrieni* of >3mm were placed in the drying pile and left to disperse for 48 hrs with data being collected after 24 and 48 hours. The experiment was replicated four times.

8.4.4.2.2 Layout A - Results

after 24 hours:	after 48 hours:
1. Humid 1, Drying 1, Dead 18	Humid 1, Drying 0, Dead 19
2. Humid 2, Drying 8, Dead 10	Humid 2, Drying 0, Dead 18
3. Humid 5, Drying 5, Dead 10	Humid 5, Drying 0, Dead 15
4. Humid 5, Drying 4, Dead 11	Humid 4, Drying 0, Dead 16

96% of dead individuals were found within 10 cm of the sides.

8.4.4.2.3 Layout A – Discussion

A proportion of individuals - on average 22.5% (min 5%, max 40%) consistently showed a reluctance to move from the dry pile during the first 24 hours. Of those that moved, only a relatively small proportion successfully reached the moist pile (between 5 and 33%). On average, only 16.25% of animals succeeded in locating the moist pile within 24 hours. This figure remained the same after 48 hours, further confirming the conclusion drawn from the two pilot experiments, that individuals need to be fully hydrated to survive movement across open spaces.

8.4.4.2.4 Layout B – Introduction

Since relatively few animals found the moist pile in Layout A and the majority of dead individuals in Layout A were found within 10 cm of the sides of the tank, it was thought possible that *A. dorrieni* may be expressing strong wall-seeking behaviour during its dispersal across open spaces. Layout B (Figure 105, below) was designed to investigate this possibility.

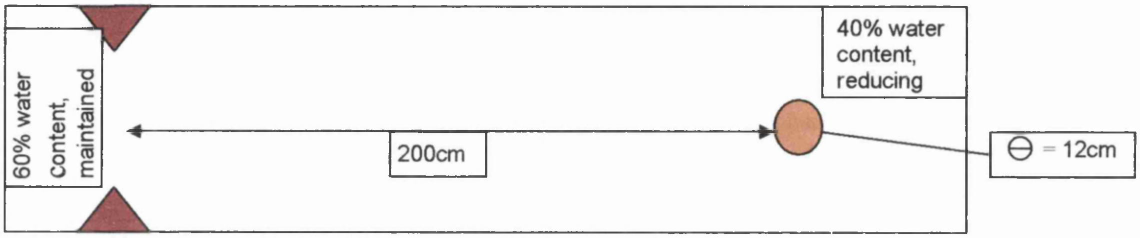

Figure 105 **Experimental arrangement in 'Layout B'.**

As in Layout A, twenty randomly selected *A. dorrieni* of >3mm were placed in the drying pile and left to disperse for 48 hrs with data being collected at the 24 hour and 48 hour stages. The experiment was replicated four times.

8.4.4.2.5 Layout B - Results

Numbers in brackets indicate the numbers of animals in each of the two triangular piles.

after 24 hours:	*after 48 hours:*
1. Humid 10 (9/1), Drying 5, Dead 5	Humid 11 (9/2), Drying 0, Dead 9
2. Humid 6 (4/2), Drying 5, Dead 8	Humid 7 (4/3), Drying 0, Dead 13
3. Humid 10 (5/5), Drying 4, Dead 6	Humid 10 (5/5), Drying 0, Dead 10
4. Humid 10 (4/6), Drying 5, Dead 5	Humid 11 (4/7), Drying 0, Dead 9

92% of dead individuals were found within 10 cm of the sides.

8.4.4.2.6 Layout B - Discussion

Considerably more animals reached the moist triangles in Layout B than the moist pile in Layout A (an average of 9.75 compared to 3.25 of 20, respectively). This result is statistically significant (Mann-Whitney U test: U=183, P=0.029), further indicating that most individuals travel along the sides of the tank, leading them, in this case, straight to the suitable habitat. Once again, all but one of the 19 individuals that were still in the drying pile at the end of 24 hours died before reaching the moist pile.

8.4.4.2.7 Layout C – Introduction

The results of Layouts A and B suggest that wall-seeking behaviour may play a significant role in dispersal across open spaces and *A. dorrieni*'s reluctance to move away from the sides seems to reduce its ability to locate suitable microhabitats where they are located away from this 'preferred' route. A number of individuals were found, however, to have died near the narrow side of the tank on the far side of the triangular piles (the side furthest from the drying pile). If all individuals had travelled consistently along the sides, this should not have been the case. Therefore, Layout C (Figure 106, page 329) was designed in such a way that all individuals covering the 200cm distance should reach suitable microhabitat, whether they travelled across open space or along the sides.

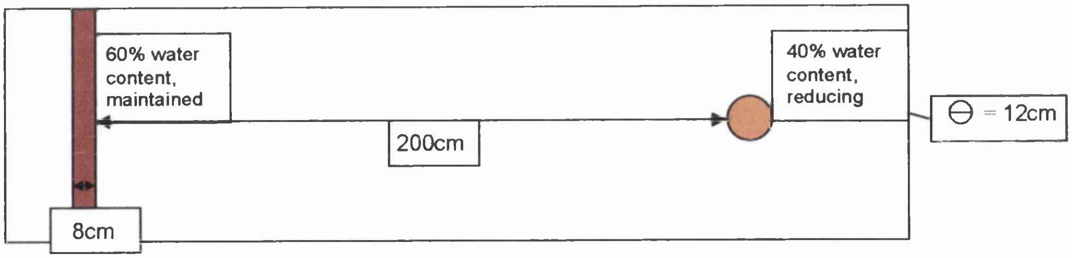

Figure 106 **Experimental arrangement in 'Layout C'.**

Introduction of animals, collection of data and replications were performed as for Layouts A and B.

8.4.4.2.8 Layout C – Results

after 24 hours:	*after 48 hours:*
1. Humid 17, Drying 3, Dead 0	Humid 17, Drying 0, Dead 3
2. Humid 12, Drying 5, Dead 3	Humid 12, Drying 0, Dead 8
3. Humid 18, Drying 1, Dead 1	Humid 18, Drying 0, Dead 2
4. Humid 17, Drying 2, Dead 1	Humid 17, Drying 0, Dead 3

100% of dead individuals were found within 10 cm of the sides.

