

# The distribution and habitat characteristics of a threatened lucanid beetle *Hoplogonus simsoni* in north-east Tasmania

M. MEGGS<sup>1,2\*</sup>, S. A. MUNKS<sup>1</sup> and R. CORKREY<sup>3</sup>

The distribution and characteristics of habitat utilized by a threatened species of stag beetle in north-east Tasmania *Hoplogonus simsoni* (Coleoptera: Lucanidae), were examined as a first step in the development of conservation management objectives for the species. The beetle was found to have a restricted distribution of 250 km<sup>2</sup> and its regional distribution appeared to be related to the occurrence of granitic geology and a moderately high rainfall at low elevations. The species was patchily distributed across its range. High-density populations of the species were restricted to the eastern part of its distribution, but over most of its range it occurred at very low densities. Relative abundances of *H. simsoni* were greatest in wet eucalypt forest, with significantly fewer beetles found in mixed forest and rainforest. Dry eucalypt forest was found to be unsuitable habitat although the beetle was found to occur in the ecotone between wet and dry eucalypt forest. Potential wet forest habitat for the species is estimated to encompass 18 200 ha or 72% of its range. The species was not found in areas of wet eucalypt forest that had been converted to pine plantation. However, *H. simsoni* was found to occur in wet eucalypt forest regenerating after clearfelling and some of the highest density populations of the species occurred in 70 year old wet eucalypt forest regenerating following a wildfire. The relationship between various habitat variables and the occurrence of the beetle was investigated using Generalized Additive Modelling and robust regression. The presence of wet eucalypt forest below 300 m altitude; slope less than 5°; a deep leaf litter layer; and a forest structure with a well-developed canopy best explained the occurrence of the beetle. These habitat characteristics probably relate to a requirement for a cool, moist, stable microclimate and an absence of wildfire for some time. The potential habitat of *H. simsoni* as identified in this study is poorly reserved across its range and a high percentage has been identified by the forest industry as having potential for conversion to pine plantation. This highlights the importance of having mechanisms for "off-reserve" conservation of threatened species, like *H. simsoni*, which are often poorly represented in or completely absent from formal reserves.

**Key words:** Lucanid beetles; Threatened species; Forestry; Pine plantation; Habitat modelling.

## INTRODUCTION

ALTHOUGH many formal reservation targets have been attained under Tasmania's Comprehensive, Adequate and Representative reserve system, a large proportion of habitats important for threatened species, particularly invertebrates, remain in the off-reserve landscape (Munks *et al.*, in press). Management objectives and prescriptions to cater for threatened fauna in production forest areas in Tasmania have been developed over the past six years for use under the Tasmanian Forest Practices System (Munks and Taylor 2000; Forest Practices Board 2001). However, for management prescriptions to be effective they must be based on a sound knowledge of the distribution and habitat characteristics of the species, as well as the specific threats to the species from off-reserve land-use practices.

Simons Stag Beetle *Hoplogonus simsoni* Parry (Coleoptera: Lucanidae) is the largest endemic stag beetle in Tasmania, and is listed as Vulnerable under the Tasmanian *Threatened Species Protection Act 1995* due to its restricted distribution, low population density and the potential adverse impacts of forestry practices within its range (Jackson and Taylor 1995). With

a body length varying between 10 and 24 mm and the greatly enlarged, elongate mandibles of the males, this flightless black beetle is considered the finest of the Tasmanian Lucanidae. It is a relatively long-lived beetle, with the larval stage lasting up to two years and adult lifespan in the range of one to two years (G. Bornemissza, pers. comm.). The larvae were believed to be log-dwelling (Jackson and Taylor 1995), but more recent information suggests that they are edaphic forming a part of the diverse soil-dwelling invertebrate fauna (G. Bornemissza, pers. comm.; Meggs 1996). The adults are free-living, wandering among leaf litter, generally at night, and sheltering under rocks, logs and leaf litter during the day. Meggs (1996) and anecdotal reports from collectors suggest that levels of activity of adult males and females appear to be highest in December/January for males, and in January/February for females.

Prior to 1996 there had been no detailed studies of *H. simsoni* and the species was known from only five localities in north-east Tasmania (Jackson and Taylor 1995). However, a preliminary investigation of the distribution, habitat and conservation status of *H. simsoni* increased the number of known localities to 18 within a restricted area of about 300 km<sup>2</sup> in the

<sup>1</sup>Forest Practices Board, 30 Patrick Street, Hobart, Tasmania, Australia 7000.

<sup>2</sup>Present address, Forestry Tasmania, 79 Melville Street, Hobart, Tasmania, Australia 7000.

<sup>3</sup>PO Box 491, Wallsend, New South Wales, Australia 2287.

\*To whom correspondence should be addressed.

north-east of Tasmania (Meggs 1996). A moderately high rainfall (1 200 mm annually) at low elevations typifies the Blue Tier region in which this species is found, and much of the region is underlain by a granitic geology known as the Blue Tier Batholith (Meggs 1996).

Little of the current known range of *H. simsoni* is contained within formal reserves and much of the forest within its range is of high value to Tasmania's timber industry. Preliminary data suggests that historical practices such as selective logging have had minimal impact on the viability of local populations of the species (Meggs 1996), but little is known of the effects of current forestry practices. Meggs (1996) suggested that the species was patchily distributed, and stressed the importance of identifying key habitats for the species within its range and the need to assess the impacts of habitat disturbance on local populations.

The present study was initiated to provide information for the formulation of management measures required to ensure the conservation of *H. simsoni* in areas subject to production forestry activities. The aims of the study were to determine the distribution and relative population densities of *H. simsoni* throughout its range, determine the characteristics of habitat utilized by *H. simsoni*, and assess the effects of current forestry practices on the beetle. The conservation status of the beetle and conservation management of its habitat is discussed.

## METHODS

### Study area

Field work for the investigation of habitat characteristics was conducted between November 1996 and May 1997 in an area encompassing the known range of *H. simsoni* in north-east Tasmania (Fig. 1). Locality records obtained subsequent to this work have been included to determine the current known range and conservation status of the species, but were not used for the analysis of habitat characteristics (Meggs, Munks and Richards, unpubl. data). The forest in the study area consisted predominantly of wet eucalypt forest communities, with some mixed forest and rainforest occurring along riparian corridors and in larger blocks of forest in the centre and southwestern corner of the area. Mixed forest was distinguished from wet eucalypt forest by the presence of rainforest species such as Myrtle *Nothofagus cunninghamii* and Sassafras *Atherosperma moschatum* as dominant understorey species. Dry eucalypt forest occurred in the eastern and northeastern parts of the study area. Approximately 80% of the study area was State Forest. Most of the remainder, occurring in the southern half of the study area along the river valleys, was private land and almost 70% of this had been cleared for agriculture in the past 150 years.

The majority of the study area is underlain by a granitic rock-type known as the Devonian Blue Tier Batholith (Groves *et al.* 1977), an extensive composite granitic intrusion of Upper Devonian age covering 1 800 km<sup>2</sup> in north-east Tasmania. It is made up of multiple intrusive bodies or plutons ranging from early mafic granodiorites to late leucocratic granites. The region is subject to relatively high annual rainfall (1 200 mm annually) at low elevations. Much of the rain in this area occurs in heavy falls associated with persistent low-pressure systems over the Tasman Sea, which are intensified by the lifting of moist easterly winds up the scarp faces at St. Helens (Mesibov 1988).

The study area forms the north-east corner of an invertebrate bioregion that has been called Plomley's Island (Mesibov 1994). This bioregion has been defined by the presence of a number of species of invertebrates that are endemic to Plomley's Island and range widely within it. The eastern and western boundaries of Plomley's Island are fairly distinct faunal breaks where species assemblages change over a relatively short distance (Mesibov 1994). The eastern boundary has been called the Goulds Country Break (Mesibov 1994) and lies within the study area.

### Beetle survey

Five broad forest types were recognized for the stratification of the beetle survey:

*Mature wet eucalypt forest:* forest communities of 70 years+ in age dominated by *Eucalyptus regnans*, *E. obliqua* and/or *E. viminalis* with a wet sclerophyll understorey.

*Mixed forest/Rainforest:* forest communities of 70 years+ in age dominated by *N. cunninghamii* and/or *A. moschatum*. Mixed forest was distinguished from wet eucalypt forest by the presence of rainforest species such as *N. cunninghamii* and/or *A. moschatum* as dominant understorey species below a wet eucalypt canopy as described above.

*Mature dry eucalypt forest:* multiple-aged forest communities, with the oldest cohort of 100 years+ in age dominated by *E. obliqua* and/or *E. amygdalina* with a dry sclerophyll understorey.

*Clearfelled wet eucalypt forest:* wet eucalypt forest communities in coupes that had been subjected to a silvicultural regime of clearfell, burn and sow (Forestry Commission 1994). The ages of the regenerating forest ranged from one to 36 years after logging. Two of the five coupes sampled were less than a year old and had not yet been subjected to a regeneration burn.

