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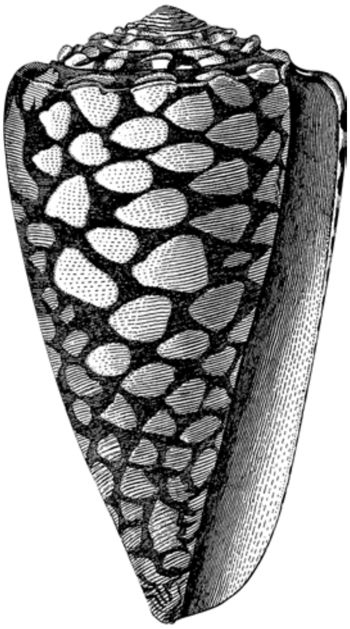

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Observations on the behaviour of the Australian land snail *Hedleyella falconeri* (Gray, 1834) (Pulmonata: Caryodidae) using the spool-and-line tracking technique

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Abstract

A brief field study of the Australian caryodid land snail *Hedleyella falconeri* (Gray, 1834), using the spool-and-line tracking method, provided detailed information concerning patterns of nocturnal movement and types of diurnal shelter site, as well as egg laying and foraging activities. *Hedleyella falconeri* was active on 74% of nights observed and, when active, moved an average of 8.70 m per night (maximum of 21.72 m in a single night), with an average straight-line displacement of 5.10 m per night (maximum of 13.96 m in a single night). Snails were more likely to be active and to move further in wet weather than dry weather. They appeared to be nomadic, moving randomly around the forest floor, with no homing behaviour observed and, contrary to preconceptions, no apparent active selection of secure diurnal shelter sites, such as beneath fallen timber. A description of diurnal shelter sites is provided, together with a description of the eggs and egg laying behaviour and observations on diet. The behaviour of *H. falconeri* is considered to reflect its equable rainforest habitat, with implications for its continued conservation. The present study demonstrates the considerable value of the spool-and-line tracking method in the field study of larger land snail species.

Additional keywords: diurnal shelter, egg laying, movement, rainforest.

Introduction

Numerous summaries of the status of research concerning the Australian land snail fauna over the past four decades have noted a paucity of ecological and biological studies. McMichael and Iredale (1959) noted that whereas the taxonomic study of Australia's land and freshwater Mollusca was far from complete, their ecology had received practically no attention. Bishop (1981) noted that the majority of Australian land snail research had focused on taxonomic studies based largely on shell morphology, to the neglect of biological or ecological studies of the living animals. Smith (1992) noted that a large proportion of Australia's terrestrial and freshwater mollusc species had never been observed in their natural habitat, with no information available on even their basic biology. Ponder (2000) noted that basic biological information for Australian molluscs was lacking for all but a few taxa. Many species of land snail in Australia and throughout the world are considered to be declining and at risk of extinction (Wells 1988; Ponder 1997; IUCN 2000). An understanding of their basic biological and ecological requirements is essential if land snails are to be properly considered in conservation and land use planning decisions.

The present project was undertaken as a pilot study to examine the feasibility and value of the spool-and-line tracking technique in studying movement patterns and shelter site selection by the Australian caryodid land snail *Hedleyella falconeri* (Gray, 1834). This technique involves attaching a small spool of thread to the subject animal, which unwinds from the inside as the animal moves about, leaving a trail of thread that can be subsequently followed to trace movement and relocate the animal. The technique is technologically

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Fig. 1. *Hedleyella falconeri* is Australia's largest native land snail and is common in rainforests in north-east NSW and south-east Queensland.

simple and low cost, but very data rich, providing a continuous and detailed record of movement over the tracking period. The spool-and-line technique has been used to study spatial and temporal patterns of habitat usage in vertebrates ranging from frogs and small reptiles to medium sized mammals (Miles *et al.* 1981; Boonstra and Craine 1986; Stott 1987; Anderson *et al.* 1988; Manning and Ehmann 1991; Carthew 1994; Key and Woods 1996). Pearce (1990) previously demonstrated and discussed the value of spool tracking in the study of land snails, noting how the technique could provide information concerning activity range, dispersal capacity, homing behaviour, behavioural interactions (such as mucous trail following) and the location of refuge and nesting sites. To the author's knowledge, the present study represents only the second use of the spool-and-line technique in studying land snails and the first for an Australian land snail species.

Hedleyella falconeri (Fig. 1) is a large land snail found in ground litter in rainforest and tall open forest from Mount Mee, south-east Queensland, to the Hunter Region in northern New South Wales (Cox 1868; Iredale 1943; Smith 1992). It is Australia's largest native land snail, with a helicoid shell up to 9–10 cm in size (Shea 1978; Abbott 1989). Despite being a large, well known species with a distribution in the highly populated eastern coastal region, little published information is available concerning its ecology and behaviour. Shea (1978) noted that *H. falconeri* was nocturnal, hiding by day under logs, heaps of leaves and sticks. Bishop (1981) described *H. falconeri* as a ground feeding species, not climbing more than 50 cm or so. He noted that it was very difficult to find by day, with a preference for giant strangler figs as diurnal shelter sites, but easily found at night on the ground around fig trees. Additional anecdotal information on the behaviour and ecology of *H. falconeri* is recorded in the unpublished newsletter of the Malacological Society of Australasia (Jahnsen 1967). This includes observations on activity patterns and movement, comments on diurnal shelter site selection and frequency of predation by ground foraging rainforest birds, as well as a description of the nest site and eggs. Previous opportunistic observations by the present author suggested that *H. falconeri* was most likely to be active on wet nights, that activity was limited to ground level, that, by day, animals were most commonly found sheltering under fallen timber and that the species was a common prey item of the noisy pitta, *Pitta versicolor* (Pittidae), a diurnal ground litter foraging rainforest bird species.