8.4.4.2.9 Layout C – Discussion

Considerably more animals reached the moist pile in Layout C than in Layouts A or B (an average of 15.75 versus 9.75 (B) and 3.25 (A)). This result is statistically significant (Kruskal-Wallis Test, P=0.009). This suggests that, while a large number of individuals travel along the sides of the tank as concluded from Layout B, there has to be a consistent proportion of individuals that move across open spaces in a straight line. This proportion of animals appears to be represented among the survivors in Layouts A and C but not in Layout B, where they probably made up the animals found dead near the far end of the tank. The fact that the total average number of survivors in Layout C (15.75) closely resembles the added totals of Layouts A and B (13), with Layout C covering an area roughly equal to that covered by Layout A and B combined, seems to confirm that finding. Again, all 11 individuals that were still in the drying pile at the end of 24 hours died before reaching the moist band.

8.4.4.2.10 Layout D – Introduction

The purpose of Layout D (Figure 107, below) was to investigate whether *A. dorrieni* would disperse more easily among or along cover (in the shape of a band of compost) than across open space. Furthermore, the effects of moist versus dry compost as cover were examined.

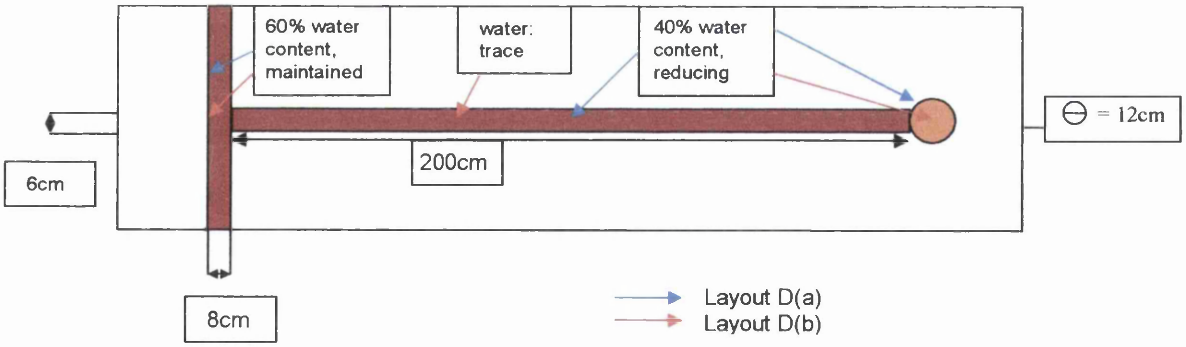

Figure 107 **Experimental arrangement in 'Layout D'.**

Introduction of animals, collection of results and replication were performed as for the previous Layouts.

8.4.4.2.11 a) Moist Bridge

Humidity as per blue arrows in Figure 107 (page 330).

8.4.4.2.12 Layout D a) – Results

after 24 hours:	*after 48 hours:*
1. Band 15, Bridge 3, Pile 1, Dead 1	Band 17, Bridge 0, Pile 0, Dead 3
2. Band 9, Bridge 3, Pile 6, Dead 3	Band 12, Bridge 0, Pile 0, Dead 8
3. Band 12, Bridge 4, Pile 4, Dead 0	Band 18, Bridge 0, Pile 0, Dead 2
4. Band 16, Bridge 2, Pile 1, Dead 1	Band 18, Bridge 0, Pile 0, Dead 2

80% of dead individuals were found within 10 cm of the sides.

8.4.4.2.13 Layout D a) – Discussion

The average proportion of animals surviving the move to the moist pile was identical to that obtained in Layout C (81.25%). This indicates that the presence of a moist band of compost as cover does not improve the survival rate or lead to an increase in the number of animals attempting the move. This further leads to the conclusion that the distance of 200 cm, which the animals had to cover in both Layouts, does not present a significant challenge where desiccation is concerned. Had desiccation been a limiting factor on survival of animals on the move in Layout C, the presence of moist substrate bridge should have increased the chances of survival of those animals in Layout D a) and led to higher numbers of survivors.

8.4.4.2.14 b) Dry bridge

Humidity as per red arrows in Figure 107 (page 330).

8.4.4.2.15 Layout D b) – Results

after 24 hours:	*after 48 hours:*
1. Band 12, Bridge 0, Pile 0, Dead 8	Band 12, Bridge 0, Pile 0, Dead 8
2. Band 10, Bridge 0, Pile 6, Dead 4	Band 10, Bridge 0, Pile 0, Dead 10
3. Band 10, Bridge 0, Pile 7, Dead 3	Band 10, Bridge 0, Pile 0, Dead 10
4. Band 9, Bridge 0, Pile 4, Dead 7	Band 9, Bridge 0, Pile 0, Dead 11

93% of dead individuals were found within 10 cm of the sides.

8.4.4.2.16 Layout D b) – Discussion

The results obtained from Layout D b) were unexpected. It was thought that the results should have been similar to (or better than) those obtained in Layout C, where animals had to travel across open space (the humidity of the dry band of compost being identical to the ambient humidity). Nevertheless, far fewer animals survived the move in D b). A possible explanation for this phenomenon could be the fact that the animals chose to use the dry compost for cover, which meant their gills came into contact with fine dry compost particles decreasing their efficiency and accelerating the desiccation process.

The difference between the number of survivors in Layout D*a* and Layout D*b* was statistically significant (Mann-Whitney U test: U=183, P=0.029).

8.4.4.3 Discussion - all Layouts

Figure 108 (below) summarizes the results of Layouts A, B, C, D a) and D b). It became obvious that, even under difficult circumstances (Layout A), a proportion of animals was capable of crossing 200 cm of open space under conditions of fairly low humidity. This proportion increased markedly where the animal's wall-seeking behaviour is taken into account (Layout B) and even more where the target area was increased (Layout C). Presence of slightly moist substrate en route did not increase the proportion of survivors at the 200 cm distance, however, presence of dry substrate decreased it markedly. The practical conclusions which may be drawn from these findings are discussed below.