*Plantation:* areas that had previously supported wet eucalypt forest but which had been converted to either pine (*Pinus radiata*) or eucalypt (*E. regnans*) plantation.

At least five different geographic locations within each forest type were selected within or immediately adjacent to the range of the study species *H. simsoni* (total of 42 locations). Locations were selected to cover the widest geographic range that would ensure sampling of all combinations of environments within the potential range of the species. At each location for a particular forest type, six sites were selected (total of 252 sites) covering the range of topography (i.e., gully/flat, mid-slope, and ridge-top), different aspects, slopes, and proximity to streams, present within a location. Where these attributes were relatively consistent within a location, sites were selected to sample as wide an area as possible. Hence sites were generally located greater than 100 m from one another. Wherever possible sites were located at least 30 m from roads, paddocks or any disturbed habitat not consistent with the forest type under investigation.

Six 1 m<sup>2</sup> plots were placed haphazardly within a 10 m radius circle, thus ensuring all potential microhabitats were sampled. The plots were systematically searched by hand for live *Hoplogonus* specimens and body parts of dead ones. Live beetles were recorded and released at the site of capture. Parts of dead beetles were recorded and stored in 70% alcohol. Identifiable body parts included male heads, female heads with thorax attached, and the thorax and abdomen of both sexes, which have distinctive humeral spines (Bartolozzi 1996).

Two measures of beetle abundance for each site were estimated from the data: beetle density (No. of individuals/m<sup>2</sup> — calculated from the minimum number of *H. simsoni* known to have been alive from dead parts and live individuals in each plot); and the frequency of occurrence of beetles at each site (calculated as the proportion of plots in which beetles were found).

The hand searching method used in this study may have led to over-estimates of absolute population sizes since the dead parts of beetles sampled may represent an accumulation from more than one season. A pilot study comparing the abundance estimates for *H. simsoni* produced by pitfall trapping relative to hand-collecting showed that the latter method resulted in estimates three times greater than those obtained by trapping (Wald Statistic = 99.7; df = 1; p < 0.01). However, there was no interaction between the method used and location, indicating that hand-collecting was as reliable a method of estimating relative abundance as pitfall trapping. Hand-collecting was thus chosen as the sampling method because of its efficiency relative to trapping and also because it allowed the use of a non-destructive sampling method for this threatened species. Hand-collecting of other litter invertebrates such as millipedes has been found

to be more efficient and to provide more accurate data on species relative abundance than pitfall trapping (Mesibov *et al.* 1995).

It was assumed that the presence and abundance of adults reflects that of the soil-dwelling larvae. It may be argued that the larvae of this species are a better indicator of presence, population size and viability, and habitat quality than the adult population. Although the two life-stages of *H. simsoni* inhabit different microhabitats, the fact that the adults do not appear to eat (P. McQuillan, pers. comm.) and are believed to be poor dispersers, in the order of 100–200 m in a lifetime (G. Bornemissza and P. McQuillan, pers. comms.), supports the assumption that adult presence, abundance and habitat requirements represents the species as a whole.

#### Habitat variables

Habitat variables recorded at each site were chosen for their anticipated value as predictors of beetle distribution and abundance, and for the ease with which they could be collected. The following habitat variables were assessed at each site: altitude (m), distance to nearest stream (<30 m; 30–100 m; >100 m), leaf litter depth (<1 cm; 1–3 cm; >3 cm), leaf litter cover (% ground cover), rock cover (very low; low; medium; high), dead wood cover (% ground cover of logs >10 cm mid-diameter), moss cover (% ground cover including on rocks and logs), average aspect (N, S, E, W, none), average slope (degrees), distance to nearest road (m), weeds (present/absent).

The forest community species composition and structure was recorded at each site. Floristic nomenclature was as per Buchanan (1999). Forest structure was measured by categorizing the forest at each site into vegetation height classes including: overstorey tree, understorey tree, tall shrub, low shrub and ground cover. For each height class present at a site the average height (m) and average canopy cover (%) was visually estimated.

Soil samples were taken from the A1 horizon at each site, placed in a sealed plastic bag, and then dried at the Mt. Pleasant Laboratories (Department of Primary Industries, Water and Environment, Tasmania) for analysis of: percentage organic carbon (Walkley and Black method); total nitrogen (modified from the Kjeldahl method); conductivity (1:5 soil/water extract); pH (1:5 soil/water suspension); and phosphorus and potassium (Colwell bicarbonate-extractable P and K). The procedures for the soil analyses conducted are described in Rayment and Higginson (1992).

Soil profile descriptions were made at eleven sites representing a range of beetle densities. The format of the profile descriptions followed Grant *et al.* (1995).

### Statistical analyses

The relative abundances of beetles in each forest type were tested for equality using Generalized Linear Modelling (McCullagh and Nelder 1989). The levels of location and site were not included in this Generalized Linear Modelling analysis as it was merely used to give an overview of differences between forest types as a prelude to the habitat modelling. Variation at the level of location and site was examined using Generalized Linear Mixed Modelling. The two measures of relative abundance were used in both analyses: beetle density (assuming a Poisson distribution and log-link function); and frequency of occurrence (assuming a binomial distribution and logit-link function). Levels of statistical significance were set at 0.01 unless otherwise stated.

Only sites occurring in wet eucalypt forest were used to examine the relationship between beetle occurrence and the measured habitat variables. Plantation and clearfelled wet eucalypt forest sites were excluded because it was decided that the influence of the physical disturbance associated with the clearfelling and associated silvicultural treatments would confound the results. Dry eucalypt forest was excluded because preliminary survey results confirmed the beetle did not prefer this forest type. Mixed/rainforest was excluded due to the small sample size of sites relative to wet eucalypt forest.

Some habitat variables needed logarithm transformation to decrease excessive skewness. These variables are indicated in the results by the prefix "L". Initial investigation indicated considerable collinearity between variables within the data, which would have led to biased and poorly estimated model terms (Myers 1990). This was avoided by selecting the model with the fewest significant variables by examination of  $C_p$  plots (Snee and Pfeifer 1983). This led to a restricted data set of the following habitat variables: Slope (LSlope), Tall shrub height (TSH), Distance to nearest road, Phosphorus, Altitude (Alt), Overstorey tree cover, Leaf litter depth, Rock cover, Weeds, Aspect, and Distance to nearest stream.

The relationship between the occurrence of *H. simsoni* and the reduced set of habitat variables recorded in wet eucalypt forest was analysed

using Generalized Additive Models (Hastie and Tibshirani 1990), incorporating all sites. These are generalized linear models that incorporate smoothed effects that make no assumption on the distribution of the data, and so can be considered non-parametric analyses. Instead of fitting a straight line, a complex curve is fitted. Separate models were constructed for each of the continuous variables crossed with one factor at a time.

Since Generalized Additive Models cannot be used for predictive models (Hastie and Tibshirani 1990), robust regression using the ROBSSPM procedure in GENSTAT (Payne *et al.* 1993) was used to construct an overall model. It was considered that this approach would lead to a conservative outcome. Only variables identified as important by the Generalized Additive Models were included. This procedure does not allow the use of factors and therefore separate models were constructed for each level of the categorical factors.

Separate analyses of variance (ANOVA) and least significance difference tests were conducted on the factors identified by the Generalized Additive Models as significantly influencing the abundance of *H. simsoni*. Significance levels were set at 0.05 for both the ANOVA and robust regression.

A multi-dimensional scaling programme in the DECODA software package (Minchin 1991) was used to examine the relationship between the structure and species composition of the vegetation communities recorded at each site and the presence/absence of beetles. The Global Non-metric Multi-Dimensional Scaling procedure was used. At least 20 starting configurations were used in each analysis in two and three dimensions. Minimum acceptable stress levels were set at 0.15.

## RESULTS

### Distribution and relative abundance of *H. simsoni*

*Hoplogonus simsoni* was present at 31 of the 42 locations sampled (119 of the 252 sites sampled). It was found in all forest types with the greatest proportion of new records occurring in wet eucalypt forest (Table 1). During this study, a sighting of a *Hoplogonus* specimen was reported from a locality south of the known distribution of *H. simsoni* (Fig. 1). The collector

Table 1. The percentage of locations and sites sampled for each forest type in which *H. simsoni* was found.

