THE EUROPEAN SOCIAL WASP, PARAVESPULA GERMANICA (F.) (HYMENOPTERA : VESPIDAE) IN TASMANIA, AUSTRALIA

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The European vespoid wasp, Paravespula germanica (F.) was first recorded in New Zealand in 1922 but did not become established until 1944 (Thomas 1960) and nests were first discovered in Tasmania during 1959 (Anon 1962a). In New Zealand, between 1945 and 1951 P. germanica spread from its original infestation locus in Hamilton to occupy most of the North Island with some outbreaks in the South Island, the dispersal being approximately 175 miles (280 Km) north and 275 miles (440 Km) south, a rate of nearly 40 miles (64 Km) per annum. In Tasmania, P. germanica is now established throughout 70 per cent of the 26,000 sq. miles state, including valleys in the uninhabited bush areas of the southwest. In Australasia, some colonies overwinter and produce nests of prodigious size during the second season. Compared to mature European colonies, there is a 10 to 100-fold increase in numbers of cells, brood and adults (Fig. 1). Nests with more than a million occupied cells have been found compared to a maximum of 12,000 cells in England (Spradbery 1971). The major factors responsible for the successful invasion of Tasmania are climatic compatability, an abundance of nest sites and forage, absence of natural enemies and a capacity to requeen colonies and thereby overwinter and increase reproductivity.

The temperate maritime climate of Tasmania is less unpredictable, with fewer days of frost than equivalent latitudes in the northern hemisphere. A variation between mean winter and summer temperatures of less than 9°C in Hobart is compared to 14°C in London, 13°C in Nice (France) and 11°C in Lisbon (Portugal). Tasmania also enjoys more sunshine than much of Europe, there being 130 per cent more winter sunshine than in London and 60 per cent more than in Bordeaux (France). In Tasmania there is comparatively more precipitation but without marked seasonal fluctuations. In Europe, P. germanica prefers the warmer, lowland areas, is rare in the north (e.g. Scotland) and is the only Paravespula species found in northwest Africa (Laidlaw 1934, Bequaert in Thomas 1960). The co-dominant European species, P. vulgaris, is more abundant than P. germanica in the cooler parts of their range but, despite nests being built in Auckland, it has not become established in New Zealand (Thomas 1960). This species occurs in some suburbs of Melbourne, but its dispersal since 1960 has been negligible and there are no reports of overwintering there (Anon 1962b, T.W. Hogan, personal communication).

Much of Tasmania is occupied by rural holdings of which two thirds are bush or uncleared scrub, their rough ground and friable soils providing good nesting areas while in coastal regions the sandy soils are easily excavated. The current distribution of P. germanica shows that all major vegetation regions (Rain Forest, Eucalypt Forest, Sedgeland and Coastal Heath) have been colonized except the mountainous moorland areas. The wasp is most abundant in suburban and coastal areas and some of

the major river valleys. Another factor favouring colonization is the abundance of rabbit and wombat burrows which make ideal nesting sites.

Many native and exotic plants flower during the Tasmanian winters. Aphids (e.g. Myzus persicae (Sulz.)), scale insects (e.g. Eriococcus coriaceus Mask.) and psyllids are common during the autumn and winter, their honeydew providing an abundant source of carbohydrate which is eagerly exploited by foraging wasps (R.J. Hardy, personal communication).

There are numerous parasites and predators of social wasps in Europe, including birds and badgers and a variety of insect parasitoids (Spradbery 1973). None of these recognised natural enemies occur in Tasmania although insectiverous birds, possums and bandicoots are potential predators. Large numbers of the migrant Spine-tailed swift (Hirundapus caudacutus) have been observed swooping on wasps in Tasmania (J.L. Madden, personal communication). The wombat, which has many similarities with the European badger is, however, a vegetarian.

During the autumn when queen rearing is being concluded and the founding queen becomes physiologically inept, the social disintegration of the wasp community normally takes place. This period is characterized by the cannibalism of brood and dominance struggles among workers, when the young queens disrupt the previously established social hierarchies (Montagner 1967). With the death of the queen, the colony dies out before the onset of winter. By contrast, in some Tasmanian colonies, young queens are recruited as egg-layers before the death of the founding queen. Two colonies were discovered late in May (equivalent to early December at northern latitudes) in which the original queens were present together with 20 and 23 young laying queens. These queens were distinguished by their ovariole development and the red pigmentation on the gastral tergites. Compared to European specimens (Spradbery, 1973) it was deduced that they had been ovipositing for approximately one month. In all other respects, the colonies were typical of mature P. germanica colonies in Europe.