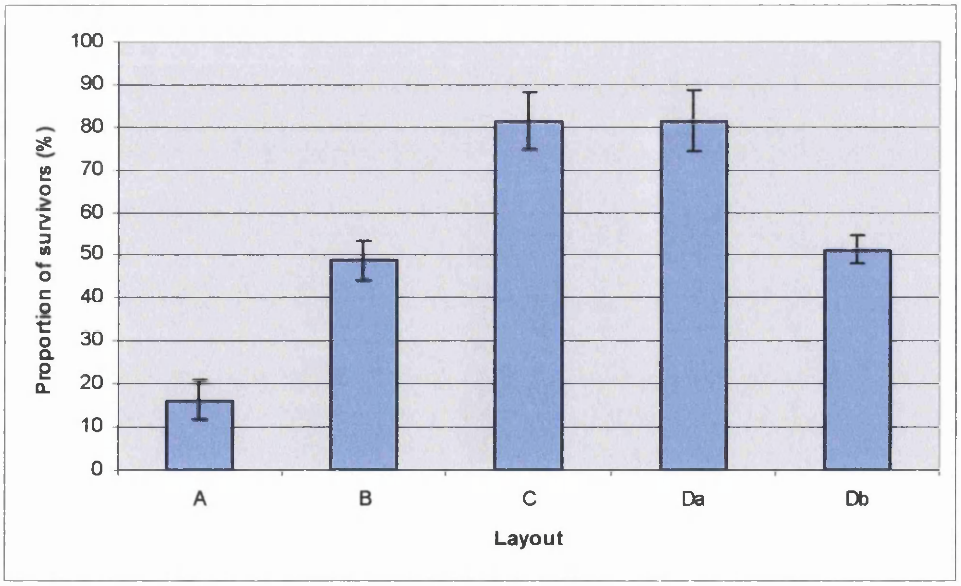

Figure 108 **Proportion of animals completing the 200 cm move successfully in the different layouts after 48 hours (mean +/- SE, n=4 for each layout).**

A. dorrieni is capable of dispersing at least 200 cm in 24 hours over open ground with an ambient humidity of 70% if conditions at the site of origin become unfavourable. Both the distance covered and the proportion of animals surviving the move are likely to be considerably greater in humid conditions (such as after rain), where animals can move along/within cover (including man-made, such as kerbs), and where alternative suitable habitat is of a reasonable size (most natural leaf litter accumulations are more than 15 cm across).

Figure 109 (page 335) illustrates an interesting point which became obvious during this series of experiments: a fairly constant proportion of animals failed to attempt to move from the inhospitable conditions during the first 24 hours. A Kruskal-Wallis test showed that the numbers of animals expressing this behaviour did not vary significantly between the layouts (P=0.648). There is a possibility that this proportion of animals is showing an alternative behavioural adaptation to unfavourable conditions of staying and waiting for the conditions to improve rather than moving away at the first signs of difficulty.

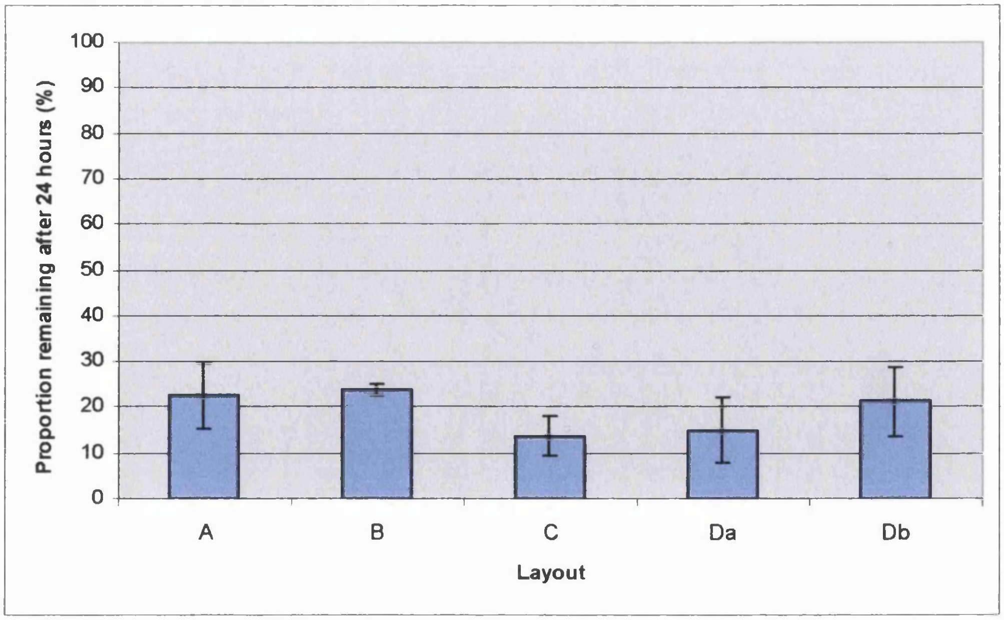

Figure 109 **Proportion of animals remaining in dry pile after 24 hours (mean +/- SE, n=4 for each layout).**

In all layouts - even those where a band of cover was provided - between 80% and 100% of dead animals were found very close to the sides of the tanks. This further indicates that most of the animals do not tend to walk around the available area randomly, but rather follow larger protective structures, thus displaying wall-seeking behaviour.

8.4.5 Experiment 2

8.4.5.1 Introduction

Morritt (1998) reports very strong hygrokinetic responses from *A. dorrieni* in a small experimental arena (14 cm diameter), and a strong preference for the maximum humidity available (in his experiments 95% and 100%, respectively). Experiment 2 was designed to investigate whether *A. dorrieni* is capable of detecting differences in relative humidity and adjusting its dispersal accordingly, on a scale more closely resembling that which it would be confronted with when dispersing in the field.

8.4.5.2 Materials and Methods

For this experiment, the same fibreglass tanks and transparent plastic covers as in Experiment 1 were used. A pile of compost of 12 cm diameter was placed centrally into each tank, and a band of 8 cm width across the tank near each end.