Forest type	Total locations sampled	Total sites sampled	% of locations with <i>H. simsoni</i>	% of sites with <i>H. simsoni</i>
Plantation	5	30	20%	7%
Wet eucalypt forest	19	114	95%	62%
Mixed/Rainforest	7	42	71%	43%
Clearfelled wet eucalypt	6	36	83%	50%
Dry eucalypt forest	5	30	40%	17%

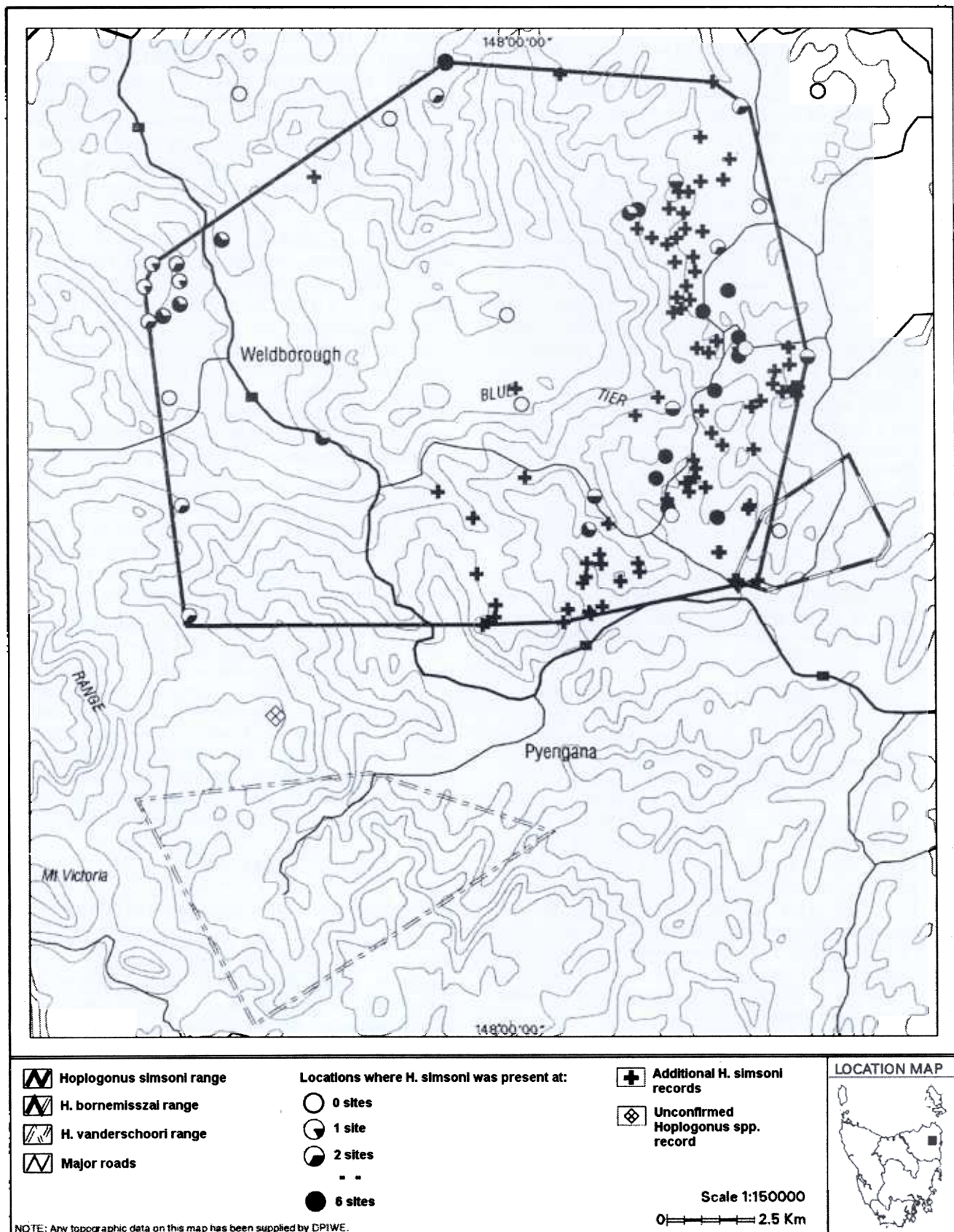


Fig. 1. Distribution of *H. simsoni* and the sites surveyed in this study (circles) in north-east Tasmania. The range boundary for *H. simsoni* includes additional records found subsequent to this study (Meggs, Munks and Richards, unpubl. data). Range boundaries for *H. bornemisszai* and *H. vanderschoori* from Munks, Richards, Meggs, Wapstra and Corkrey (unpubl. data).

was familiar with the characteristics of the genus and it is considered a reliable sighting.

The known range of the species was extended by 10 km<sup>2</sup> in a west/north-westerly direction, by 50 km<sup>2</sup> to the north/north-east and 5 km<sup>2</sup> to the south. The range was reduced by 15 km<sup>2</sup> in the south-east due to the mistaken identification of a female *H. bornemisszai* Bartolozzi specimen by Meggs (1996). Subsequent survey work has further increased the known range of the species by another 10 km<sup>2</sup> to the north/north-east (Meggs, Munks and Richards, unpubl. data).

The extent of occurrence of *H. Simsoni*, calculated as the area contained within the shortest boundary that encompasses all known sites of occurrence (IUCN Species Survival Commission 1994) is now over 250 km<sup>2</sup> (25 300 ha) (Fig. 1). This represents an increase of approximately 60 km<sup>2</sup> from that reported by Meggs (1996), recalculated at the 1 km grid square scale as 190 km<sup>2</sup>.

*H. simsoni* was found to occur at very high densities (>5/m<sup>2</sup>) at only one location, in high densities (3–5/m<sup>2</sup>) at three locations and in moderate densities (1–3/m<sup>2</sup>) at four locations, but over most of its range it occurred at less than one per square metre. Densities varied significantly between locations within forest types (estimate of variance component on the log scale was 2.293, se = 0.685, df = 33, Schall (1991)) and between sites within locations (scale parameter for an over-dispersed Poisson was estimated as 3.747, se = 0.362, df = 213, Schall (1991)).

The beetle was patchily distributed between locations within the forest (estimate of variance component on the logit scale was 3.655, se = 1.027, df = 33, Schall (1991)). It also appeared to be patchily distributed between sites within locations, but this was not statistically significant, occurring in less than 20% of plots at roughly half of the sites where it was found. These sites largely correspond to those where it was found at low densities. It was more evenly distributed within sites and locations where it occurred at moderate to high densities, such as in the eastern part of its distribution. Overall, within locations, beetle distribution was fairly uniform across sites but actual densities suggested high aggregations for particular sites.

#### Forest types and the occurrence of *H. simsoni*

*Hoplogonus simsoni* was found in all of the forest types sampled (Fig. 2). However, abundance of *H. simsoni* differed significantly between the five forest types for both abundance measures, density ( $\chi_4 = 231$ ,  $p < 0.01$ ) and frequency of occurrence ( $\chi_4 = 51.3$ ,  $p < 0.01$ ). Relative abundances of beetles were highest in wet eucalypt forest and lowest in plantation (Figs 2a and b).

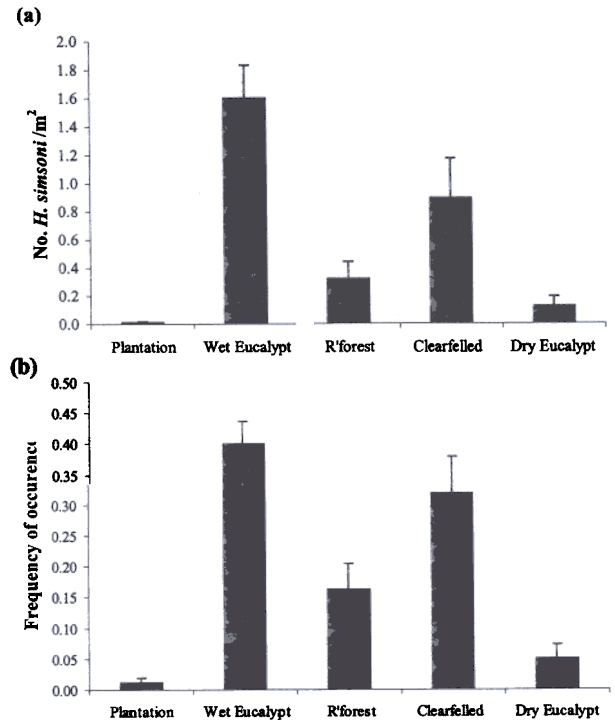


Fig. 2. The (a) density and (b) frequency of occurrence of *H. simsoni* in each of the five forest types (mean  $\pm$  se; n = 30, 114, 42, 36, 30).

Two body parts of *H. simsoni* were found in two plots at one site within a 12-year-old eucalypt plantation adjacent (within 50–100 m) to mature native eucalypt forest. No body parts of *H. simsoni* were found in any of the pine plantation sites sampled, including a site in a 30 year old plantation immediately adjacent to mature wet eucalypt forest that had the highest density of beetles found in the study. Two males were captured in pitfall traps in this 30 year old pine plantation during the preliminary survey but the absence of any body parts in all of the plots hand-searched in this study suggests that these individuals were vagrants from the adjacent native forest.