During the winter months in Tasmania (May-September), there is little or no nest building although disused combs and the peripheral cells of other combs are generally papered over with carton, which would improve the insulation qualities of the nest. Brood rearing is continued at a reduced level throughout the winter (Fig. 1), with males, queens and workers being produced in approximately equal numbers. In the spring, the rearing of reproductives decreases and the colony reverts primarily to worker production. Second-season nests are often characterized by rings of worker cells built around the periphery of the queen combs (Thomas 1960, and personal observations). During the summer and autumn (December-March) the number of cells and inhabitants increases and laying queens are recruited until populations in excess of 100,000 workers and an estimated thousand or more functional queens are produced.

The productivity of such colonies has undoubtedly contributed to the outstanding success of P. germanica in its colonization of Tasmania. In terms of the numbers of queens produced per queen per day under European conditions, P. germanica is the outstanding vespine species with a mean of 4.2 and a maximum of 7.8 (Spradbery 1971) in contrast to

P. vulgaris which has a maximum of 3.1 (Archer 1972). Under Tasmanian conditions, queen productivity is considerably higher, although with many functional queens present, the value of queens produced per queen per day may well be lower.

What factors regulate requeening in autumn colonies and thereby permit overwintering? The two crucial steps are the recruitment of young queens and the absence or curtailment of ovariole diapause. Normally, only one queen is present in a vespine wasp colony and the introduction of, or attempted usurpation, by foreign queens and workers is met with great hostility. However, in late summer and autumn, there develops an increased tolerance towards strangers by both functional queens and workers. Ishay et al (1970) were able to combine up to five colonies of the Oriental Hornet, Vespa orientalis F., towards the end of the season. There is, undoubtedly, a physiological change in the ageing queen that causes a diminished animosity towards foreign queens. It is at this stage in the colony cycle that requeening begins in Tasmanian colonies.

Under European conditions, young queens spend some time in the parental colony, foraging for food and feeding off larval saliva until large reserves of depot fat are accumulated (Spradbery 1973). These queens finally leave the nest and enter hibernation before the onset of winter (Duncan 1939) and, for the next five to seven months, undergo an ovariole diapause. When recruitment of queens takes place in Tasmania, it is most probable that they are daughters of the original founding queen, rather than from other colonies. It is doubtful whether they have an ovariole diapause, for recruitment begins within four to six weeks of the start of queen rearing (Fig. 2).

Diapause in insects is invariably induced by environmental factors acting on a diapause-susceptible stage. The most likely candidate factor is daylength. At similar latitudes in the northern and southern hemispheres, seasonal changes in daylength are the same, but queen rearing occupies different parts of the daylength cycles (Fig. 2). For example, in the northern hemisphere queen rearing begins in mid-August and generally finishes by mid-October when the photoperiod is decreasing (e.g. 14 to 10 hours in London at 52°N; 14 to 11 hours in Lisbon at 40°N; and $13\frac{1}{2}$ to $11\frac{1}{2}$ in Algeria at 35°N). In Tasmania at 42°S, queen production begins in early April when daylength is $11\frac{1}{2}$ hours and continues until it reaches 9 hours per day in mid-winter (June) with requeening beginning in early May when daylength is less than 10 hours (Fig. 2). The rates of declining daylength are similar in both latitudes and it seems unlikely that the wasps respond by perceiving small changes in photoperiod. If ovariole diapause is a response to the actual duration of light, the evidence suggests that queens are susceptible to a definite photoperiod of approximately 10-14 hours but do not respond when the photoperiod is less than 10 hours.

While imprudent to ignore the possibility of a non-diapausing genetic strain of P. germanica in Australasia, it seems probable that environmental factors, especially daylength, are primarily responsible for the lack of ovariole diapause in queens which results in the successful overwintering of colonies.