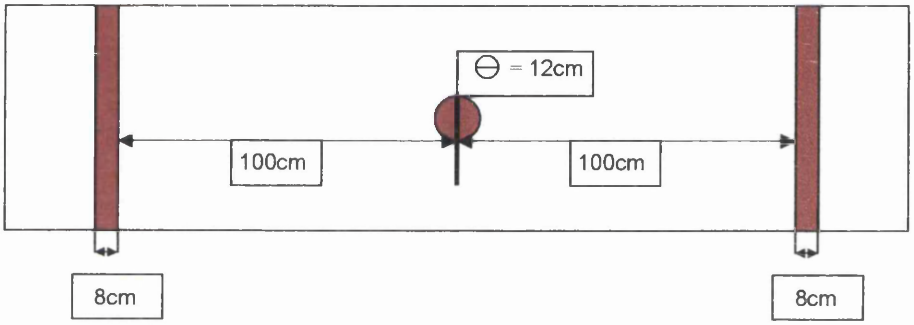

Figure 110 Experimental arrangement for Experiment2, Layouts A-C.

Moist compost again contained 60% water, and this level was maintained for the duration of the experiment. Drying compost initially contained 40% water and was allowed to dry, dry compost (as used for one of the bands in Layouts B and C) contained only traces of water. No food was provided. Twenty randomly selected specimens of *A. dorrieni* of >3 mm were placed into the central pile and left to disperse for 24 hours, at which point data was collected. The experiment was replicated 5 times for each layout. Air humidity at each end of the tank was measured by means of a hygrometer (*Zeal*, Gallenkamp Griffin UK) and calculated by using a psychrometic table.

Layout A was designed to assess the baseline dispersal level - the pile and both bands of compost contained 60% water. Any dispersal taking place would be motivated by factors other than lack of humidity, such as the search for food, mates, or random movement. Air humidity was 68% on both ends of the tank. Movements over 24 hours were expected to be few, and random in direction.

Layout B was designed to assess whether animals whose dispersal is not triggered by desiccation stress would direct their movement towards higher air humidity. The band on the right was dry. Air humidity was 68% on the left and 55% on the right. Movements over 24 hours were expected to be few and mainly to the left.

Layout C was designed to assess whether animals whose movement is motivated by desiccation stress would be able to direct their movements towards an area of higher humidity. Movements over 24 hours were expected to be many and mainly to the left.

8.4.5.3 Results

The results from the three layouts are summarized in Table 8-2, Table 8-3 and Table 8-4, below.

Replicate	Moist band live	Moist band dead	Middle live	Middle dead	Moist band live	Moist band dead
1	4	1	14	0	1	0
2	0	1	15	2	2	0
3	1	0	11	1	5	2
4	11	0	7	0	2	0
5	1	1	11	1	6	0

Table 8-2 Results – Layout A (baseline dispersal levels).

Replicate	Moist band live	Moist band dead	Middle moist live	Middle moist dead	Dry band live	Dry band dead
1	5	4	10	1	0	0
2	12	0	8	0	0	0
3	4	0	15	1	0	0
4	1	0	18	0	0	1
5	1	0	18	1	0	0

Table 8-3 Results – Layout B (possible directed dispersal - no desiccation stress).

Replicate	Moist band live	Moist band dead	Middle drying live	Middle drying dead	Dry band live	Dry band dead
1	1	0	16	1	0	2
2	4	0	13	1	2	0
3	1	0	8	4	0	7
4	7	1	1	6	0	5
5	5	0	6	0	0	9

Table 8-4 Results – Layout C (possible directed dispersal - desiccation stress).

In Layout B, the numbers of animals moving towards the humid side of the tank was statistically significant (Mann-Whitney U test: U=1, P=0.016), but in Layouts A and C there was no significant difference (U=6.5, P=0.222, in both cases).

The total number of animals moving was, as expected, somewhat greater where they were put under pressure by the drying substrate in Layout C than in Layouts A and B, but the differences were not statistically significant (Mann-Whitney U test for A-C: U=4.5, P=0.095, for B-C: U=6, P=0.172).

The total number of animals that died was greater in Layout C than in either of the other Layouts (Mann-Whitney U test, U=1, P=0.016, in both cases).

8.4.5.4 <u>Discussion</u>

It appears that *A. dorrieni* is unable to detect a humidity gradient of ca 13% over a distance of 200cm and direct its movements accordingly. The significant result obtained in Layout B may be a random occurrence due to the small number of replications that could be undertaken. Alternatively, since the majority of animals moved to the humid end on all four occasions, they may have been attracted by an unknown factor. If *A. dorrieni* had been able to detect the humidity gradient, undoubtedly the already stressed individuals in Layout C would have followed this gradient rather than dispersing randomly.

Further experiments involving stronger humidity gradients and a larger number of replicates would be needed to ascertain whether *A. dorrieni* is capable of utilizing humidity gradients to orient its movements on a larger scale, for example when crossing open spaces such as paths or roads.

8.4.6 General Discussion

This chapter provides an initial insight into some of the behaviours of *A. dorrieni* necessary for dispersal. It was shown that animals tend not to become active on the surface of the leaf litter when this is present at sufficient depth and is of adequate humidity. This behaviour may change on rainy nights, a fact warranting further investigation. *A. dorrieni* possesses a pronounced diel activity rhythm with most of its activity confined to the hours of darkness, and it is able to successfully cross distances of 200cm under conditions of relatively low air humidity. Casual observations have further revealed that the animals tested in Experiment 1 (page 324) may not have followed a straight path to their final destination, but rather moved around the tank to a much greater extent during the course of the night, both into and out of the piles of compost in which they were eventually found. As mentioned in section 8.2.4, experiments using infra-red night vision equipment would undoubtedly produce very interesting results, and provide a much more realistic picture of the landhopper's actual dispersal capabilities than has been possible here. Night vision equipment should also be used for observations under natural conditions, both during wet and dry conditions and in different temperatures, to investigate *A. dorrieni's* natural dispersal.

9 Aspects of particular relevance to future studies

This chapter comprises four topics which were investigated to some degree in the course of this study, and on each of which future research may be based.

9.1 Pitfall trapping

There has been much controversy over the usefulness and the accuracy of the results obtained by pitfall trapping, and it appears that the answer varies from species to species (Vandenberghe, 1992). Pitfall traps only catch animals which are walking on the surface during their nocturnal activity and generally produce reliable results for species which are regularly active in such a manner, for example some species of semi-terrestrial amphipods (e.g. (Scapini *et al.*, 1992). Many landhopper species, however, are reluctant to leave the leaf litter layer as long as conditions are favourable, and calculations of population parameters based on pitfall trap catches may therefore be highly inaccurate (Friend & Richardson, 1977; Richardson *et al.*, 1984). Nevertheless, pitfall trapping has been used for sampling terrestrial amphipod populations, with varying degrees of success (Lindeman, 1991; Richardson, 1992; Richardson *et al.*, 1984; Richardson *et al.*, 1996; Richardson *et al.*, 1991).

