The Developmental Dynamics of *Tipula paludosa* and the Relation of Climate to Its Growth Pattern, Flight Season and Geographical Distribution

A. Meats

School of Biological Sciences, University of Sydney, Sydney, N.S.W. 2006

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Summary. The model of Meats (1974a) is tested against Laughlin's (1967a) data on growth in the field. A good measure of agreement is found. The model is then used to investigate the consequences of the univoltine *T. paludosa* starting its life cycle (flight season) at various dates in the range quoted by Coulson (1962)—i.e. from July to October. Similarly the influence of increased or decreased monthly temperatures is also investigated. The model indicates that growth will be poorer the later the life cycle starts or the lower the mean monthly temperature.

Populations at Moor House (high Pennines) are probably obliged to start their cycle earlier by shortening the prepupal/pupal period because the relatively colder average temperatures would otherwise prevent the attainment of a suitably sized adult. Lowland populations from Canada, England, Germany and Poland differ in developmental schedule depending on prevailing temperatures but usually achieve sufficient growth despite a relatively prolonged prepupal/pupal period and late flight season. Dry conditions (which, like low temperatures, can slow growth) are not associated with advanced flight seasons. In areas where low temperatures are critical, successful growth may be restricted to wet soils. The relation of climate to prepupal diapause is discussed and developmental dynamics is related to potential geographical range.

Introduction

*Tipula paludosa* Meigen (Diptera, Nematocera) is a common univoltine inhabitant of grassland and pest of cereal crops in northern Europe and in parts of North America. It spends most of its life passing through immature stages in the top 100 mm or so of the soil. According to most accounts, eggs are laid and hatch in late summer and early autumn; larval growth is greatest in autumn and the following spring; larvae reach peak weight in June following which they pupate. They then emerge after a variable interval.

There are differences between published accounts of the schedule of growth and development. Hatching and early larval growth may be delayed (Milne et al., 1965); development from first to third instar may be typically slow (Maercks, 1939) or it may be fast or slow (Laughlin, 1967a). Late larval growth may be poor or it may be quite marked and associated with considerable damage to crops (Laughlin, 1967a; Williams and MacCarthy, 1967). This paper will use the development model of Meats (1974a, b) to relate the above differences to differences in climate and to the known effects of soil moisture and temperature on growth and development.

Most accounts of the flight season (by contrast to those of development) are remarkably similar—despite differences in climate. In low lying areas of northern
England, north Germany and British Columbia, virtually all flight activity occurs from early August to the middle of September with a peak around August 31 (Coulson, 1962; Laughlin, 1967; Sellke, 1936; Maercks, 1939; Wilkinson and MacCarthy, 1967). There are, however, records of earlier and later flight seasons. In the high Pennines of northern England (where the relatively cold wet climate is similar to that of coastal Iceland) the flight season is early, extending through July and August with a peak around July 31 (Coulson, 1962). At Rothamsted in southern England the flight season was late in the relatively warm years of 1933–1936. Virtually all flight activity took place between mid-August and early October with a peak between September 9–14 (Robertson, 1939).

The significance and possible causes of the above similarities and differences in flight season will be explored by means of the model of Meats (1974a, b) and will be discussed in relation to prepupal diapause, pupal development and particular aspects of climate.

**Methods**

The model of Meats (1974a, b) is used to predict development rates. Briefly, it utilises the fact that development rate has a sigmoid relationship with both the temperature and the moisture-tension of the soil. Development at any one temperature is prevented at tensions above 1560 kPa and rises sigmoidally as tension drops to zero. Similarly at any one tension, development is virtually prevented below 2°C but its rate rises sigmoidally with increase in temperature. Hence warm weather may not promote growth, if the soil is dry and neither may moist soil if temperatures are too low.

Developmental increments may be calculated for any interval of time and hence size at any particular date may be estimated by summation of increments as detailed in Meats (1974a).

Weather data was obtained from Walter and Leith (1960) and from Professor A. Milne and the British Meteorological Office to whom the author is grateful.

**Results**

1. Comparison of Model Estimates with Field Results

Fig. 1 compares the growth estimates of the model (solid line) with equivalent field estimates (dotted line) of Laughlin (1967a, b). Laughlin gives sufficient data with some of his estimates to enable the calculation of 95% fiducial limits. These are plotted as vertical lines on Fig. 1 and give some idea of the width of the “confidence band” on either side of each “field” curve and the extent to which the equivalent model curve stays within it.

Despite some relatively wide departures the model accounts for 78% of the variance in field estimates. Some lack of fit is to be expected because of the shortcomings of the model (Meats, 1974a) and because the model used meteorological data from a station 30 km from the nearest of Laughlin’s sites. Fits are expected to be worse for the early parts of each growth curve as the model assumes a distribution of larval weights which is skewed to include a proportion of very small larvae early in the season. This is quite possible considering that the flight season does not end until mid September at the sites in question (Laughlin, 1967a). Field sampling involving the St. “Ives” method described in the latter paper would make it extremely difficult to recover very small larvae. Such field