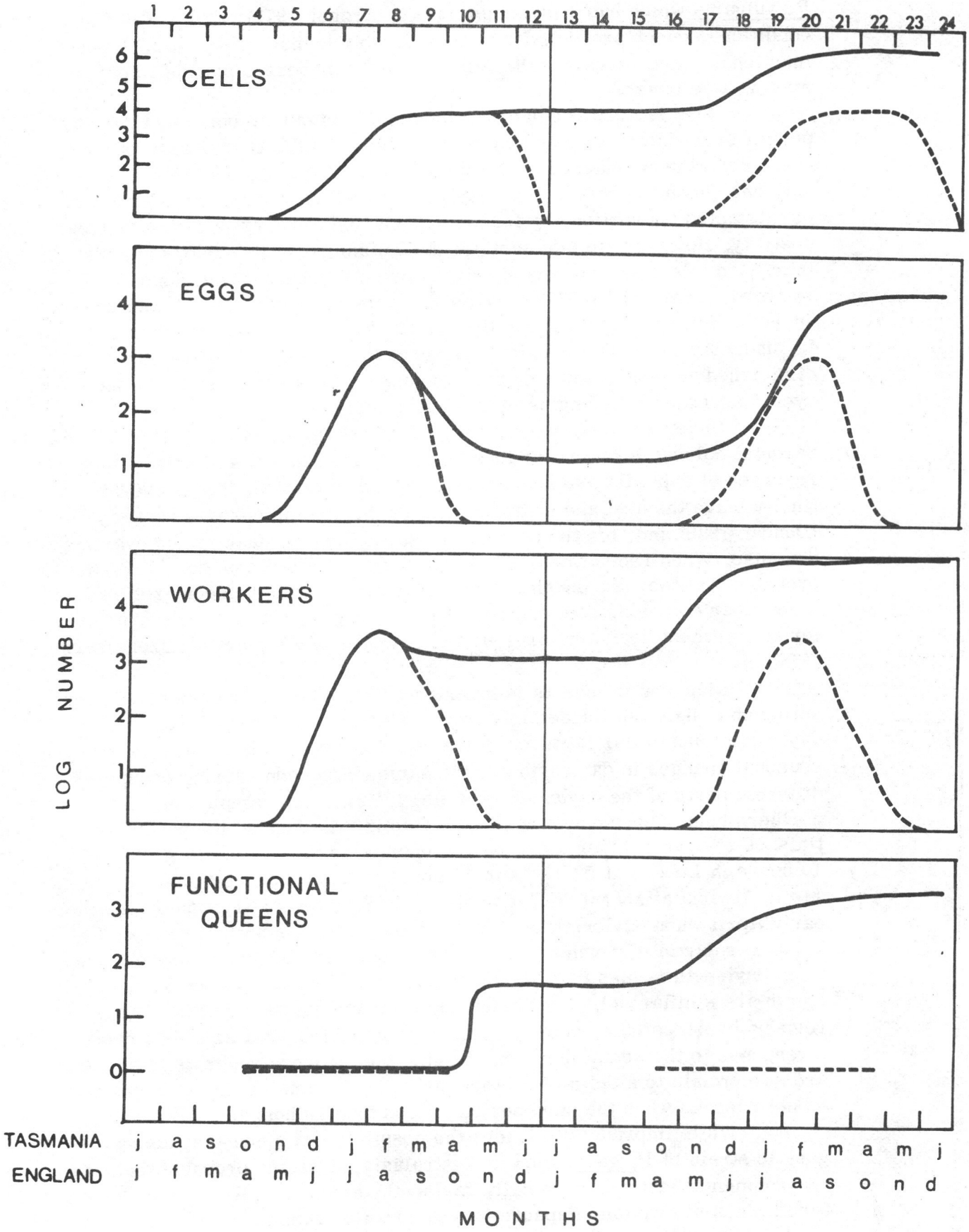

Figure 1 Comparison of seasonal population changes in European (broken line) and Tasmanian (solid line) colonies of Paravespula germanica.