Beetles were present in five of the six clearfelled sites sampled, including two sites in recently logged coupes, and sites in coupes, which were regenerating three years, seven years and 36 years after logging. No beetles were found at the sites in 12 year old *E. regnans* forest regenerating after logging. This patch of wet eucalypt forest occurred within an area of predominantly dry eucalypt forest just outside the known range of the species and hence it is possible that the species did not occur in the area prior to logging.

#### Relationship between the occurrence of *H. simsoni* and measured habitat variables

The Generalized Additive Modelling of *H. simsoni* habitat indicated that the following seven habitat variables significantly influenced the

Table 2. Robust estimates of regression coefficients for *H. simsoni* habitat in wet eucalypt forest (s.e. = standard error; t = the t-statistic, used as a rough guide to test whether each of the factors differs from the first level; % Var. accounted for = the percentage of variance in the data set accounted for by each model; L = logarithm transformation; Alt = Altitude; TSH = Tall Shrub Height; TSH2 = TSH\*TSH).

Variable	Estimate	s.e.	t(*)	p-value	%Var. accounted for
<i>Leaf litter and weeds excluded</i>					
Constant	38.6700	4.0400	9.57	<0.001	
Alt	-0.0629	0.0105	-5.99	<0.001	
TSH	-0.7830	0.2650	-2.96	0.004	
LSlope	-2.2700	1.0000	-2.27	0.025	
No. beetles = 38.67 - 0.0629×Altitude - 0.783×Tall Shrub Height - 2.27×LSlope					
<i>Leaf litter &lt;1 cm and weeds excluded</i>					
Constant	1.795	0.291	6.16	<0.001	
LSlope	-0.452	0.136	-3.32	0.008	
No. beetles = 1.795 - 0.452×LSlope					
<i>Leaf litter 1-3 cm and weeds excluded</i>					
Constant	40.1700	4.2500	9.46	<0.001	
TSH	-3.1480	0.7670	-4.10	<0.001	
Alt	-0.0413	0.0108	-3.84	<0.001	
LSlope	-2.4300	1.0000	-2.43	0.018	
TSH2	0.1326	0.0553	2.40	0.020	
No. beetles = 40.17 - 0.0413×Alt - 3.148×TSH - 2.43×LSlope + 0.1326×TSH2					
<i>Leaf litter &gt;3 cm and weeds excluded</i>					
Constant	27.2400	6.7800	4.02	<0.001	
Alt	-0.0548	0.0230	-2.38	0.026	
No. beetles = 27.24 - 0.0548×Altitude					
<i>Weeds included and leaf litter excluded</i>					
Constant	61.4000	15.1000	4.05	0.003	
Alt	-0.1371	0.0525	-2.61	0.028	
No. beetles = 61.4 - 0.1371×Altitude					

abundance of beetles in wet eucalypt forest: Altitude, Overstorey tree canopy cover, Distance to nearest road, Tall shrub height, Slope, Weeds, and Leaf litter depth. The robust regression of *H. simsoni* habitat, which was used to develop overall models using variables identified as important by Generalized Additive Models, confirmed the importance of most of these variables in wet eucalypt forest and their relationships with beetle numbers. The exceptions were overstorey tree canopy cover and distance to nearest road, which did not appear in any of the models. The models that best explain the variation in beetle abundance in wet eucalypt forest are presented in Table 2.

Beetle abundance increased with increasing leaf litter depth. Sites with a shallow litter layer (<1 cm) had significantly lower numbers of *H. simsoni* than sites with deeper litter layers ( $F_{2,110} = 3.14$ ;  $p = 0.047$ ). Although on average sites with the deepest leaf litter (>3 cm) had the greatest numbers of beetles, these were not significantly higher than those with leaf litter between one and three centimetres. Numbers of *H. simsoni* were also significantly higher at sites where weeds were present ( $F_{1,112} = 12.68$ ;  $p < 0.001$ ), in the order of three times greater than at sites without weeds.

The abundance of beetles decreased with increasing altitude and increasing slope. At sites with a shallow litter layer and with weeds present

the decline of beetle abundance with increasing slope was less pronounced. Abundance of beetles also declined with increasing distance from a road, but this trend was not apparent where litter layers were shallow.

There was a complicated relationship between tall shrub height and beetle abundance. Numbers of beetles declined with increasing tall shrub height but the graph shows a bowl-shaped curve (Figs 3a and b). This relationship differed for sites with weeds compared to those without (Fig. 3b).

The Global Non-metric Multi-Dimensional Scaling analysis found no clear relationship between plant community species composition and the presence or absence of *H. simsoni*, neither was the presence of *H. simsoni* related to a particular forest structure.

## DISCUSSION

### Distribution and relative abundance of *H. simsoni*

The results from this study have shown that *H. simsoni* is more widely distributed in the north-east of Tasmania than was thought when it was first listed as threatened (Meggs 1996). It was recorded from 38 localities in north-east of Tasmania, which with the addition of recent records (Meggs, Munks and Richards, unpubl.

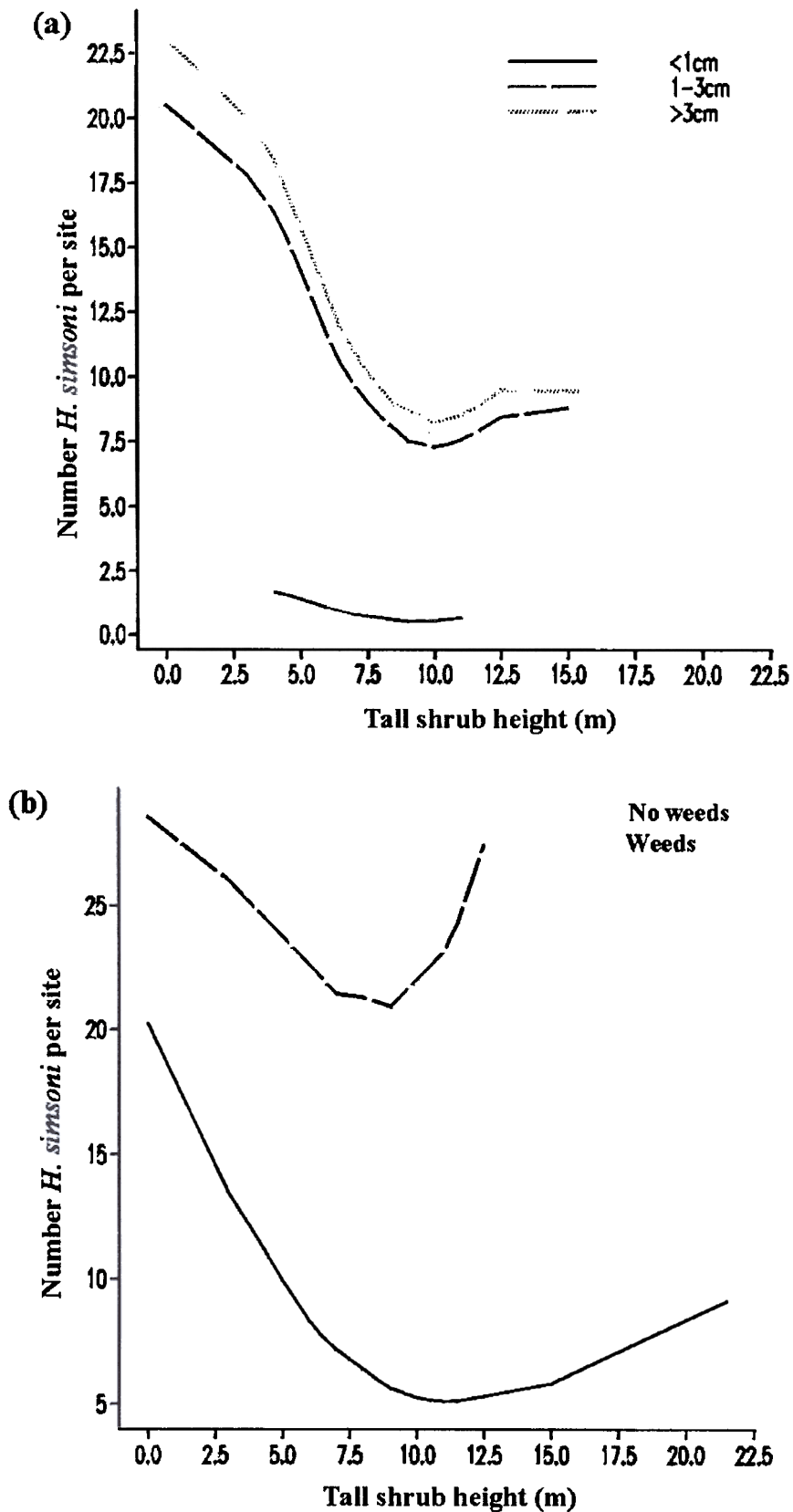


Fig. 3. The relationship between numbers of *H. simsoni* per site and tall shrub height for (a) varying leaf litter depth and (b) sites with and without weeds in wet eucalypt forest from the Generalized Additive Models analysis. The fitted lines are smooth curves obtained from the Generalized Additive Models and indicate trends and non-linearities in the data. The length of the lines corresponds to the range of the data collected.