The above observations and comments provide some insight into the ecology of *H. falconeri*; however, being typically based on anecdotal or opportunistic sightings, they are subject to potential observer bias and subjectivity. The present spool-and-line tracking study enabled the collation of a dataset of continual observations of movement patterns and diurnal shelter site selection over a period of approximately 2 weeks. These quantitative and qualitative findings have been compared with previous anecdotal or opportunistic information.

Materials and methods

The study area was located in Bruxner Park Flora Reserve (30°15´S 153°06´E), near Coffs Harbour on the north coast of New South Wales, Australia. The study area was approximately 60 × 30 m in area and was located adjacent to Bucca Bucca Creek in the central part of the Reserve, at an elevation of 140 m Australian height datum. The vegetation of the study site was subtropical rainforest with scattered emergent flooded gum, *Eucalyptus grandis*. One mature strangler fig, *Ficus watkinsiana*, was present within the study area. The ground surface was covered by a layer of leaf litter and scattered rotting logs.

Nocturnal searches for *H. falconeri* in the study area were undertaken over two consecutive nights during a period of wet weather in mid-February 2000. Each search was of approximately 1 h duration and involved looking for active snails with the aid of a 50 watt spotlight. Two adult snails were found active on the forest floor in the study area on the first night and a third was found on the second night. The three snails were measured, weighed and marked with an identifying number on the shell (Table 1). (Note, the three snails were numbered 2, 3 and 4 because one snail in the study area had previously been marked as snail 1 in an earlier unsuccessful tracking attempt using a rotating spool system.) A spool of fine nylon thread (Danfield bobbin no. 10 white; Penguin Threads, Prahran, Victoria, Australia) wrapped in electrical tape was affixed to the rear of each animal's shell using electrical tape and cyanoacrylate 'super glue' (Fig. 2). Spools weighed 5 g and measured 38 mm long and were 16 mm in diameter at the middle, tapering to 11–12 mm diameter at each end. The snails were released at point of capture within 15 min of collection, with the free end of the thread secured to a stick in the ground next to the snail.

The study site was visited daily each morning for 17 days following marking of the snails (16 days for the snail marked on the second night), giving a total dataset of 50 nights of spool tracking data from the three tracked snails. On each visit the thread trail of each animal was traced and interpreted for activity and the animal located. The actual distance travelled (length of spool thread trail) and straight-line displacement over the previous night was measured, the location of the animal was marked and mapped, and notes were made on overnight activity and diurnal shelter site.

An additional two *H. falconeri* specimens found in the study area during the spool tracking study were also individually marked (as snails 5 and 6) and observations on their behaviour noted.

Information on the weather conditions over the course of the spool tracking study was recorded. There were 8 nights during the study when weather conditions in the study area were wet and 9 nights with dry conditions. This equated to 23 wet snail nights and 27 dry snail nights for the pooled dataset of 50 snail nights.

At the end of the 17 day study period, the spools were removed and the snails were released at last point of collection. The straight-line distance between each snail's last point of collection and original point of collection was measured to provide the straight-line displacement over the entire spool tracking study. Identification numbers were left on the animals so that they could be identified on subsequent inspections.

Nocturnal searches in the study area and adjacent areas were undertaken during or following rain on three subsequent occasions in an attempt to relocate the five marked snails and determine the straight-line displacements over longer periods. One search was in late March 2000 (24 nights since removal of spools), one in late May 2000 (87 nights since removal of spools) and one night in late December 2000 (303 nights since removal of spools). The search effort each night was between 30 and 60 min. When a snail was found, its location was marked for future reference and the straight-line distance between its current and last recorded location was measured. Two marked snails were relocated in late March, of which one was found again in late May. No marked snails were found in late December.

Table 1. Size of snails observed in the present study
Note: shell height and width are straight-line measurements using calipers

Animal	Weight (g)	Shell height (mm)	Shell width (mm)
Snail 2	118.5	75.2	54.0
Snail 3	118.0	81.6	53.3
Snail 4	68.5	62.9	43.4
Snail 5	–	–	–
Snail 6	–	72.2	49.3

Fig. 2. *Hedleyella falconeri* with spool attached to enable tracking. The 50 cent coin shows the scale.

Results

Movement of snails

A combined total of over 320 m of movement by the three spool tracked snails was recorded over the 50 snail nights comprising this study. The tracking spatial data for the three snails (snails 2, 3 and 4) is shown in Fig. 3. The location of each of the two additional snails (snails 5 and 6) found in the study area during the spool tracking study is also shown. The area of movement mapped for snail 2 did not overlap with any other identified snail. Snails 3 and 4 had partially overlapping areas of movement but did not meet. Snail 3 was found sheltering with one of the additional snails (snail 6) on 1 day, but had moved on by the following day, while snail 6 remained there for another 2 days, as described under breeding observations below.