In this study, pitfall trapping at the sampling sites in Bishop's Wood, Caswell was not practical. On some sites this was due to the amount of limestone fragments among the surface layer of the soil which would have prevented a correct fit of the trap in the surrounding ground, and on others this was due to the gradient of the slopes the sampling sites were located on. Therefore, in order to achieve a preliminary assessment of the usefulness of pitfall trapping in the study of *A. dorrieni*, pitfall traps were placed in five locations in the University's Botanic Gardens, at varying distances from a compost heap around which the landhopper was abundant (illustrated in Figure 111 and Figure 112 (below and pages 342).

Trap 1

Located near hedge planted along compost heap among some loose litter

Trapped: 19% of total catch

Trap 2

Located directly next to compost heap among a quanitiy of loose litter

Trapped: 73% of total catch

Figure 111 Illustration and description of traps 1-2, red arrows indicate location of trap.

Trap 3

Located in border across path from compost heap with little loose litter in the vicinity

Trapped: 4% of total catch

Trap 4

Located in mulched bed ca. 2m from compost heap

Trapped: 4% of total catch

Trap 5

Located in grassy area between beds across path from compost heap

Trapped: 0

Figure 112 Illustration and description of traps 3-5, red arrows indicate location of trap.

Trapping took place during August. The traps consisted of polystyrene drink cups (diameter 7cm) which were sunk into the ground until their rims were level with the ground. Lindeman (1991) showed that catches of *Cerrorchestia hyloraina* were not influenced by the presence or absence of baits or preservatives in the traps. They were therefore filled with ca. 2 cm of soapy water and protected by petri dishes supported on twigs 3-5 cm above the cups. The petri dishes were weighed down by stones, both to prevent them from becoming dislodged and to reduce the amount of light entering the (white) traps, which might possibly deter animals from entering the trap during moonlit nights. The traps were emptied every day for five days.

92% of all animals caught were collected from traps 1 and 2, those nearest the compost heap, indicating that *A. dorrieni* belongs to the landhopper species which preferentially remain in the leaf litter and do not venture far from suitable habitat (this could be further confirmed in Chapter 8). The animals caught consisted of 13% adult males, 2% adult females and 83% juveniles. The majority of juveniles was caught in the trap nearest the compost heap. Overall numbers of landhoppers caught decreased somewhat over the 5 days of sampling, indicating that replacement of trapped animals by those from other areas is slow. These preliminary results indicate that surface activity is greatest in juveniles and adult males, whereas it appears to occur rarely in females. Lindeman (1991) similarly reports a 2:1 m:f ratio in pitfall catches of *C. hyloraina*, (a ratio much higher than that found in the overall population) indicating that surface activity may also be more common in males than in females in other landhopper species.

The composition of *A. dorrieni* populations in August, based on the Bishop's Wood population, is 15% adult males, 57% adult females and 28% juveniles. Thus, pitfall trapping greatly misrepresented the proportions of females and juveniles in the population. The fact that the proportion of males in the population and in the pitfall traps corresponded very closely is most likely coincidental.

No landhoppers were caught in the trap set among short grass, confirming that *A. dorrieni* does not favour such habitat (see Chapter 3).

Overall, pitfall trapping may be a useful tool for detecting the presence of *A. dorrieni* at a location. Under most circumstances, however, the presence of landhoppers is fairly easily ascertained by hand searching (compared to many other litter dwelling invertebrates). Since this method is much less labour intensive than pitfall trapping, it will therefore often be the method of choice.

It appears that catches obtained by pitfall trapping are not representative of the population as a whole, so in order to obtain reliable data, core sampling methods will have to be applied.

9.2 Marking

Marking is a very useful tool for population studies, since the results from mark-recapture experiments allow accurate calculation of population densities. Unfortunately, marking of landhoppers is notoriously difficult due to their unusually smooth cuticle which even lacks most microscopic structures present in other crustaceans (Halcrow *et al.*, 1987). Whole body marking of landhoppers with dyes such as neutral red [as used for sandhoppers (Scapini *et al.*, 1992)] is not practical due to the darker colour of the landhoppers, which makes the stain almost impossible to detect in the field. This was the proved to be the case when dying with dilute methylene blue (1:4 dilution in distilled water, exposure time 3 minutes) was attempted. This dye was only visible when the animal was viewed against a white background and, additonally, had virtually disappeared after 24 hours, having been excreted with the faeces.

Attempts to mark landhoppers with nail polish have been reported to have failed, even where this was only applied lightly to the uropods (Lindeman, 1991), and were therefore not repeated in this study. Instead, marking with two different types of 'Humbrol' paint (Humbrol, Marfleet, Hull, UK), as suggested for use in woodlice (Sutton, 1980), was attempted. Animals had to be anaesthetized prior to marking as described in section 5.3. Blue paint was chosen in order to minimize the possibility of making the animal more conspicuous or producing an aposematic effect when the mark would be used in the field. Survival to 48 hours of animals marked with acrylic water based paint was virtually identical to control animals which had only been anaesthetized. Most animals marked with enamel paint, however, died shortly after application due to the paint's viscosity and slow drying time, and all marked animals had died after 24 hours. Unfortunately, however, the initially successful acrylic paint marks only lasted for 2-3 days on the surviving animals, and often, even when applied very carefully, the paint would fuse adjoining segments of the animals, affecting their ability to jump. When animals were placed among leaf litter, the marks disappeared even more rapidly.

A mark which did not affect survival to 1 week (again tested on 20 animals which were anaesthetized and marked and an equal control group which were only anaesthetized) was water-based typewriter correction fluid (Tipp-Ex Ltd., Camberley, Surrey, UK). These marks lasted for a minimum of 2 days on animals kept singly without leaf litter and lasted equally in conditions where litter was present. In order to test the persistence of the mark under natural conditions, 20 animals marked in such a manner were released under the tree trunk where they had been collected (a habitat where losses through capture by visually hunting predators would be minimized). Marked animals were found in this location for 2 days, at a decreasing rate of 6 on the first day and 2 on the second. Since the numbers of marked animals found decreased so rapidly towards the previously determined end of the durability of the mark, it is likely that at least a proportion of the originally marked animals was still present, but had lost their mark, rather than dispersed. Similar problems were faced by Lindeman (1991), who found that all her mark-recapture experiments failed.