data) results in a range of roughly 250 km<sup>2</sup>, centred on the Blue Tier, of which 182 km<sup>2</sup> is considered potential habitat. Although small extensions of its range beyond that found by Meggs (1996) have been made, it is unlikely that future searches will extend its range any more than a few kilometres beyond that presented here. Much of its current known range is surrounded by unsuitable habitat (e.g., dry eucalypt forest, altitudinal barriers). Where potential habitat does exist, studies on other litter invertebrates have failed to find *H. simsoni* (e.g., Bashford 1990; Mesibov and Ruhberg 1991; Meggs 1996; Mesibov *et al.* 2002; Taylor, unpubl. data). The occurrence of two new species of *Hoplogonus* (*H. bornemisszai* and *H. vanderschoori* Bartolozzi) on the south-west and east/south-east boundaries of *H. simsoni*'s range (Richards, unpubl. data) supports the argument for the south-west and east/south-east boundaries of *H. simsoni* range. Apart from a minor overlap in the distributions of *H. simsoni* and *H. bornemisszai* in a small part of the boundary (Marguerita ridge) the species have not been found to co-occur, yet all three species appear to inhabit forests of the same type (Richards, unpubl. data). In addition, the east/south-east range boundaries of *Hoplogonus* species coincide with part of an invertebrate faunal boundary, respected by at least eight species of invertebrates with minimal overlap, called the Goulds Country Break (Mesibov 1994). This boundary may be explained at an ecological level by the presence of a steep environmental gradient but its maintenance at a species level is unknown (R. Mesibov, pers. comm.).

*Hoplogonus simsoni* occurred at relatively high densities at only a handful of locations. Over most of its range it occurred at very low densities. Most species exist as metapopulations, since habitat heterogeneity and breeding systems divide them into a series of populations that interact by dispersal between them (Caughley and Gunn 1996). The classic metapopulation structure is characterized by local extinctions and recolonizations. This may take the form of patchy populations in localized and ephemeral habitats, characterized by high rates of individual dispersal between patches which lessens the chance of local extinctions. At the other end of a continuum of metapopulation patterns is the mainland-island population structure where a large core population supplies immigrants to recolonize islands as local extinctions occur. In contrast to this structure is the source-sink structure where it is not the core population size but habitat quality that determines metapopulation structure. The source population occupies high quality habitat that supplies dispersers to recolonize sink populations in patches of poor quality habitat

(e.g., Ehrlich and Murphy 1987; Mladenoff *et al.* 1995). Although there were areas within the range of the beetle which were not sampled in this study and hence make it difficult to be certain of the overall structure of its population, the results suggest that *H. simsoni* does have at least one, or possibly two, mainland or source populations. Only four locations of high beetle density (>3/m<sup>2</sup>) were found in this study and they occurred within close proximity of one another in the south-eastern corner of its range (i.e., along the southern end of Murdochs Road). Approximately 10 km to the north of this area, near the intersection of Murdochs Road and New England Road, is a grouping of moderate density (1–3/m<sup>2</sup>) locations (Fig. 1). However, over the rest of the beetle's range it occurred in low numbers. The beetle's dispersal abilities are believed to be limited, in the order of 100–200 m for an individual in its life-time (G. Bornemissza and P. McQuillan, pers. comms.). Therefore, it is probable that the northern and western populations are the most vulnerable to habitat disturbance or environmental change, since they lack any high-density populations nearby to supply re-colonizers when local populations go extinct.

#### Characteristics of habitat utilized by *H. simsoni*

All but seven of the locations where the beetle was found to occur in this study were on a granitic rock known as the Devonian Blue Tier Batholith. This batholith is an extensive composite granitic intrusion of Upper Devonian age covering 1 800 km<sup>2</sup> in north-east Tasmania (Groves *et al.* 1977). With a range of only 250 km<sup>2</sup> the beetle only occupies a small portion of this batholith and therefore this geology alone is clearly not indicative of the beetle's presence. It is likely that a complex relationship between this geology, topography and the amount and pattern of occurrence of the rainfall particular to the Blue Tier area, as described by Meggs (1996), is influencing the regional distribution of *H. simsoni*. In terms of broad forest types, *H. simsoni* showed a preference for wet eucalypt forest and species abundance was clearly influenced by altitude, slope, leaf litter depth and a specific forest structure. Specifically, the beetle occurred in highest numbers in areas within wet eucalypt forest where the altitude is below 300 m, slope is less than 5°, there is a deep litter layer (at least 1–3 cm) and a well developed upper understorey layer (i.e., tall shrub layer).

The majority of these characteristics may relate to the beetle's requirement for a relatively cool, moist, stable micro-climate. The preference for a particular forest structure and a deep litter layer indicates that the beetle prefers relatively mature forest that has not been subject to major disturbance, such as severe wildfire, at least for

50 years but possibly longer. Studies of other forest-dwelling ground beetles in evergreen forest have also found that a particular forest structure influences the occurrence of different species (Niemela and Spence 1994; Ings and Hartley 1999). Leaf litter is likely to be the major source of soil organic matter for *H. simsoni* larvae and therefore ultimately its major food source. Ashton (1975) has shown that in *E. regnans* forest the humified layer of leaf litter, which may be mixed with top-soil to a depth of 30 cm, can contain 56% organic matter compared with 12% for normal soil at the same depth. In addition to being a potential food source a deep layer of litter may also maintain a cool and moist microclimate for both *H. simsoni* larvae and adults and provide refuge for adult beetles from predators.

The lack of a relationship between the soil chemical or physical characteristics measured in this study and the abundance of *H. simsoni* is surprising given that larval *H. simsoni* are soil-dwellers and are apparently the only life-stage that feeds (P. McQuillan, pers. comm.). It also contrasts with the results of other studies of ground-beetles, which have found that beetle community composition has been related to soil properties (Dufrene 1990; Luff *et al.* 1992; Niemela *et al.* 1992; Sanderson *et al.* 1995). It may be that soil properties such as texture and drainage are more important to *H. simsoni* than soil chemistry. Soil profile descriptions were only made at eleven locations representing a range of beetle densities. At locations of high beetle density the soils were of the Stronach type (Grant *et al.* 1995), characterized by a deep (20–40 cm), dark organic clay loam A<sub>1</sub> horizon, with variable levels of coarse sands and gravels. There was then a gradual boundary to the B<sub>2</sub> horizon of light medium clay. The absence of mottles in the topsoil on flat ground indicated that these soils are relatively well drained (M. Laffan, pers. comm.). In contrast, the soils at locations of low beetle density were often as deep, but had a lighter texture and lacked the coarse sands and gravels. These differences were not pronounced and any apparent preference for soils of a particular structure will require more detailed investigation.

The significance of the presence of weed species to the occurrence of the beetle as identified in the habitat modelling is unclear. Beetle numbers were found to be significantly higher when weeds were present. Weeds were present in less than a fifth of sites sampled and generally occurred at low densities of 1–2% ground cover. It is possible that the presence of weeds is indicative of habitat disturbance such as road construction and may reflect the coincidence between the preferences of land managers for locating roads and the beetle's preferred

habitat. Roads have long been recognized as an important vector for weed dispersal. If such an indirect relationship does exist, it would suggest that the beetle can tolerate this type of disturbance at least at the current level of intensity.

#### Impacts of current forestry practices on *H. simsoni*

The majority of wet and mixed eucalypt forest coupes (averaging 50 ha in size) within the range of *H. simsoni* are currently harvested by clearfelling often followed by a high intensity regeneration burn and aerial sowing — a clearfell, burn and sow or CBS silvicultural regime (Forestry Commission 1994). Current sustainable yield models indicate that the regenerating forest may then be subject to harvesting again at approximately 90-year intervals (Forestry Tasmania 2002). Studies of the effects of clearfelling on invertebrates have generally found that initially a significant reduction in individuals and changes to the community structure occurs, including the complete loss of some species and invasion by new species (Huhta *et al.* 1967; Vlug and Borden 1973; Lenski 1982; Szysko 1991; Niemela *et al.* 1993; Michaels and McQuillan 1995; Taylor *et al.* 2000). These effects are thought to be a result of the direct impacts of clearfelling on soil and leaf litter microhabitats, including increased light reaching the soil surface, greater temperature extremes, and changes in moisture conditions (Huhta *et al.* 1967). In addition, some studies suggest that high intensity burns used to regenerate the forest after clearfelling significantly increase the impact on soil and leaf litter fauna (e.g., Huhta *et al.* 1967; Koch and Majer 1980; O'Dowd and Gill 1985; Christensen and Abbott 1989; Moldenke and Lattin 1990; Neumann 1991; Beaudry *et al.* 1997; Strehlow *et al.* 2002). Generally species that disappear from areas of forest subject to CBS usually correspond to those classified as mature forest or old-growth specialists (Niemela *et al.* 1993; Michaels and McQuillan 1995). The characteristics of habitat preferred by *H. simsoni* determined in this study suggest that this species is a late-successional or mature forest specialist. Hence, it was surprising that the species was found to occur in recently harvested sites. It is possible that the body parts found in the recently harvested sites were a legacy of pre-logging conditions, since chitin may take a number of years to break down and the sites were in areas where the beetle occurred in high numbers prior to harvest (Meggs 1996). In addition, two of the coupes sampled had not yet been burnt. It is also possible that sufficient moist refuges (e.g., under decayed logs and rocks), demonstrated as important by Madden *et al.* (1976) and Moldenke and Lattin (1990), remained within these coupes enabling survival of individuals.