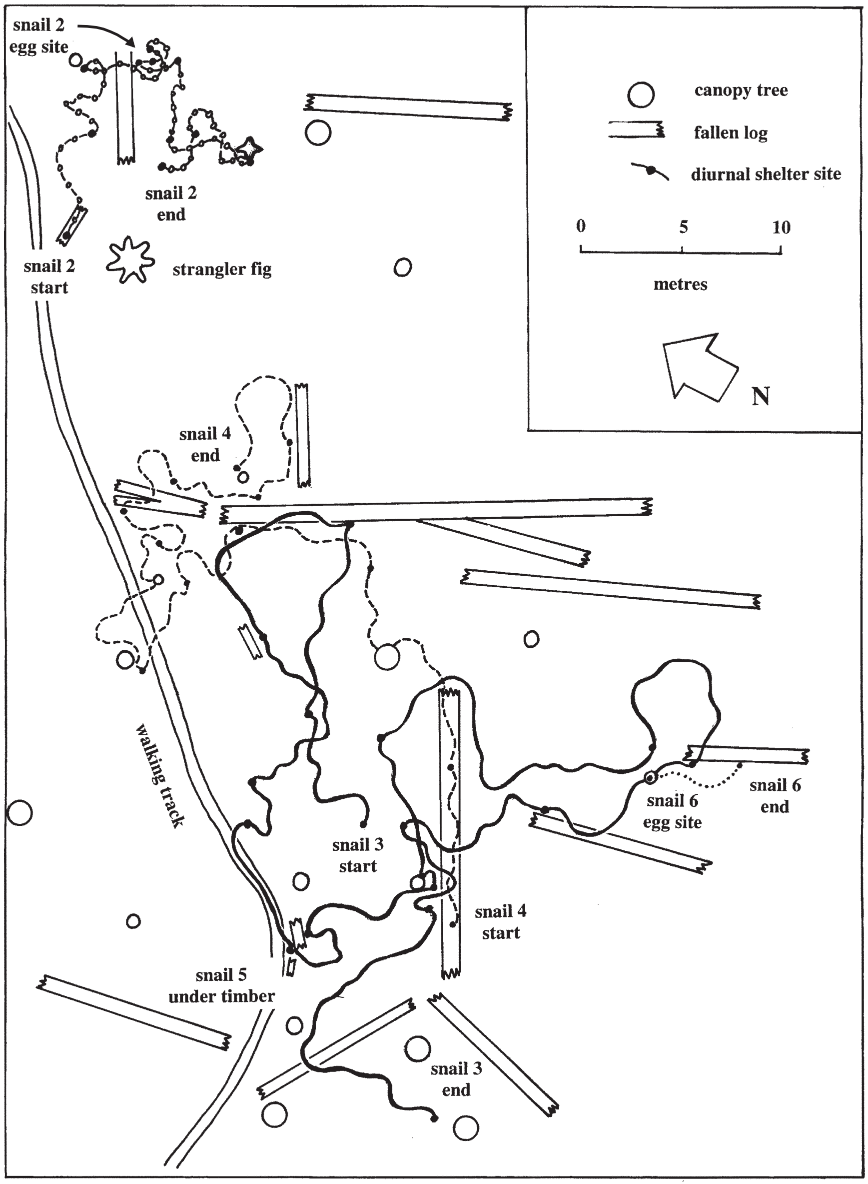

Fig. 3. Map of the study area showing movement patterns and diurnal shelter sites of three spool-tracked *Hedleyella falconeri*. The location of two additional *H. falconeri* found in the study area is also shown, together with the approximate location of the two nest sites recorded in the present study.

Average distances moved per night by each snail in wet and dry conditions during the spool tracking are shown in Table 2. Data were randomly deleted to give a balanced dataset of 7 nights per snail (three snails) per weather type (wet or dry) for statistical analysis. A two factor analysis of variance of this data indicated that there was a significant difference between the snails ($F = 14.19$ with 2, 36 d.f., $P<0.01$) and a significant difference between wet and dry nights ($F = 10.71$ with 1, 36 d.f., $P<0.01$), with no significant interaction

Table 2. Average distances travelled per night by snails during spool tracking study (mean ± SEM)

	Snail 2	Snail 3	Snail 4
Wet nights	3.64 ± 0.97 m (8 nights)	13.89 ± 1.45 m (8 nights)	8.62 ± 2.28 m (7 nights)
Dry nights	1.72 ± 0.80 m (9 nights)	7.90 ± 1.78 m (9 nights)	3.86 ± 1.24 m (9 nights)

Table 3. Average straight-line displacements per night by snails during spool tracking study (mean ± SEM)

	Snail 2	Snail 3	Snail 4
Wet nights	2.41 ± 0.67 m (8 nights)	8.39 ± 1.06 m (8 nights)	5.14 ± 1.46 m (7 nights)
Dry nights	0.99 ± 0.54 m (9 nights)	3.75 ± 0.96 m (9 nights)	2.55 ± 0.88 m (9 nights)

between these factors (F = 1.34 with 2, 36 d.f., P>0.05). It was therefore concluded that individual snails differed in the average distances moved overnight, but that all snails tended to move further on wet nights than dry nights. The greatest overnight movement recorded during the study was 21.72 m by snail 3 on a wet night.