A possible effective alternative which could not be tried in this study would be radioactive tagging, which has been used successfully in the study of the mobility of leaf-litter dwelling oribatid mites (Berthet, 1964). Such a technique would have to be carefully assessed for its potential for environmental contamination (Stimmann, 1991). Furthermore, landhoppers would have to be tested for their tolerance to the radioactive material, and the distances at which tagged individuals were to be released would have to be increased considerably compared to those used in Berthet's study (the maximum distance covered by one of the mites in his study was 17.5cm in 24 hours). Such a study would be likely to yield interesting and much needed results on the mobility and dispersal of *A. dorrieni* under natural conditions, with the advantage that, since detection of marked animals is non-destructive, movements of the same animal could be monitored for an extended period.

9.3 Cold resistance

It is generally assumed that low temperatures limit the spread of *A. dorrieni* in Britain as a result of the amphipod's inability to tolerate freezing (e.g. Cowling *et al.*, 2003; Richardson, 1980). Where low temperature tolerances were tested for this species, the ambient temperature was often lowered rapidly (1°C per minute in Cowling, *et al.,* 2003.), and continued until all experimental animals had died. No attempt was made to assess the effect of prolonged exposure to low, but not lethal, temperatures, and to graduallly increase the temperature again after such exposure, thus more closely replicating natural conditions. Additionally, no work was performed on the responses of similar native invertebrates (such as isopods) to equally low temperatures. Most native invertebrates, including semi-terrestrial amphipods, overwinter in sheltered conditions [for example *T. saltator*, which, in South Wales, spends November – April buried deeply in sand well above high water (Bregazzi *et al.*, 1972)]. These animals have no need for extensive physiological frost tolerance, as they are behaviourally adapted to surviving the adverse conditions.

Due to time restraints, only very limited, preliminary experiments could be conducted to test differential survival of landhoppers and woodlice under regimes of slowly reducing temperatures. The experiments were conducted in cooled incubator (LMS Model 303, LMS Ltd., Sevenoaks, UK) with an accuracy of +/- 0.1°C. All experimental animals were collected during a cold spell in January and acclimatized for 24 hours at 5°C followed by 24 hours at

1°C before the start of the experiments. Standard size petri dishes equipped as described in section 5.2.2, but with only minimal quantities of leaf litter, were used to house 5 landhoppers and 5 woodlice (*P. scaber* and *O. asellus*) of similar sizes per dish. In the initial experiment, involving only one petri dish, the temperature was lowered by 1°C per day and the behaviour of the animals, as well as deaths noted. These results are summarized in Table 9-1, (below).

Following this experiment, which indicated that landhoppers may possess a similar cold tolerance to native woodlice, and that neither group can tolerate a temperature of less than -3°C, experiments at -1°C, -1.5°C and -2°C were performed and continued for 1 week. Each of these was replicated three times. Survival was recorded after 24 hours and at the end of the experiments. Subsequently, the ambient temperature for the surviving animals was slowly (at a rate of 1°C per hour) returned to 5°C. Once they had regained their ability for movement, they were released. The results from these experiments are summarized in Table 9-2 (page 351).

Air temperature °C	Amphipods	Isopods
0	all alive, upright, capable of movement	all alive, capable of movement
-1	as above	as above
-2	all alive, on side, capable of some movement	all alive, somewhat sluggish
-3	all dead – frozen solid (did not recover after slow thawing)	all dead – frozen solid (did not recover after slow thawing)

Table 9-1 Results of preliminary slow-cooling experiment of amphipods and isopods.

Air temperature °C	Alive after 24 hours (listed per petri dish)	Alive after 1 week (listed per petri dish)	% of total landhoppers alive after 1 week	% of total woodlice alive after 1 week
-1	2L, 5W 3L, 5W 3L, 5W	2L, 5W 1L, 5W 2L,4W	33%	93%
-1.5	0L, 5W 0L, 2W 1L, 3W	0L, 5W 0L, 2W 1L, 3W	6%	67%
-2	1L, 4W 5L, 5W 2L, 4W	1L, 3W 5L, 5W 2L, 4W	53%	80%

Table 9-2 Results of replicated slow cooling experiments of amphipods and isopods (L=landhopper, W=woodlouse).

These experiments showed that a proportion of the landhopper population is capable of surviving prolonged exposure to sub-0 air temperatures. This proportion is lower than that of the native woodlice, but would nevertheless be sufficient to maintain the population once the frost had passed. This is contrary to the findings by Cowling *et al.* (2003), in whose experiments no landhopper survived a temperature of below 0°C, but the cause of this is probably the difference in experimental methodology used, as described previously. The low number of survivors of both landhoppers and woodlice at -1.5°C is probably due to a factor other than the temperature (such as low humidity), as the survival rate increased again at an even lower temperature. It may be of note that most deaths occurred during the first 24 hours at the low temperature, and that most animals which survived this time period tolerated the respective temperature regime for the duration of the experiment. No particular adaptive behaviours to cope with the low temperatures, such as aggregation, could be observed. Under natural conditions, it is unlikely that landhoppers would not be exposed to sub-0 temperatures without shelter for an uninterrupted period of time such as was tested here. Instead, they would be able to seek shelter in the substrate (possibly making use of heat generated by decomposition) and daytime temperatures would rise considerably, particularly in the sun, all of which would probably increase survival.

Further experiments replicating natural conditions as closely as possible are urgently required in order to build up a realistic picture of the invasive potential of *A. dorrieni* in relation to winter temperatures. Additionally, dataloggers should be placed in sheltered areas (such as accumulations of leaf litter or friable soil, compost heaps, hollow tree stumps) accessible to landhoppers and other invertebrates during the winter, both in already colonized areas as well as in areas of potential invasion, to record the temperatures that the amphipod is actually exposed to, as opposed to just recording air or grass minimum temperatures. Even comparatively thin layers of leaf litter or soil can have a surprisingly strong insulating effect (Firbas, 1927). Furthermore, the rate of frost penetration into moist humus (lacking protective covering) is only 0.6 cm per day (Geiger, 1966). Since landhoppers are known to bury to a depth of 5 cm (Clark, 1954), continued frost of over 1 week's duration would be needed to reach those individuals buried to this depth.