The regenerative patterns for groups of invertebrates that are impacted by clearfell, burn and sow operations are variable (Friend 1995). Most studies have found that within a period of 20–50 years the numbers of litter and soil invertebrates build up again and in some studies this is linked with the recovery of leaf litter depth (Bornemissza 1969; Madden *et al.* 1976; Springett 1976; Michaels and McQuillan 1995). Madden *et al.* (1976) suggested that wet forests may need to be over 50 years old before the litter fauna return after clearfelling and burning. Similarly, in a study of the abundance and species composition of soil fauna in managed forests in America, old-growth forest taxa were not present until the new canopy was 20–40 years old (Moldenke and Lattin 1990). The results from this study suggest that 30 year old *E. regnans* can sustain a viable population of *H. simsoni*. Beetle parts were also found in three year old and six year old regeneration, but in very low numbers. It should be noted that no live beetles were found in any of these coupes. All of them were adjacent to large areas of unlogged wet eucalypt forest where beetles occurred in high densities, circumstances that could enhance the chances of recolonization of the harvested areas.

As wet eucalypt forest appears to be the preferred habitat of *H. simsoni*, it is clear that the species has evolutionary experience of fire. Wet eucalypt forests are naturally fire-prone, and wildfires of various scales and intensities, with a return interval of 20–400 years (Hickey *et al.* 1999; McCarthy *et al.* 1999; Alcorn *et al.* 2001) are thought to be the main source of large-scale natural disturbance. Many elements of CBS silviculture are qualitatively different from the effects of wildfire, including the resultant forest age structure and the landscape-scale spatial pattern of disturbance (McCarthy and Burgman 1995; McCarthy and Lindenmayer 1998; McCarthy *et al.* 1999). For this reason, and due to the small number of coupes of different ages sampled in this study, caution should be exercised in drawing conclusions on the recovery pattern of *H. simsoni* following CBS. Without sampling over time it cannot be established whether populations in harvested areas are in decline, increasing, or stable (e.g., Koivula 2002; Strehlow *et al.* 2002). Considering the limited evidence from this study, including the fact that the areas of forest containing high densities of *H. simsoni* largely consisted of 70 year old regrowth from the 1929 wildfires (G. Richardson, pers. comm.), it is possible that regenerating forest may attain the characteristics of optimal habitat for the beetle within current planned harvesting rotations of 90 years.

While by no means biological deserts (Bonham *et al.* 2002), pine and eucalypt plantations have

a lower species diversity of invertebrates compared to native forest (Ahern and Yen 1977; Taylor 1991; Mesibov, unpubl. data). The results of this study suggest that replacement of native wet eucalypt forest with exotic pine plantations can result in the local extinction of populations of *H. simsoni*. This is likely to be a consequence of the intensive nature of plantation forest management, which includes a high level of soil disturbance, and the divergence of these forests' microhabitats from the natural forest habitat of the species, both of which may be exacerbated over successive rotations (15–30 year intervals). As *H. simsoni* larvae appear to inhabit the upper soil layer, regular disturbance during plantation establishment is likely to have a significant cumulative impact on populations of the beetle. The microclimate of single-aged plantation stands lacking in understorey is likely to be much more variable than that found in optimal *H. simsoni* habitat, exposing the beetle to greater extremes of temperature. Of perhaps greatest significance for the beetle is the development of leaf litter dominated by a dense mat of pine needles. Ahern and Yen (1977) attributed reduced species richness and number of individuals of litter invertebrates, including beetles, in pine plantations in Victoria to the homogenous composition of the plantation leaf litter and the chemical nature of the pine needles. Although no significant differences in soil chemical or physical properties between pine plantations and native forest were found in this study, a change in the composition of the leaf litter may in the long term affect the quantity and quality of food available for the larvae.

The results of this study were insufficient to determine the suitability of eucalypt plantations for *H. simsoni*. Only one eucalypt plantation was sampled in which two abdomens of *H. simsoni* were found in an area adjacent to mature wet eucalypt forest. It is likely that the establishment of eucalypt plantations will have a similar negative impact on the species as observed in pine plantations; the same intensive management practices are used and the microclimate is dramatically altered. Bashford (1990) found no breeding populations of carabid species in six year old eucalypt plantations in north-east Tasmania that were adjacent to undisturbed native forest where carabids occurred. He suggested that the lack of a carabid breeding population was due to the loss of a dense ground cover and thick litter layer, resulting in an increased chance of desiccation and a significant reduction in prey availability. Some information suggests that eucalypt plantations may be less favourable for native litter invertebrate fauna than pine plantations (Bonham *et al.* 2002). Although eucalypt plantations managed for sawlog production may have a

lesser impact than eucalypt pulpwood plantations due to their longer rotation times (at least 30 years compared with 15 years), it is unlikely that there is sufficient time or opportunity for the recovery of many of the native forest habitat characteristics important to a late-successional or mature forest specialist such as *H. simsoni*. Baguette and Gerard (1993) found that 10–15 year old spruce plantations had a very depauperate carabid fauna relative to 70-year-old plantations. They found that it was only in the oldest plantations, as native understorey complexity increased, that forest specialists began to appear in the invertebrate fauna sampled.

### Conservation considerations

Although this study and Meggs (1996) extended the range of *H. simsoni*, it still meets the criteria of a vulnerable taxon under the *Tasmanian Threatened Species Protection Act 1995* due to its restricted distribution, the inadequate reservation of its preferred habitat, and the likely negative impact of modern forestry practices, particularly the conversion of areas of native forest to pine plantation. Potential habitat for *H. simsoni* (or the predicted area of occupancy of *H. simsoni*) may be broadly defined as all relatively undisturbed wet forest types (including mixed/rainforest) within the species range. This was estimated to be 18 200 ha (182 km<sup>2</sup>) or 72% of the beetles extent of occurrence (Table 3). Although 33% of potential habitat of *H. simsoni* occurs in Tasmania's Comprehensive, Adequate and Representative reserve system, the majority of this is marginal habitat in the form of mixed forest and rainforest. Wet eucalypt forest, the preferred habitat of the species, is relatively poorly reserved with only 19% (1 700 ha) of this forest type occurring in Comprehensive, Adequate and Representative reserves, equivalent to 9% of the potential habitat available to the species throughout its range. The majority of potential habitat occurs in State Forest, with 43% of its total habitat potentially subject to forestry practices, including 56% (5 000 ha) of wet eucalypt forest. A further 12% of potential habitat occurs as private land (Table 3). Thirty-eight per cent

of potential habitat for *H. simsoni* has high or moderate potential for conversion to pine plantation (Forestry Tasmania, unpubl. data). These estimates demonstrate the potential loss of *H. simsoni* habitat that could occur under the current intensification of forest management in north-east Tasmania (Forestry Tasmania 1998) in the absence of "off-reserve" management strategies for this species.

Criteria have been established for determining levels of reservation for forest communities in Australia (JANIS 1997), but there are no similar established criteria for adequate levels of reservation for threatened species. Under the *Guidelines for the listing of species under the Tasmanian Threatened Species Protection Act 1995* (Scientific Advisory Committee 1998) the conservation requirements of nominated fauna species are assessed on a case-by-case basis. It is generally accepted that the protection of threatened fauna should aim for the maintenance of viable populations throughout the species range (i.e., 100% conservation) (Grove *et al.* 2002). This does not necessarily equate with 100% reservation or protecting every individual of the species or every patch of its habitat. The specific conservation actions required to meet this aim depend on the status, degree of threat and range of the species. A variety of conservation management approaches ranging from reservation to management by prescription or the development of species recovery plans may be required to achieve adequate levels of protection.

"Off-reserve" conservation strategies to ensure the maintenance of viable populations of *H. simsoni* across its range need to include limits on the area of potential habitat that may be converted to plantation. Areas of wet eucalypt forest with the characteristics of optimal habitat as identified in this study should be excluded from plantation development. In accordance with the recommendations under the *Tasmanian Regional Forest Agreement* (Commonwealth of Australia and State of Tasmania 1997) for the conservation of the species, the high-density

Table 3. The distribution of potential habitat for *H. simsoni* (wet eucalypt forest and mixed/rainforest) within its range according to land-use category prior to any species-specific land-use changes on State Forest. Other public land category includes miscellaneous land uses such as HEC land.