Average straight-line displacements per night by each snail in wet and dry conditions during the spool tracking study are shown in Table 3. Data were randomly deleted, as above, to give a balanced dataset for statistical analysis. A two factor analysis of variance of this data indicated that there was a significant difference between the snails (F = 8.41 with 2, 36 d.f., P<0.01) and a significant difference between wet and dry nights (F = 15.17 with 1, 36 d.f., P<0.01), with no significant interaction between these factors (F = 3.07 with 2, 36 d.f., P>0.05). It was therefore concluded that individual snails differed in the average straight-line displacements overnight, but that all snails tended to move further on wet nights than dry nights. The greatest overnight straight-line displacement recorded during the study was 13.96 m by snail 3 on a wet night.

Zero overnight movement by a spool tracked snail was recorded on 13 occasions. Three of these (23.1%) were on wet nights, whereas 10 (76.9%) were on dry nights. A Chi-square 'goodness of fit' analysis indicated that these observed proportions were significantly different from that expected on the basis of the relative number of wet snail nights (46%) and dry snail nights (54%) experienced during the study (χ^2 = 21.1 with 1 d.f., P<0.01). It was therefore concluded that snails were more likely to remain inactive on dry nights than wet nights.

Overall, tracked snails were active on 74% of snail nights observed and, when active, moved an average of 8.70 m per night, with an average straight-line displacement of 5.10 m per night. Snails were significantly more likely to be active and to move greater distances on wet nights than dry nights.

A summary of distances moved and straight-line displacements by the three snails tracked during the spool-and-line study is provided in Table 4. The index of daily directness of movement (indicating the degree to which once-daily straight-line measurements reflected actual movements) was similar for the three snails, ranging only from 55.3% (snail 3) to 63.1% (snail 2). In contrast, the index of directness of movement over the entire study

Table 4. Summary comparison of distances moved and straight-line displacements during and following the spool-and-line study

	Snail 2	Snail 3	Snail 4
Duration of spool tracking (nights)	17	17	16
Sum daily distances moved during spool tracking (m)	44.64	182.24	95.07
Sum daily straight-line displacements during spool tracking (m)	28.16	100.84	58.92
Index of daily directness of movement (sum daily straight-line displacements/sum daily movements; %)	63.1	55.3	62.0
Overall straight-line displacement from start to end of spool tracking (m)	6.10	16.22	25.50
Index of directness of movement over the period of study (overall straight-line displacement/sum daily movements; %)	13.7	8.9	26.8
Straight-line displacement between early and late March (24 nights; m)	1.66	47.55	–
Straight-line displacement between late March and late May (63 nights; m)	31.6	–	–
Straight-line displacement between late May and late December (216 nights)	–	–	–

Table 5. Above-ground movements by spool tracked snails (summed for three snails)

Object climbed	No. times recorded	Average height (cm)	Maximum height (cm)	Proportion of total movement by snails (%)
Over or along mossy fallen logs	15	29	58	8.0
Up base of tree trunks	6	24	42	1.0
Over surface tree roots and prostrate lianas	6	14	20	0.5
Over sticks and other debris	6	16	26	0.7

period (indicating the degree to which a single straight-line measurement between the start and end of the study period reflected actual movements) was more variable, ranging from 8.9% (snail 3) to 26.8% (snail 4). The measurements of straight-line displacement for animals relocated subsequent to the spool tracking study are also summarised in Table 4 and can be seen to also be highly variable. The final known location of both snails relocated was outside the immediate study area.

The majority of movement recorded during the spool tracking study was on the ground. Of the total distance traced (three snails pooled), 89.8% was on the forest floor. Above-ground movements (climbing) by the spool tracked snails were rare and generally of limited extent. Vertical movements were recorded on a total of 33 occasions (three snails pooled; Table 5). These movements usually comprised snails climbing over low obstructions, such as fallen logs and other debris, although on a few occasions snails were recorded climbing short distances up tree and sapling trunks. The greatest height above the ground recorded for a snail was 58 cm on a mossy fallen log and the longest single above-ground movement recorded was 9.10 m along the length of a mossy fallen log.

Table 6. Diurnal shelter sites of spool tracked snails (summed for three snails)

Location of shelter	No. times recorded	Proportion of total (%)
In open (>2 m from logs or trees)	17	46
Against logs (within 10 cm of log)	9	24
Near logs (within 25–50 cm of log)	6	16
Base of trees (within 20 cm of tree trunk or between buttress roots)	4	11
On logs	1	3
Total	37	100

Diurnal shelter sites

The locations of diurnal shelter sites recorded over the course of the study are shown in Fig. 3. No spool tracked snails were recorded returning to previously used shelter sites. A total of 37 different diurnal shelter locations were recorded for the three tracked snails (Table 6), some of which were occupied for 2 or more consecutive days during periods of nil overnight movement. Almost half the recorded sites were on the open forest floor. All shelter sites but one were on the ground, the exception being a site on top of a large mossy log. At all 37 diurnal sites spool tracked snails were found partially or fully buried in leaf litter.