There is little doubt that low temperatures have a deleterious effect on landhopper populations (as could be seen in Chapter 3), but it may be found that these are not capable of completely excluding *A. dorrieni* from most of the

UK, as is currently believed. Already, there are a number of thriving populations of the amphipod in areas which experience occasional severe winter conditions, and one well-established population in Budshead Wood (near Plymouth) regularly experiences winter frosts and snow cover (Harding *et al.*, 1988).

9.4 Rearing A. dorrieni under laboratory conditions

In order to gain insights into a species' growth rates, moult intervals, life expectancy and similar aspects of its biology, rearing and breeding of this species has to be performed under controlled circumstances. While the entire life cycles of a number of amphipod species have been successfully observed in the laboratory (e.g. (Duncan, 1969; Sutcliffe & Carrick, 1981), some landhopper species are notoriously difficult to rear under laboratory conditions (Tamura *et al.*, 1974). In a number of amphipod species it is possible to relate the number of segments on the flagellum of the second antenna to instar, as a fixed number of segments are added at every moult (Duncan, 1969; Sutcliffe *et al.*, 1981). Such data are of great use in the study of population dynamics, but the initial data can only be obtained by rearing specimens individually in the laboratory and observing their moult intervals.

While it is possible to breed *A. dorrieni* in leaf litter as described in section 5.2, this species has not yet been successfully reared to adulthood under more controlled laboratory conditions. Where suitable individuals were obtained in the process of other experimentation during the course of this study, initial attempts were made to rear these singly under controlled conditions and record the findings. The results from these trials are described here for the benefit of future researchers attempting to follow the complete life cycle of *A. dorrieni* in the laboratory (and hopefully succeeding in this endeavour!).

At an ambient temperature of 20°C, females (n=3) were found to produce eggs within a maximum of 8 days of a moult (in the presence of a male) and to carry those for 12 -14 days before releasing the young. During the last 4-5 days of gravidity, larvae were carried. These larvae (illustrated in Figure 113, below) measured 2.5mm and were pale whitish with remnants of the grey yolk showing through the translucent body surface. Attempts to keep such larvae alive in Crustacean Ringer solution [in g/l: NaCl:12, KCl:0.4, $CaCl_2$: 1.5, $MgCl_2$: 0.25, $NaHCO_3$: 0.2; pH=7.55, after Van Homeveld (1936)] failed.

Figure 113 Larval *A. dorrieni* extracted from marsupium, note the dark yolk showing through transparent body surface.

During prolonged (1.5 hours) observation of a pair immediately after the female had moulted, no sign of mating behaviour could be recorded. The male merely rested near the female (which remained in a curled-up position) and touched her with his antennae and legs (Figure 114, page 356).

Figure 114 Male showing interest in newly-moulted female; note touching of female with antennae and legs (female on top in left photograph, on left in right photograph). Note also bluish hue of newly moulted female due to haemocyanin.

The maximum number of young released by one female was six. The young (n=23, including those from females mentioned previously) measured 3mm on release, weighed <1mg and possessed 8 antennal segments (Figure 115, below).

Figure 115 Newly-released *A. dorrieni*, note empty gut prior to first meal.

When housed singly in small petri dishes (as described in section 5.2) and fed on Birch (*B. pendula*) leaf tissue, no growth took place and animals died within 3 weeks. Survival times were marginally longer when Crustacean Ringer solution was used in place of distilled water. When the young were fed Birch and Oak (*Q. robur*) leaf tissue in conjunction with Crustacean Ringer solution to dampen the substrate, some growth became apparent. A first moult was observed at 7 days post-release, after which the animals possessed 9 antennal segments and measured 3.5 mm in length, and a second moult at 34 days post-release, after which the animals still had 9 antennal segments, but had grown to 4mm. This group of animals died shortly after their second moult. The batch of young (n=6) surviving the longest was housed as a group with the adult female in mixed deciduous leaf litter with Crustacean Ringer used to dampen the substrate. All juveniles showed similar growth rates. Occasionally, one or two individuals had not reached the size indicated in the table by the date shown. Those individuals had, however, invariably caught up with their siblings by the next date. The observed moult intervals are illustrated in Table 9-3, below.

Date	Length (mm)	Antennal segments	% alive
23/7	3	8	100
1/8	3.5	9	100
15/8	4	10	100
4/9	5	13	100
19/9	5	14	50
30/9	6	15	50
15/10	6.5	16	33
31/10	6.5	17	0

Table 9-3 Moult intervals and growth of juvenile *A. dorrieni.*

The maximum survival time of a juvenile *A. dorrieni* housed in a petri dish was 69 days, during which time the animal had moulted seven times and more than doubled both its body length and its number of antennal segments. It appears that, as a rule, 1 antennal segment is added at each moult. Moult intervals (after the first moult) appeared to be approximately 2 weeks. The lack of growth at some moult stages may have been caused by the unnatural rearing conditions. The fact that juveniles survived much longer, and showed significantly better growth, in the presence of an adult and mixed litter indicates that they benefitted either from the presence of the adult (possibly by utilizing symbiotic bacteria or nutrients contained in its faeces), from the different leaf tissue types, or a combination of the two factors. The fact that, eventually, all juveniles died before reaching maturity means, however, that some essential factor was still missing in the confines of the petri dish that was present in the larger amounts of litter in which specimens of *A. dorrieni* matured successfully.

Rearing and breeding of *A. dorrieni* in the laboratory should be given priority in future research, so that a better understanding of this species' reproductive biology and growth may be reached, which may subsequently lead to important insights into its potential population dispersal rates.