Land use	Wet eucalypt forest (ha)	Mixed/rainforest (ha)	Total potential habitat (ha)
Formal reserves	900	3 700	4 600 ( 25%)
Informal reserves	800	600	1 400 ( 8%)
State forest (couped)	5 000	2 900	7 900 ( 43%)
State forest (uncouped)	1 000	900	1 900 ( 10%)
Other public land	100	100	200 ( 1%)
Private property	1 200	1 000	2 200 ( 12%)
Total	9 000	9 200	18 200 (100%)

Source: GIS Section, Forestry Tasmania.

populations of the species in the eastern part of its range should be reserved. Over the rest of the species' range, the long-term survival of *H. simsoni* in areas subject to CBS forestry practices is likely to be largely dependent on emigration from source or mainland populations. Therefore, the retention of contiguous undisturbed areas of forest throughout the beetle's range is important to increase the chance of maintaining genetic exchange between populations and as sources of individuals to recolonize regenerating forest as it becomes suitable. It is important that the species is conserved in all parts of its range in order to maintain genetic diversity as a buffer against long-term environmental change. This could be further facilitated by ensuring the dispersal of harvesting in both space and time in order to allow sufficient time for the regeneration of suitable habitat for *H. simsoni* before an adjacent area is harvested.

The intensification of forestry activities in "off-reserve" forested areas recently increased following Tasmania's *Regional Forest Agreement* (Commonwealth of Australia and State of Tasmania 1997), resulting in an upsurge in clearing of the native forests in the north-east of the State for conversion to plantations (Munks and McArthur 2001; Lindenmayer and Franklin 2002). At the time of this intensification of forest disturbance there were 20 forest-dependent fauna species (both vertebrates and invertebrates, but with hydrobiid snails lumped as one group) listed under the Tasmanian *Threatened Species Protection Act 1995*, including *H. simsoni*, which were known to occur in areas identified as having potential for production forestry activities (Forest Practices Board 1998). The development of management prescriptions to maximize retention of quality habitat and/or minimize adverse effects of disturbance for these species has been severely hampered by a lack of knowledge of the characteristics and extent of habitats they occupy, and the species-specific impacts of the planned disturbance regimes (Munks and Taylor 2000). The information collected in this study provides a basis for predicting the distribution of habitats important to *H. simsoni* and the areas where the conservation of the species would conflict most strongly with planned forestry activities.

#### ACKNOWLEDGEMENTS

The majority of this work was funded by the W. V. Scott Bequest Fund, with additional funds obtained from Forestry Tasmania. In-kind support was provided by the Forest Practices Board and Eastern Tiers and Bass Districts. Thanks go to Mark Wapstra (FPB) for assistance with the initial development of the study and field assistance. Additional field assistance was

provided by Greg Finnigan, Helen Otley, Gary Mondon, Malcolm Banfield, Emma Clement and Danielle Warfe. George Bornemissza provided useful advice on many aspects of the beetle's ecology, while Bob Mesibov (QVMAG) brought our attention to the broader evolutionary aspects of the work. Soils advice was obtained from Mike Laffan (FPB) and Leigh Sparrow (DPIWE). Steve Candy (FT) provided additional statistical advice. The GIS analyses were conducted by Luke Ellis (FT) and Ian Harvey (FT). Alastair Richardson (Uni. of Tas.), Peter McQuillan (Uni. of Tas.), Mick Brown (FT), Graham Wilkinson (FPB) and three anonymous referees provided useful feedback on earlier drafts of this manuscript.

#### REFERENCES

- Ahern, L. D. and Yen, A. L., 1977. A comparison of the invertebrate fauna under *Eucalyptus* and *Pinus* forests in the Otway Ranges, Victoria. *Proc. Roy. Soc. Vic.* **89**: 127–36.
- Alcorn, P. J., Dingle, J. K. and Hickey, J. E., 2001. Age and stand structure in a multi-aged wet eucalypt forest at the Warra silvicultural systems trial. *Tasforests* **13**: 245–60.
- Ashton, D. H., 1975. Studies of litter in *Eucalyptus regnans* forests. *Aust. J. Bot.* **23**: 413–33.
- Baguette, M. and Gerard, S., 1993. Effects of spruce plantations on carabid beetles in southern Belgium. *Pedobiologia* **37**: 129–40.
- Bartolozzi, L., 1996. Description of a new species of *Hoplogonus* Parry, 1875 from Tasmania (Coleoptera Lucanidae). *Redia* **79**: 91–95.
- Bashford, D., 1990. The dispersal of ground beetles into different aged eucalypt plantations in North Eastern Tasmania. *Tasforests* **2**: 43–51.
- Beaudry, S., Duchesne, L. C. and Cote, B., 1997. Short-term effects of three forestry practices on carabid assemblages in a jack pine forest. *Can. J. For. Res.* **27**: 2065–071.
- Bonham, K. J., Mesibov, R. and Bashford, R., 2002. Diversity and abundance of some ground-dwelling invertebrates in plantation vs. native forests in Tasmania, Australia. *For. Ecol. Mgmt.* **158**: 237–47.
- Bornemissza, G. F., 1969. The re-invasion of burnt woodland areas by insects and mites (abstract). *Proc. Ecol. Soc. Aust.* **4**: 138.
- Buchanan, A. M., 1999. A Census of the Vascular Plants of Tasmania and Index to the Student's Flora of Tasmania. Tasmanian Herbarium, Hobart.
- Caughley, G. and Gunn, A., 1996. Conservation Biology in Theory and Practice. Blackwell Science, Cambridge.
- Christensen, P. and Abbott, I., 1989. Impact of fire in the eucalypt forest ecosystem of southern Western Australia: a critical review. *Aust. For.* **52**: 103–21.
- Commonwealth of Australia and State of Tasmania, 1997. Tasmanian Regional Forest Agreement. Commonwealth of Australia and State of Tasmania, Hobart.
- Dufrene, M., 1990. Zoogeographical analysis of carabid beetles in Belgium. Pp. 383–87 in *The Role of Ground Beetles in Ecological and Environmental Studies* ed by N. E. Stork. Intercept, Andover.
- Ehrlich, P. R. and Murphy, D. D., 1987. Conservation lessons from the long-term studies of checkerspot butterflies. *Cons. Biol.* **1**: 122–31.