Snails 5 and 6 were recorded opportunistically when they were found with or near spool tracked snails. Snail 5 was observed only on a single day (Day 7), when it was found sheltering on the ground surface hidden in the space under a slab of fallen wood. Snail 5 had moved away from this site on the following day and, although the site was checked several times throughout the remainder of the study, it was not found there again. Snail 6 was observed with one of the spool tracked snails (snail 3) partially buried in leaf litter on the open forest floor on Day 13. It remained here for two more nights (as described under breeding observations below) and then moved to a new site against a fallen log, after which it was not recorded again. Whereas the two diurnal shelter sites recorded for snail 6 were consistent with those recorded for the spool tracked snails, it is of note that the diurnal shelter site where snail 5 was found (a hidden cavity under fallen timber) was of a type not recorded for any of the spool tracked animals.

Breeding observations

Two egg-laying events were observed during the course of the study. Observations concerning these events are documented below. Table 7 provides a summary of breeding information for *H. falconeri* based on an amalgamation of the two observed events.

Breeding event 1

On Day 5 of the spool tracking study (mid-February), snail 2 was found partly buried under leaf litter close up against the side of a mossy fallen log. It remained here without moving for the next 4 nights and days. After it had moved away on the fifth night, the site was inspected and a clutch of 16 creamy white, rubbery shelled subspherical eggs were noted. The eggs were in a mass in a 5 cm deep, 8 × 4 cm wide hole in the soil below the leaf litter and were covered by leaf litter. The weight of the entire clutch of eggs was 35.5 g, which comprised 30.0% of the bodyweight of the snail at the start of the study. The average size of the eggs, based on measurement of a random sample of five eggs, was 18.8 × 16.4 mm and the average weight 2.2 g. The eggs swelled slightly over the next few days to become turgid creamy white spheres.

Table 7. Summary of breeding information for *Hedleyella falconeri*

Egg laying season:	mid to late February
No. eggs laid:	11–16 eggs laid over 3–5 nights
Egg size and weight:	mean size 18.3 × 15.7 mm; mean weight 2.1 g
Relative clutch mass:	30.0% of original bodyweight
Nest site:	4–5 cm deep hole in soil below leaf litter, close against fallen log or on open forest floor
Incubation period:	eggs hatch between 40 and 46 days
Shell size at hatching:	mean 14.9 mm high × 11.9 mm wide
Shell size at 145 days old:	mean 21.8 mm high × 15.1 mm wide
Shell size at 200 days old:	mean 22.3 mm high × 18.5 mm wide

The nest site was examined again in early April (46 days after egg laying finished) and the eggs were found to have hatched. Three live hatchling snails and one empty hatchling snail shell were observed within the nest site. The average hatchling shell size, based on the four shells noted, was 14.9 mm high by 11.9 mm wide. Hatchling shell shape was similar to that of adult *H. falconeri*.

Breeding event 2

On Day 13 of the spool tracking study (late February), snail 3 was found next to a new snail (snail 6), partly buried under leaf litter on the open forest floor. Both snails were situated side by side with the front end of the shell over a shallow 4 cm deep depression in the soil. Snail 3 was retracted entirely within the shell, whereas the body of snail 6 was partly extruded into the depression. Interpretation of the spool trail indicated that snail 3 had climbed onto and over snail 6 during the previous night.

On the following morning (Day 14), snail 3 had moved away but snail 6 had not moved and remained partially covered by leaf litter, with the front of the shell down in the shallow depression. Four creamy white, rubbery shelled eggs had been deposited in the deepest part of the depression over the previous 24 h. Snail 6 was still at the nest site on Day 15, when a total of eight eggs was counted. On Day 16, snail 6 had moved away from the nest site and a total of 11 eggs was counted in the nest. The eggs were in a 5 × 5 cm wide mass in a 4 cm deep hole in the soil below the leaf litter and were partly covered by the leaf litter (Fig. 4). The weight of the entire clutch of eggs was 22.5 g, giving an average egg weight of 2.0 g. The average size of the eggs, based on measurement of a random sample of five eggs, was 17.8 × 15.0 mm (Fig. 5).

In early April (39 days after egg-laying finished), the nest site was examined again and the eggs were noted to be close to hatching, with shelled snails clearly visible inside the transparent eggshells. Six eggs were collected and retained in captivity and hatched over the next few days. By early September (approximately 145 days after hatching), the average size of these snails was 21.8 mm high by 15.1 mm wide and by late October (approximately 200 days after hatching) the average size was 22.3 mm high by 18.5 mm wide.

Two hatchling snails and one intact egg were lodged in the Queensland Museum Malacology collection (specimen no. 67294).

Foraging observations

On two occasions, interpretation of spool tracks indicated that the snails had been feeding on fruiting bodies of the fungus *Polyporus varius* (Order Aphyllophorales) during nocturnal movements. Snails were usually retracted inside the shell when observed during

Fig. 4. Nest site of *Hedleyella falconeri* with the covering of leaf litter removed. The eggs were laid over a period of several days in a small hollow in the soil beneath the leaf litter.

Fig. 5. Size of *Hedleyella falconeri* eggs. The large eggs each weighed approximately 2 g.

the day. However, on two occasions (separate to breeding observations), snails were found with their bodies partly extruded into the leaf litter beneath the shell and may have been feeding on rotting leaf litter material during diurnal resting.

