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FORUM

Response to R. Eikelboom

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We agree with Eikelboom (2001) that the number of wheel revolutions divided by the number of 1-min intervals with any running activity ('average speed') may be an inadequate measure of an instantaneous running speed. However, we think it is still a meaningful measure of an intensity of locomotor activity in the context of our study on physiological and behavioural responses to selection for high voluntary wheel running in mice (Swallow at al. 1998; Koteja et al. 1999). Even if a single running bout lasts only one or a few seconds, the aerobic metabolism covering the energy demand associated with the activity is extended to the range of minutes (e.g. Baker & Gleeson 1998).

Motivated by Eikelboom's (2001) commentary, we have examined our computer-recorded data for an additional piece of information that bears on possible differences in running speeds. Specifically, we examined the single highest l-min interval of running that was ever recorded for each individual mouse (i.e. the single interval within a 24-h period that had the greatest number of revolutions). These data were not available for our original study (Koteja et al. 1999), so we turned to a recent generation. Table 1 reports wheel-running descriptive statistics for mice from generation 24 of our ongoing artificial selection experiment. This table can be compared with Table 2 in our original report (Swallow et al. 1998), except that we did not previously report the data for single highest intervals. Mice from our selected lines show single highest intervals that average more than 1.8-fold greater than in the random-bred control lines. This difference also suggests, but does not prove, a difference in instantaneous running speeds.

As also indicated by Eikelboom (2001), estimating running speed based on wheel-running data presents at

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Table 1. Summary statistics for wheel running of mice from generation 24 of our ongoing artificial selection experiment (values are means of days 5+6 of a 6-day exposure to wheels)

	Sex*	Selected	Control	Ratio
Total revolutions	F	14 458	5205	2.78
	M	12 390	4493	2.76
Number of 1-min intervals with any revolutions	F	564.0	472.9	1.19
	M	530.8	400.3	1.33
Average revolutions/min	F	25.79	10.88	2.37
	M	23.41	11.07	2.12
Revolutions in highest 1-min interval	F	41.38	21.28	1.94
	M	38.51	22.08	1.74
Body mass (g)†	F	21.78	24.06	0.91
	M	27.81	30.89	0.90
Age (days)‡	F	52.27	53.04	0.99
	M	52.25	52.73	0.99

*F=females (*N*=300); M=males (*N*=264).
†Mean of values recorded at start and end of 6-day trial.
‡At midpoint of 6-day trial.

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least one more difficulty. Based on visual observations, we (Koteja et al. 1999) reported that a large proportion of wheel revolutions is made with the mice coasting (hanging in a rotating wheel) rather than actually running (see also: De Kock & Rohn 1971; Drickamer & Evans 1996). When a mouse runs and then takes a short break, the wheel continues to rotate for some time. An automated revolution counter cannot detect short breaks, so the length of 'running' bouts is overestimated.

Because we found no significant difference in the percentage of coasting episodes between the selected and control lines (Koteja et al. 1999), we thought that the selected mice indeed ran faster, not only more regularly than the control mice. However, an estimate of instantaneous speed would be unbiased only if the rate of rotations with the animal coasting were the same as with the animal running, which cannot be strictly true based on principles of physics. Neither increasing the frequency of counting nor applying a tachometer, as recommended by Eikelboom (2001), can solve the problem. The only way of measuring accurately the instantaneous running speeds is by using a video-based system, which would allow setting off the periods with actual running. Such analyses are currently under way.

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