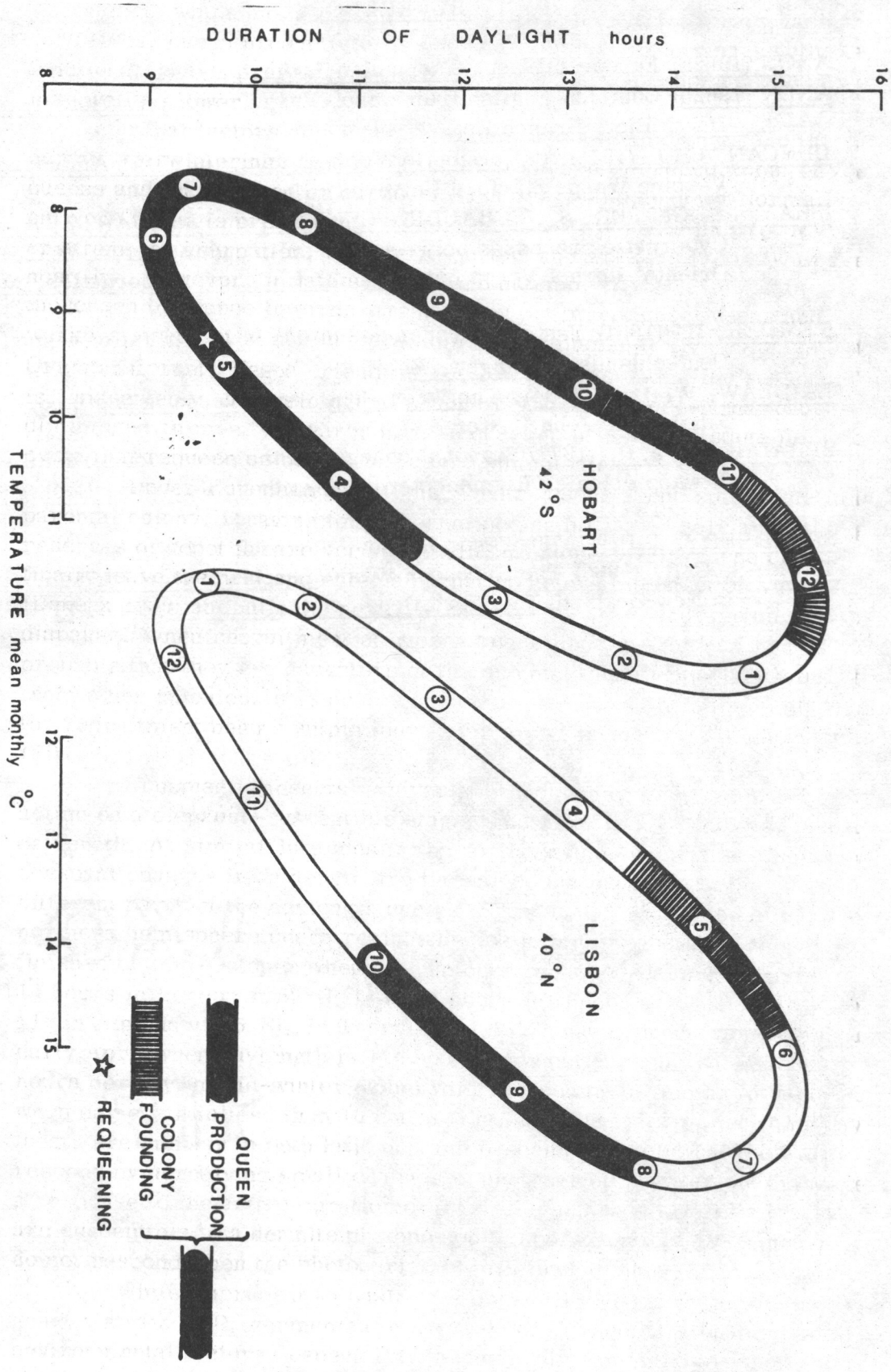

Figure 2 Daylength and temperature data in Hobart, Tasmania and Lisbon, Portugal in relation to queen production and colony founding in Paravespula germanica.

REFERENCES

ANON (1962a) European Wasp. Tasmanian J. Agric., 341-2

ANON (1962b) Common English fruit wasp, Vespula vulgaris Victoria Agri. Dept. Biol. Branch Rpt. 2, 44

DUNCAN, C.D. (1939) A Contribution to the Biology of North American Vespine Wasps Stanford University Press

ISHAY, J., GITTER, S., SCHAUDINISCHKY, L. and SCHWARTZ, A. (1970) Cybernetic processes between the adults and the larvae of the Oriental Hornet Vespa orientalis. Int. Congr. Cybernetics, Namur, 1-16

KEMPER, H. (1961) Nesterunterschiede bei den sozialen Faltenwespen Deutschlands. Z. angew. Zool. 48, 31-85

LAIDLAW, W.B.R. (1934). The Wasp. The genus Vespa in Scotland. Edinburgh, John Baxter

SPRADBERY, J.P. (1971) Seasonal changes in the population structure of wasp colonies (Hymenoptera : Vespidae). J. Anim. Ecol. 40, 501-23

SPRADBERY, J.P. (1973) Wasps London, Sidgwick & Jackson

THOMAS, C.R. (1960) The European Wasp (Vespula germanica Fab.) In New Zealand. Inf. Ser. Dep. Scient. ind. Res. N.Z. 27, 1-73