Discussion

The present study is the first investigation of spatial and temporal patterns of habitat usage in an Australian land snail species that documents detailed quantitative and qualitative information at the scale of individual animals. Whereas the number of animals examined in this pilot study was low and caution needs to be exercised in extrapolation of the results, the findings have provided an increased understanding of the biology and ecology of *H. falconeri*. This is one of the first studies where the spool-and-line tracking technique has been applied to land snails. The first reported use of the spool-and-line technique in behavioural study of land snails was by Pearce (1990), comparing movement patterns and interactions between three North American land snail species. Other studies of movement patterns of land snails have typically relied on mark/recapture (Baker 1988; Baur and Baur 1988, 1990, 1992; Staikou *et al.* 1989; Cavagnaro *et al.* 2000). Time lapse cinephotography (Cook 1980; Bailey 1989), radiotracking (Tomiyama and Nakane 1993) and continuous observation (Cook 1979) have also occasionally been used. Both Pearce (1990) and the present study have demonstrated the significant value of the spool-and-line technique in ecological study of land snails.

Movement patterns and diurnal shelter sites

The results presented in this study concerning general activity patterns in *H. falconeri* supported a number of earlier observations of this species. Snails were found to be only nocturnally active, as previously noted by Jahnsen (1967), Shea (1978) and Bishop (1981), and were more likely to be active and to move greater distances on rainy nights than dry nights, consistent with earlier comments by Jahnsen (1967). McMichael and Iredale (1959) reported that, in general, the large land snail species from eastern Australian rainforests are very sensitive to dry conditions, appearing only at night and after rain and hiding away in moist places at other times. Similar correlation of activity with humid conditions or darkness has been reported in many other land snail species, including the European species *Helix aspersa* and *Helix lucorum* (Helicidae) (Bailey and Lazaridou-Dimitriadou 1986; Bailey 1989; Staikou *et al.* 1989) and the giant African snail *Achatina fulica* (Achatinidae)

(Tomiyama and Nakane 1993). It is likely to be a general behavioural pattern in many land snail species, assisting to minimise evaporative loss of body fluids and to reduce the high cost (Copley 2000) of mucous trail production. Many gardeners would probably attest to the veracity of the correlation between snail activity and wet nights.

Bishop's (1981) description of *H. falconeri* as a ground living species not climbing more than 0.5 m was also supported by the present study, with almost 90% of all movement recorded over the course of the study occurring on the ground surface and most climbing limited to passage over low obstacles, such as tree roots and fallen logs. Unlike sympatric land snail and slug species, such as *Thersites novaehollandiae* (Camaenidae) and *Triboniophorus graeffei* (Athoracophoridae), which can often be observed at moderate to high heights on tree trunks as well as on the ground (personal observations), *H. falconeri* does not appear to forage or shelter in trees.

The only previous reference to distances moved by *H. falconeri* is a single record, based on following a slime trail, of a juvenile snail (shell width 5 cm) moving a distance of approximately 30 m over an unknown time period (Jahnsen 1967). In the present study, *H. falconeri* moved an average of almost 9 m per night on the nights when it was active, with a maximum of over 21 m in a single night. Much of this movement (up to 45%) was meandering, but still resulted in straight-line displacement of up to 25.5 m over 16 nights and 47.55 m over 24 nights. It is evident that *H. falconeri* has considerable dispersal capacity provided there is continuity of habitat. Baur and Baur (1990) found that an 8 m wide paved road with low traffic density and, to a lesser extent, a 3 m wide unpaved track were sufficient to form a significant dispersal barrier for the European land snail *Arianta arbustorum* (Helicidae). However, movement in *A. arbustorum* (shell diameter 16–22 mm) averages only 0.58 m per day, with a maximum of up to approximately 4.4 m per day (Baur and Baur 1992), substantially less than that recorded for *H. falconeri* in the present study, and it is anticipated that greater barriers (e.g. wider or busier roads) would be needed to significantly obstruct movement and isolate populations of *H. falconeri*.

Comparison with other land snail species indicates that daily distances moved by *H. falconeri* are generally relatively large, probably reflecting, in part, its greater body size. Baur and Baur (1988) reported that the tiny European land snail *Punctum pygmaeum* (Endodontidae) (shell diameter 1–1.5 mm) had an average displacement of only 47 mm per 12 h. *Cernuella virgata* (Helicidae) (shell diameter 10–15 mm) was found to move on average between 0.1 and 0.4 m per day (Baker 1988). Pearce (1990), spool tracking three different land snail species with shell sizes of 15–25 mm diameter, recorded average daily movements of 0.76 to 2.25 m per day. Daily movements of an extent similar to *H. falconeri* were recorded in juveniles of the large land snail species *A. fulica* (shell length 50–57 mm), averaging between 5 and 9 m per day (Tomiyama and Nakane 1993).

