Spontaneous Locomotor Activity as a Test for the Rate of Living Theory

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Recently, Lints et al. [1] reported results of a study dealing with the relationship between spontaneous locomotor activity (SLA) and life span in *Drosophila melanogaster*. SLA was found not to be correlated with life span. Lints et al. seemed to believe, as also indicated by the title of the paper, that their study tested the 'rate of living' theory of Pearl. They also reviewed results of previous studies dealing with the rate of living theory and concluded that 'Pearl's hypothesis has not yet received any definite confirmation'. The objective of this letter is to point out that the experimental design employed in this study is inadequate to draw any specific or broad inferences about the validity of the rate of living theory.

Lints et al. placed individual flies in Petri dishes (5.5 cm in diameter and 5 mm deep) where, according to the authors, 'only very few attempts to fly were observed'. Each fly was observed in turn and recorded as active or inactive if the fly showed two consecutive signs of activity within a 5-second observation period. Activity was defined as any motion of the fly, i.e., walking or attempt to fly. Since 'only very few attempts to fly were observed', it can be surmised that SLA measured was limited to walking activity. A maximum of 75 observations, each 5 s long, totalling 6.4 min were thus made on each fly. All the SLA observations on a fly were made within one 12-hour period, although the average life span of different groups of flies varied from 50 to 80 days. After a fly was scored for relative SLA, it was placed in a vial, and age at death was recorded. No relationship between SLA and life span was observed at the individual (except in one out of six groups) or population level.

An examination of the protocol employed in this study indicates that the authors were attempting to determine the effects of locomotor activity under housing conditions which were highly restrictive of physical activity. In the vials, flight activity of *Drosophila* is quite rare [see Maynard Smith in ref. 2, p. 60]. In insects, flying activity requires a much greater expenditure of energy than walking, for example, metabolic rate of *D. melanogaster* increases 8-fold or more during flight as compared to the resting/walking state [3]. Although the authors found significant differences in the propensity of flies

Spontaneous Locomotor Activity as a Test for the Rate of Living Theory
333

to walk or to fly, these behavioral tendencies would not be adequately expressed as actual differences in physical activity among different flies due to limitations imposed by the housing conditions. It would seem that under the housing conditions employed, Lints et al., in reality, studied the correlation between behavioral tendency for physical activity and life span. In physically restricted flies, the actual differences in the level of physical activity among different

individuals would be minimal. A more desirable experimental design would have involved housing of flies in a large cage where metabolically demanding flying activity was possible. Quite obviously, if one is testing the rate of living theory, it is advantageous to employ conditions which will maximize rather than minimize the differences in metabolic expenditure among different test animals. Effects of SLA on life span, if any, are more likely to emerge under the conditions permitting relatively high levels of physical activity. It has been previously shown by us that significant differences in the life spans of male and female houseflies observed under conditions which permit flying activity become insignificant under conditions which abolish flying activity [4].

Another limitation of the experimental protocol used by Lints et al. is that life time estimates of SLA cannot be reliably made on the basis of observations on a single day, as was done by these authors. It has been amply demonstrated that physical activity of individual insects varies greatly on different days [5]. For example, individuals that fly for extended periods on some test days fly only briefly or not at all on other days. This daily variation in activity can introduce a major experimental error if life time extrapolations are made on the basis of observations on a single test day.

The main factual point which emerges from the study of Lints et al. is that spontaneous walking activity of *Drosophila* is not correlated with life span. It is very likely that the deleterious effects of physical activity on life span, if any, would occur above a certain threshold level of activity. This threshold may not have been exceeded by the voluntary walking activity of a fly confined within a small vial.

Lints et al. also opined that the decreased life span of houseflies, previously reported by us [4, 6, 7], under conditions of relatively high physical activity is a 'simple phenomenon of exhaustion'. Among other data, we also reported that houseflies confined singly in 0.09 cm³ cages, where they can fly, have a shorter life span than those kept singly in a vial, where they are unable to fly [7]. It would seem highly improbable that flies undertaking voluntary flight in a cage of this size would undergo physical exhaustion and die from it, as inferred by Lints et al.

Finally, it is not my intention here to debate whether or not the rate of living theory is true, I would simply like to point out that Lints et al. have not provided a valid test of the rate of living theory. Deficiencies in their experimental design do not permit a validation of their broad inferences. Studies dealing with the rate of living theory have been recently reviewed elsewhere [8].

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334

Sohal

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