**Patterns of growth, development and body size towards the end of the season in the yellow dung fly.**

Seasonality imposes a time constraint to which ectotherms have to adjust their life cycle and development period (Roff 1980, 1983). Winter diapause is one prominent phenomenon that has been addressed in this context (Tauber et al. 1986; Danks 1987; Leather et al. 1993), the drying of ephemeral ponds is another. Both situations often require acceleration of development as the season progresses so that a specific life stage is reached in time (Roff 1980, 1983; Rowe and Ludwig 1991). The fitness consequences are rather obvious: individuals will die if they do not meet the time constraint. On the other hand, if they have the time, individuals may extend the period of development and grow larger, as body size is often proportional to development time in ectotherms (Roff 1980, 1992). Larger body size typically confers higher fitness, most prominently a fecundity advantage to female ectotherms (e.g. Wooton 1979; Shine 1988) but also an advantage to males in sexual selection (Andersson 1994). This trade-off is supported by many intra-specific studies showing decreases in body size later in the season as well as smaller average body sizes where seasons tend to be short (e.g. Mousseau and Roff 1989a; Rowe and Ludwig 1991; Blanckenhorn 1994; Blanckenhorn and Fairbairn 1995).

In ectotherms, temperature is supposed to have straightforward effects on body size, development time and related characters. Within limits (Ratte 1985), lower temperatures prolong development and reduce growth rates, resulting in larger final body size (Roff 1980; Atkinson 1994). Even though the mechanism is not entirely clear (Ratte 1985), and contrary to theoretical expectations (Berrigan and Charnov 1994; Sibly and Atkinson 1994), this rule holds in a majority of species from protozoans to plants, insects and amphibians, though there are exceptions (Atkinson 1994). A positive correlation between development time and body size has featured centrally in many life history models (see Roff 1980, 1992; Stearns 1992). The underlying assumption is that individuals, while generally maximising their rate of growth, can adaptively adjust their rate of development to optimise body size in a given (temperature) environment. However, several authors have pointed out the advantages of adjusting growth rate independently of (i.e. in addition to) development time (Case 1978; Sibly and Calow 1986; Atkinson 1994; Nylin 1994; Abrams et al. 1996). This mechanism could explain deviations both from the expected positive correlation between development time and body size and from the negative correlation between temperature and development time (and body size; Atkinson 1994; e.g. Smith-Gill and Berven 1979; Sigurjónsdóttir 1984; Nylin 1994). Consequently, development time and growth rate should be investigated independently (Abrams et al. 1996).

As temperature affects "physiological time" (Taylor 1981) and, in particular, rates of development, its effects need to be controlled for when comparing responses of organisms to treatments under variable conditions (Taylor 1981; Ratte 1985; Atkinson 1994). This is particularly important in field studies. The concept of degree-days has proven useful for this purpose (Roff 1992, p. 163). Instead of calendar days, development time is expressed as the cumulative number of degrees above a critical lower threshold, below which development ceases and which can be determined empirically in the laboratory for a given species or population (e.g. Danks 1987).

In this study, I investigated the effects of rearing temperature on growth, development and body size in the yellow dung fly, *Scathophaga stercoraria*. I allowed replicate full-sib families of larvae to develop in the field beginning at ever closer times to the onset of winter, thus imposing a time limitation. I investigated the phenotypic growth and diapause responses and the correlations between development time and body size, both in real time and and in degree-days.

**Materials and methods**

*The study animal*

The yellow dung fly occurs world-wide in temperate regions (Gorodkov 1984). Its distribution up to Iceland reveals a preference for colder temperatures. Indeed, in the warmer regions of their distribution yellow dung flies typically decline in numbers in summer, evidently avoiding the hottest time of the year (Hammer 1941; Parker 1970; Gibbons 1987; Ward and Simmons 1990), but whether they survive this period in the adult or the pupal stage is still unclear. Thus a spring and an autumn season can be distinguished, both likely featuring no more than two overlapping generations (Blanckenhorn 1997). Females lay clutches of 30-70 eggs into fresh dung, which the developing larvae feed on and thereby deplete. Individuals have to complete larval development in order to overwinter as pupae (Luvchiev and Tsankova 1982), at which point adult body size has been fixed, but pupal development (i.e. metamorphosis) still requires time to be completed. Body size in this species is greatly influenced by the amount of dung individuals feed on as larvae (Amano 1983; Sigurjónsdóttir 1984), but it is also partially heritable (Simmons and Ward 1991; Mühlhäuser et al. 1996). Males are larger than females on average (Borgia 1981, 1982; Simmons and Ward 1991). Large size confers a mating advantage to males (Borgia 1982; Otronen 1993; Parker and Simmons 1994; Sigurjónsdóttir and Snorrason 1995) and a fecundity advantage to females (Borgia 1981).

*Field rearing experiment*

An experiment was conducted during the autumn fly season 1994/95 at a field site near the University of Zürich, Switzerland. I allowed offspring of field-collected *S. stercoraria* pairs (henceforth COHORTs) to develop under field conditions for 5 successive weeks starting 29 August 1994. Copulating or guarding pairs were randomly collected every week from dung pats at the nearby town of Fehraltorf (N47°23', E8°44'). The pairs were transported to the laboratory and allowed to copulate again in a 50 ml glass vial containing a smear of fresh dung, into which the females then deposited their eggs. Every week, ten eggs of each of 16 females (FAMILIES) were counted onto a small piece of wet filter paper and then transferred into 50 ml plastic containers with 20 g of dung. The containers were kept for a maximum of 24 h in the laboratory until hatching of the larvae could be scored. Thereafter they were transferred to the field site, where they were placed on the ground in the open under the roof of a shed (yielding constant shade).

I checked for emerging adults at least every other day. This yielded the data on development times from egg to adult prior to winter. Individual development times in days (DEVTIME) were later converted into degree-days (DEVTIMDD) >2°C (2°C is the lower temperature threshold) using daily temperature averages supplied by the Swiss Meteorological Service for the nearest available site (Zürich-SMA; ca. 1 km away). I measured the hind tibia length of all individuals (SIZE), and individual growth rates were calculated as hind tibia length divided by development time in days (GROWTH) and degree-days (GROWTHDD).

The data were analysed with family containers as independent statistical units. For the individual measures body size, development time and growth rate I produced family means, separately for both sexes (SEX: 2= FEMALES, 1=MALES). The NUMBER of individuals of each sex that emerged is also given.

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