Appendix B

Measures for linear displacement can be converted into estimates of μ, but this conversion may introduce bias. Suppose an experiment was terminated after 1 day. Then a biased estimated of μ could be calculated using equation 2:

$$\hat{\mu} \approx \frac{1}{4}\bar{d}^2 \qquad \text{eqn B.1}$$

Where $\bar{d}$ is the average movement distance. This estimate of μ from $\bar{d}$ underestimates the true value of motility because of the variability in the distance covered around the mean and the convex (upward curving) relationship between μ and $\bar{d}$ (Jensen's inequality, e.g. Hilborn & Mangel, 1997, p. 58). A better estimate of μ is achieved by including the effect of the non-linear relationship between $\bar{d}$ and μ by using the Delta method (Hilborn & Mangel, 1997, p. 58):

$$E\left(g\left(d\right)\right) = g\left(\bar{d}\right) + \frac{1}{2}g''\left(\bar{d}\right)\mathrm{var}\left(d\right) \qquad \text{eqn B.2}$$

Where *E* denotes the mathematical expectation, *g* is a non-linear function linking motility and dispersal distance of individual beetles, i.e.

$$\mu_i = g\left(d_i, t_i\right) = \frac{1}{4}\frac{d_i^2}{t_i} \qquad \text{eqn B.3}$$

g'' is the second derivative of *g* with respect to *d,* and var(*d*) denotes the variance of dispersal distance. The second derivative of *g* is

$$g''\left(d_i, t_i\right) = \frac{1}{2t_i} \qquad \text{eqn B.4}$$

At chosen t_i, the Delta method then yields:

$$\hat{\mu} \approx \frac{1}{4}\bar{d}^2 + \frac{1}{4}\mathrm{var}\left(d\right) \qquad \text{eqn B.5}$$