Some earlier reports suggested that *H. falconeri* actively selected particular types of sites for diurnal shelter. Jahnsen (1967) suggested that the selection of secure diurnal shelter sites was essential for *H. falconeri* to avoid predation by diurnal ground foraging rainforest birds and reported finding snails sheltering under large rocks and slabs of fallen timber. Bishop (1981) reported that *H. falconeri* preferred diurnal shelter sites among the twisted roots of strangler fig trees, implying a high degree of active site selection. The results presented here do not support the notion of active and frequent selection of secure diurnal shelter sites. Almost half the shelter sites recorded in the present study simply comprised partial or complete burial under leaf litter on the open forest floor and the remainder were merely close to or up against the sides of logs or tree bases. None of the spool tracked snails was recorded using shelter sites that would be secure against diurnal predators, despite the availability in the study area of a fig tree with suitable crevices and root spaces at ground level and an abundance of fallen logs and pieces of timber, as well as the presence in the study area of the noisy pitta (a known predator) and other likely diurnal predators, including the superb lyrebird *Menura novaehollandiae* (Menuridae) and Australian brush turkey *Alectura lathami* (Megapodidae). Nevertheless, the three tracked snails all successfully avoided predation during the 17 day duration of the spool tracking study, with at least two of the three surviving a further 24 days following the end of the tracking study and at least one surviving a further 87 days. It is not known whether the other snails not relocated in these later searches were alive but not found or had been predated, but the fact that the last known site of the two relocated snails was outside the original study area suggests it is quite likely they were simply beyond the area searched.

One of the additional *H. falconeri* found and marked during this study (snail 5) was found in a secure diurnal shelter site under a slab of fallen timber, although it was not found there again during the remainder of the study. The author has previously found *H. falconeri* by day in similar sites on numerous occasions. This study, however, suggests that such secure shelter sites are not actively sought for every night by *H. falconeri*, but are simply used as they are randomly encountered and are not consistently re-used once found. Previous conclusions regarding the significant use of secure diurnal shelter sites, such as under logs and rocks, may be the result of paradigm based search pattern biases of the researcher rather than a true pattern of the snail. Certainly, the species is more abundant when observed at night than one would surmise based on diurnal searches (Bishop 1981; personal observations).

As noted above, all the diurnal shelter sites recorded in this spool tracking study involved partial or complete burial under leaf litter. Sheltering under leaf litter probably serves the dual function of providing a moist refuge and a degree of concealment from diurnal predators. Evidently simply hiding below leaf litter on the open forest floor is sufficient for *H. falconeri* to usually evade diurnal snail researchers, although concealment from diurnal predators is obviously not absolute, because *H. falconeri* is a common prey item of the noisy pitta.

The present study recorded no instances of return to and re-use of shelter sites once snails had moved away. Even the non-tracked snail found in a secure site under a fallen piece of timber was not found there again on subsequent inspections. This, together with the observation that the two marked snails relocated after the end of the spool tracking study had both moved beyond the original study area, suggests that *H. falconeri* does not occupy a home range, but is nomadic, moving randomly around the forest floor and sheltering wherever it finds itself at the end of the night. Jahnsen's (1967) description of two *H. falconeri* found by day retracted inside their shells in the middle of a bush road, having failed to completely cross during the previous night, is consistent with the type of behaviour observed in the present study. Pearce (1990) found a similar result spool tracking three North American land snail species, with snails re-using refuges only occasionally. Baur and Baur (1992) also found no evidence of homing behaviour in *A. arbustorum*, snails showing no preference in direction of movement, with directions chosen on consecutive days being independent from each other.

The apparently nomadic behaviour observed in the present study contrasts with studies of some other land snail species, which have reported homing behaviour and re-use of diurnal shelter sites (Edelstam and Palmer 1950; McLauchlan 1951; Cook 1980). Staikou *et al.* (1989) suggested that homing behaviour may be more advantageous in open habitats, where temperature and evaporation rates are more extreme, than in the favourable environments provided in well vegetated habitats. Therefore, the nomadism of *H. falconeri* may be a reflection of the equable environment for land snails in subtropical rainforest.

Nomadism and homing to a precise site represent the two end-points of a spectrum of possible movement behaviours for land snails. Examples of intermediary behaviours include *H. aspersa*, which Bailey (1989) reported as tending to choose particular areas for roosting but rarely returning to the exact same spot, and *A. fulica*, in which older adults maintain discrete home ranges but within which diurnal resting sites are not fixed (Tomiyama and Nakane 1993).

Some studies have reported seasonal or other longer scale homing or directional movement behaviour in some land snail species. McLauchlan (1949) reported *Strangesta capillacea* (Rhytididae) in an urban garden environment moving around in relatively open areas during periods of wet weather of up to 3 weeks duration, returning again to shelter in moist, sheltered refuge areas during intervening dry conditions. Baker (1988) recorded directional seasonal movement between pasture and roadside vegetation by *C. virgata*. Bailey (1989), citing references to seasonal migration of *Helix pomatia* (Helicidae) to traditional shelter sites, suggested that choice of a traditional shelter site may be more advantageous than on-the-spot assessment, particularly if the selection had to be made before the conditions that made the site suitable became apparent. The present study extended over only 17 nights and did not investigate seasonal scale differences or longer term patterns in movement by *H. falconeri*. Further study would be required to identify whether any longer term patterns exist in this species.