10 General Discussion and Conclusions

Invasive exotic species are causing dramatic changes in many ecological systems worldwide, and there is no question that invasive species are profoundly altering many communities and ecosystems (Gurevitch & Padilla, 2004). There has been increasing controversy regarding the presence of invasive alien species and what (if any) steps should be taken as a consequence of their presence. While some sources argue in favour of the alien species, regarding them as positive additions to the native flora or fauna, others campaign in favour of their eradication (Downie, 2001; Simberloff, 2003). In reality, the situation is generally such that, while some species present real threats to native biodiversity, others turn out to be harmless. In order to determine which group an invasive species belongs to, it would have to become the focus of extensive research (Manchester & Bullock, 2000). The obvious drawback of such a 'case-by-case' assessment strategy is the amount of money and resources needed to implement it successfully. Current policies in the UK advise in-depth study only of those alien species which are most likely to present a threat. The UK Biodiversity Research Advisory Group (part of the Joint Nature Conservation Committee) attempts to provide a classification of species according to the potential risk they pose to native biodiversity.

It has been suggested that alien predators and pathogens are far more likely to cause extinction of native species than alien competitors (Davis, 2003). If this is indeed the case, *A. dorrieni* may be in a position to become a widespread member of the British leaf-litter fauna without endangering any native species. Nevertheless, species are still regularly threatened or driven to extinction by alien competitors (Manchester *et al.*, 2000). Despite the fact that there is growing public awareness of invasive species issues through increasing exposure in the media (e.g. (Brown, 2003; Farrar, 2005)), *A. dorrieni* and the effects it may have on native species is still generally overlooked, by science and the public alike. This oversight may, in the future, prove to not to have been the cause of undesirable consequences in the case of *A. dorrieni*, but it could just as easily turn out to have been the cause of irrevocable changes in, or damage to, native ecosystems and, possibly, the extinction of species. It is therefore essential that the risk status of *A. dorrieni* in Britain is assessed in detail and that populations are monitored regularly. Such assessment and monitoring are particularly important in the case of *A. dorrieni*, because, although small and unobtrusive, this alien is virtually impossible to eradicate once it has become established.

The aim of this study was to cover as much ground as possible, within the given constraints of time and resources, towards a better understanding of *A. dorrieni's* role as an invasive species, and to examine this role from a variety of different angles. A number of aspects which are not commonly considered in the study of invasive species, but nevertheless play an important part in determining a species' invasive potential, were included in an attempt to produce a coherent picture of the factors influencing populations of *A. dorrieni* in Britain. The food preferences of *A. dorrieni* and its activity rhythms are among such aspects examined here.

In Chaper 3 it could be shown that densities of the alien amphipod were lower in deciduous woodland than in the Irish locations of mixed or coniferous woodland examined previously by other workers. The distribution of individuals at the study location, however, was less patchy than had been thought, being even less patchy than that of the native isopods.

It was confirmed that *A. dorrieni* is a year-round breeder, but it appears that none of the young released at the second reproductive peak in winter reach maturity. Considerable fluctuations in population density were observed, and a possible link with late frosts could be established (Chapter 3).

Comparisons of the native fauna of the litter layer between a location colonized by *A. dorrieni* and a closely matched 'control' location revealed no statistically significant differences. It appeared, however, that some species occurred in greater numbers where *A. dorrieni* is present, whereas the densities of others seemed to be reduced. It is suggested that further study will show up statistically significant effects of landhopper presence on native faunal assemblages (Chapter 4).

A number of different methodologies were developed for laboratory studies involving *A. dorrieni*, and descriptions are included for the benefit of future workers (Chapter 5). Due to the scarcity of terrestrial amphipod research to date, much additional research is needed in the majority areas of the biology of *A. dorrieni*, and numerous suggestions for further work are incorporated in the relevant locations in the main text and described in Chapter 9. These are, however, not the only areas warranting further investigation. Among the many aspects which still require attention are:

- Grooming behaviour – Terrestrial amphipods face very different challenges with regard to fouling of their body surfaces than do their aquatic relatives, and their grooming behaviour may have adjusted accordingly. To date, only one study has investigated the grooming behaviour of a landhopper (*Talitroides alluaudi*) in any detail (Holmquist, 1985), and only very few other publications so much as make reference to this subject (e.g. Lindeman, 1991).

- Escape mechanisms – These are unusual in semi-terrestrial and terrestrial amphipods in that they combine initial erratic display behaviour [also referred to as 'protean' behaviour (Humphries & Driver, 1967)] with subsequent death feigning. These escape mechanisms have received little attention, particularly in landhoppers. A few publications include some reference to the subject (Holmes, 1903; Lindeman, 1991; Spicer *et al.*,

1987) but there is much potential for a study, possibly of a comparative nature, investigating triggers of the escape response, the timing, duration and distance covered by jumps [using methodologies similar to those used in the study of the jumping of *O. cavimana* (Bracht, 1980)], and the conditions required for the onset as well as the duration of the subsequent death feigning.

- Turn alternation and similar behavioural aspects - The presence of a number of behaviours known to exist in terrestrial isopods, in particular turn alternation (Hughes, 1992; Hughes, 1987), has not yet been investigated in terrestrial amphipods. There is much scope for the study of such behavioural aspects, in *A. dorrieni*, or, indeed, in other landhopper species.

In Chapter 6, the feeding rates and food preferences of *A. dorrieni* were investigated. From these it was possible to calculate the biomass of, and the amount of litter consumed by, a population of the amphipod at a deciduous woodland location.

The biomass of *A. dorrieni* was an estimated 7% of the total litter-soil animal biomass, a value similar to that of the Gastropoda and the Diplopoda, and significantly higher than that of the Isopoda. Further, *A. dorrieni* was calculated to consume between 25% and 35% of the total annual litter fall. Values such as these strenghten the view expressed in Chapter 4, that populations of *A. dorrieni* are very likely to affect native faunal assemblages. A. dorrieni was further shown to comparatively readily consume leaf tissue avoided by most other leaf-litter feeders until a much more advanced stage of decomposition. This may provide the amphipod with a competitive advantage over native leaf litter feeders.

Chapter 7 showed that *A. dorrieni's* British populations probably face considerable predation pressure, as representatives of all major groups of potential predators readily accepted it as a prey item.

Finally, it could be shown that *A. dorrieni* regularly becomes active during the night even in the presence of adequate food and humidity, and that it is capable of successfully crossing at least 2 metres of open ground at relatively low ambient humidity.

Overall, this study showed that *A. dorrieni* has much potential for continued spread across the British Isles, and that this species is an excellent potential subject for further research, both in its own right and in its role as an invasive species.

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