- Forest Practices Board, 1998. Forest Practices Board Annual Report 1997-98. Forest Practices Board, Hobart.
- Forest Practices Board, 2001. Threatened Fauna Adviser (revised version), Expert System Program. Forest Practices Board, Hobart.
- Forestry Commission, 1994. Silvicultural Systems. Native Forest Silviculture Technical Bulletin No. 5. Forestry Commission (now Forestry Tasmania), Hobart.
- Forestry Tasmania, 1998. Forest growth plan. Forestry Tasmania, Hobart.
- Forestry Tasmania, 2002. Sustainable high quality eucalypt sawlog supply from Tasmanian State forest — Review No. 2. Forestry Tasmania, Hobart.
- Friend, G. R., 1995. Fire and invertebrates — a review of research methodology and the predictability of post-fire response patterns. *Calm Science Supp.* 4: 165-74.
- Grant, J. C., Laffan, M. D., Hill, R. B. and Nielsen, W. A., 1995. Forest soils of Tasmania: a handbook for identification and management. Forestry Tasmania, Hobart.
- Grove, S., Meggs, J. M. and Goodwin, A., 2002. A review of biodiversity conservation issues relating to coarse woody debris management in the wet eucalypt production forests of Tasmania. Technical Report No. 22 to Forestry Tasmania, Hobart.
- Groves, D., Cocker, J. and Jennings, D., 1977. The Blue Tier Batholith. *Bull. Geol. Surv. Tas.* No. 55.
- Hastie, T. J. and Tibshirani, R. J., 1990. Generalised Additive Models. Chapman and Hall, London.
- Hickey, J. E., Su, W., Rowe, P., Brown, M. J. and Edwards, L., 1999. Fire history of the tall eucalypt forests of the Warra ecological research site, Tasmania. *Aust. For.* 62: 66-71.
- Huhta, V., Karppinen, E., Nurminen, M. and Valpas, A., 1967. Effect of silvicultural practices upon arthropod, annelid, and nematode populations in coniferous forest soil. *Ann. Zool. Fenn.* 4: 87-143.
- Ings, T. C. and Hartley, S. E., 1999. The effect of habitat structure on carabid communities during the regeneration of a native Scottish forest. *For. Ecol. Mgmt.* 119: 123-36.
- IUCN Species Survival Commission, 1994. IUCN Red list categories. IUCN Council, Switzerland.
- Jackson, J. and Taylor, R. J., 1995. Threatened fauna manual for production forests in Tasmania. Forest Practices Unit, Forestry Tasmania, Hobart.
- JANIS, 1997. Nationally agreed criteria for the establishment of a Comprehensive, Adequate and Representative Reserve System for forests in Australia. A report by the Joint ANZECC/MCFFA National Forest Policy Statement Implementation Sub-committee. Commonwealth of Australia, Canberra.
- Koch, L. E. and Majer, J. D., 1980. A phenological investigation of various invertebrates in forest and woodland areas in the south-west of Western Australia. *J. Roy. Soc. W.A.* 63: 21-28.
- Koivula, M., 2002. Alternative harvesting methods and boreal carabid beetles (Coleoptera, Carabidae). *For. Ecol. Mgmt.* 167: 103-21.
- Lenski, R. E., 1982. The impact of forest cutting on the diversity of ground beetles (Coleoptera: Carabidae) in the southern Appalachians. *Ecol. Ent.* 7: 385-90.
- Lindenmayer, D. B. and Franklin, J. F., 2002. Conserving Forest Biodiversity, A Comprehensive Multiscaled Approach. Island Press, Sydney.
- Luff, M. L., Eyre, M. D. and Rushton, S. P., 1992. Classification and prediction of grassland habitats using ground beetles (Coleoptera, Carabidae). *J. Env. Man.* 35: 301-15.
- McCarthy, M. A. and Burgman, M. A., 1995. Coping with uncertainty in forest wildfire planning. *For. Ecol. Mgmt.* 74: 23-36.
- McCarthy, M. A. and Lindenmayer, D. B., 1998. Multi-aged mountain ash forest, wildlife conservation and timber harvesting. *For. Ecol. Mgmt.* 104: 43-56.
- McCarthy, M. A., Gill, A. M. and Lindenmayer, D. B., 1999. Fire regimes in mountain ash forest: evidence from forest age structure, extinction models and wildlife habitat. *For. Ecol. Mgmt.* 124: 193-203.
- McCullagh, P. and Nelder, J. A., 1989. Generalised Linear Models, Second Edition. Chapman and Hall, London.
- Madden, J. L., Hickman, J. L., Richardson, A. M. N. and Hill, L., 1976. Effect of cutting and regeneration practice on the invertebrate fauna of litter and soil. Woodchip Symposium Papers. 47th A.N.Z.A.A.S. Congress. Tasmanian Forestry Commission, Hobart.
- Meggs, J. M., 1996. Distribution and conservation status of two threatened species of lucanid beetle in Tasmania. Unpublished report to Forestry Tasmania and the Australian Heritage Commission, Hobart.
- Mesibov, B., 1988. Tasmanian Onychophora. Unpublished report to the Dept. of Land, Parks and Wildlife, Hobart.
- Mesibov, R., 1994. Faunal breaks in Tasmania and their significance for invertebrate conservation. *Mem. Qld Mus.* 36: 133-36.
- Mesibov, R. and Ruhberg, H., 1991. Ecology and conservation of *Tasmanipatus barretti* and *T. anophthalmus*, parapatric onychophorans (Onychophora: Peripatopsidae) from northeastern Tasmania. *Pap. Proc. Roy. Soc. Tas.* 125: 11-16.
- Mesibov, R., Taylor, R. J. and Brereton, R. N., 1995. Relative efficiency of pitfall trapping and hand-collecting from plots for sampling of millipedes. *Biodiv. Conserv.* 4: 429-39.
- Mesibov, R., Bonham, K. J., Doran, N., Meggs, J., Munks, S., Otley, H. and Richards, K., 2002. Single-species sampling in Tasmania: an inefficient approach to invertebrate conservation? *Invert. Syst.* 16: 655-63.
- Michaels, K. and McQuillan, P. B., 1995. Impact of commercial forest management on geophilous carabid beetles (Coleoptera: Carabidae) in tall, wet *Eucalyptus obliqua* forest in southern Tasmania. *Aust. J. Ecol.* 20: 316-23.
- Minchin, P., 1991. Database for Ecological Community Data, version 2.04. Australian National University, Canberra.
- Mladenoff, D. J., Sickley, T. A., Haight, R. G. and Wydeven, A. P., 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the Northern Great Lakes Region. *Conserv. Biol.* 9: 279-94.
- Moldenke, A. R. and Lattin, J. D., 1990. Dispersal characteristics of old-growth soil arthropods: the potential for loss of diversity and biological function. *The Northwest Env. J.* 6: 408-09.
- Munks, S. and McArthur, C., 2001. Plantation design and fauna conservation in Tasmania: Part 1, Workshop abstracts. *Tasforests* 12: 161-72.
- Munks, S. and Taylor, R., 2000. Conserving threatened fauna in production forests: the Tasmanian process. Pp. 670-74 in Nature Conservation 5: Nature Conservation in Production Environments: Managing the Matrix ed by J. L. Craig, N. Mitchell and D. A. Saunders. Surrey Beatty & Sons, Chipping Norton.

- Munks, S., Richards, K., Meggs, J. and Brereton, R., in press. Can off-reserve management prescriptions for threatened species be effective? Implementing, monitoring and upgrading swift parrot, *Lathamus discolor*, conservation measures in Tasmania. In Conservation of Australia's Forest Fauna 2nd edn (in press) ed by D. Lunney. Roy. Zool. Soc. NSW, Sydney.
- Myers, R. H., 1990. Classical and Modern Regression with Applications. Duxbury Press, Belmont, California.
- Neumann, F. G., 1991. Responses of litter arthropods to major natural or artificial ecological disturbances in mountain ash forest. *Aust. J. Ecol.* **16**: 19–32.
- Niemela, J. K. and Spence, J. R., 1994. Distribution of forest dwelling carabids (Coleoptera): spatial scale and the concept of communities. *Ecography* **17**: 166–75.
- Niemela, J. K., Langor, D. and Spence, J. R., 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. *Conserv. Biol.* **7**: 551–61.
- Niemela, J. K., Spence, J. R. and Spence, D. H., 1992. Habitat associations and seasonal activity of ground-beetles (Coleoptera, Carabidae) in central Alberta. *Can. Ent.* **124**: 521–40.
- O'Dowd, D. and Gill, M., 1985. Effects of a high-intensity fire on ants and other invertebrates in the Brindabella Range. Pp. 87–90 in Soil and Litter Invertebrates of Australian Mediterranean-type Ecosystems ed by P. Greenslade and J. D. Majer. Wait School of Biology Bulletin No. 12, Adelaide.
- Payne, R. W., Arnold, G. M. and Morgan, G. W., 1993. Genstat 5 Procedure Library Manual. Release 3[1]. Lawes Agricultural Trust, Rothamsted Experimental station.
- Rayment, G. E. and Higginson, F. R., 1992. Australian Laboratory Handbook of Soil and Water Chemical Methods. Inkata Press, Melbourne.
- Sanderson, R. A., Rushton, S. P., Cherrill, A. J. and Byrne, J. P., 1995. Soil, vegetation and space: an analysis of their effects on the invertebrate communities of a moorland in north-east England. *J. Appl. Ecol.* **32**: 506–18.
- Schall, R., 1991. Estimation in generalised linear models with random effects. *Biometrika* **78**: 719–27.
- Scientific Advisory Committee, 1998. Guidelines for the listing of species under the Tasmanian Threatened Species Protection Act 1995. Dept. Primary Industries, Water and Environment, Hobart.
- Snee, R. D. and Pfeifer, C. G., 1983. Graphical representation of data. *Encyclo. Statist. Sci.* **3**: 488–511.
- Springett, J. A., 1976. The effect of prescribed burning on soil fauna and litter decomposition in Western Australian forests. *Aust. J. Ecol.* **1**: 77–82.
- Strehlow, K., Bradley, J. S., Davis, J. and Friend, G. R., 2002. Short term impacts of logging on invertebrate communities in jarrah forests in south-west Western Australia. *For. Ecol. Mgmt.* **162**: 165–84.
- Szysko, J., 1991. Influence of deciduous underwood on carabids (Carabidae, Col.) in pine forests (Polish with an english summary). *Sylvan* **135**: 27–32.
- Taylor, R. J., 1991. Fauna Conservation in Production Forests in Tasmania. Tasmanian Forestry Commission, Hobart.
- Taylor, R., Michaels, K. and Bashford, D., 2000. Occurrence of carabid beetles in retained unlogged strips within production forests of southern Tasmania. Pp. 120–27 in Nature Conservation 5: Nature Conservation in Production Environments: Managing the Matrix ed by J. L. Craig, N. Mitchell and D. A. Saunders. Surrey Beatty & Sons, Chipping Norton.
- Vlug, H. and Borden, J. H., 1973. Soil Acari and Collembola populations affected by logging and slash burning in a coastal British Columbian coniferous forest. *Env. Ent.* **2**: 1016–023.