Size or age related differences in movement patterns have been reported in some land snail species. Baur and Baur (1988), for example, found a positive correlation between shell size and average displacement in *P. pygmaeum*. In contrast, Tomiyama and Nakane (1993) found a negative correlation between age and average dispersal distance in *A. fulica*, with juveniles being significant dispersers and young adults having continuously shifting home ranges, whereas older adults maintained a more restricted and constant home range. Baur and Baur (1989) found no age related correlation in *A. arbustorum*. These different patterns (or lack of pattern) probably reflect different life history strategies between different land snail species. Tomiyama and Nakane (1993), for example, proposed that the negative correlation found in *A. fulica* was related to its protandrous maturation, allowing younger sperm producing adults to increase their reproductive fitness by searching widely for older egg producing adults. Further study with a greater sample size including a range of age classes would be necessary to determine whether any age related movement patterns exist in *H. falconeri*.

Breeding observations

The observations of egg laying in *H. falconeri* made during the present study were an unexpected bonus and illustrate the value of close observation of natural behaviour required in such studies. The descriptions of egg size, clutch size and nest site for *H. falconeri* presented here are consistent with those provided by Jahnsen (1967), who maintained the species in captivity and described two separate clutches of marble sized (15 mm diameter) white eggs, one of 14 eggs and the other of 16 eggs, both deposited in small depressions in the soil and then covered with debris to a depth of approximately 2.5 cm. Jahnsen (1967) recorded *H. falconeri* eggs in December and January, 1–2 months earlier than the present study, and also reported observing *H. falconeri* mating in September. Information detailed in the present study concerning relative clutch mass, time taken to lay eggs, incubation period, hatchling size and early growth rate details has not previously been described for *H. falconeri*.

Unfortunately, little information is available to enable comparison of reproductive details in *H. falconeri* with other Australian land snail species (Bishop 1981). Smith (1992) noted that large eggs were typical of many caryodid land snail species. Hedley (1892) reported that *Pygmipanda atomata* (Caryodidae) laid large white hard-shelled eggs. Jahnsen (1967), who maintained *P. atomata* in captivity, provided further details, including that egg size was approximately 5 mm in diameter, clutch size between 13 and 20 eggs, laying occurred in November and December, the nest site comprised a small cavity in the soil under leaf litter and eggs hatched in approximately 32 days, with progressive hatching of eggs, a few per day, presumably reflecting laying over several days. Similarities between *P. atomata* and *H. falconeri* in addition to the large egg size include approximate clutch size, nest site and probably egg laying extending over several days.

The nest sites recorded in the present study were not in secure locations, such as under fallen logs, and would be vulnerable to predation by ground litter foraging birds. However, there was no indication of the eggs apparent from the surface of the leaf litter at the two nest sites recorded and it is probable that discovery of nest sites by predators, such as birds, relies on random chance, with sufficient nest sites escaping discovery to maintain population levels.

Feasibility and value of the spool-and-line tracking technique

The spool-and-line tracking technique was found to work well for field study of *H. falconeri*. The spools were very easy to affix to the hard dry shell surface, stayed firmly in place for the duration of the study and, attached to the rear of the shell, did not appear to impede movement of the animals. Distances moved by *H. falconeri* were such that a single spool per animal was amply sufficient for the duration of the present study and, in fact, would probably have sufficed for at least 25 days. *Hedleyella falconeri* was sufficiently large to ensure that the 5 g spool mass used in the present study did not exceed the recommended level of 10% of the subject animal's body mass for tracking devices on small animals (Richards *et al*. 1994). Lighter spools are available that would be suitable for use on medium sized land snail species. Pearce (1990) used a modified spool measuring only approximately 25 mm by 6–8 mm and weighing less than 1 g on land snails with a shell diameter of 15–25 mm.

As discussed above, the application of the spool tracking technique enabled the collection of detailed quantitative and qualitative data for several aspects of ecology and biology that would otherwise be difficult to study in the field. Direct monitoring of snail movements in natural habitats is difficult, with observation related disturbance potentially altering the snails' behaviour (Baur and Baur 1990). Furthermore, the most mobile individuals that leave the search area and the least mobile individuals that remain hidden are likely to be underrepresented in mark/recapture sampling (Baur and Baur 1990). The spool tracking technique enabled continuous and detailed monitoring of movement by an indirect means, thereby minimising observation-related disturbance, and allowed animals to be relocated regardless of distance moved, avoiding sampling biases. Comparison of spool trail length and straight-line displacements in the present study (on both a daily basis and over the course of the study) demonstrated the significant degree to which movement studies based on point locations, such as mark/recapture or radiotracking studies, can underestimate actual distances moved. It is considered that the cheap, simple and effective spool-and-line technique has great potential in the study of medium to large land snail species and can provide much information concerning their behaviour and ecology to assist with their conservation.

Conservation implications and conclusions

This study indicated that *H. falconeri* is reliant on the leaf litter layer on the rainforest floor for foraging, shelter and breeding. Degradation or loss of this key habitat component through impacts such as fire, intensive forestry or grazing by domestic stock is likely to significantly and adversely affect the species. *Hedleyella falconeri* does not appear to rely on known or traditional diurnal shelter sites, but gambles on finding suitable shelter wherever its nomadic movements lead it. On the one hand, this nomadism, together with the distances the species is able to cover, provides a relatively high dispersal capacity, so that recolonisation of regenerating habitat is likely if populations survive nearby. On the other, it is a strategy that works well in the highly favourable conditions for land snails provided by eastern Australian rainforests, but is reliant on the continued conservation of those rainforest habitats.

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