The disposable soma theory (Kirkwood, 1977, 1981, 1990; Kirkwood & Holliday, 1979) is a solution to two key questions of gerontology: "Why does ageing occur?", and "How is ageing caused?". The first question is a problem of evolutionary biology and its primary relevance is to gain insights into the genetic factors that control lifespan in present-day species. The second question is a problem of physiology and concerns the molecular and cellular mechanisms through which senescence comes about.

The disposable soma theory explains ageing through asking how best an organism should allocate its metabolic resources, primarily energy, between on the one hand keeping itself going from one day to the next (maintenance), and on the other hand producing progeny to secure the continuance of its genes when it itself has died (reproduction).

No species is immune to hazards of the environment, such as predation, starvation and disease. These hazards would set a limit to the average survival time, even if senescence did not occur. It follows that maintenance is only needed to an extent which ensures that the body (soma) remains in sound condition until an age by which most individuals will have died from accidental causes. In fact, a greater investment in maintenance is a disadvantage because it eats into resources that in terms of natural selection are better used for reproduction. The theory concludes that the optimum course is to invest fewer resources in the maintenance of somatic tissues than are necessary for indefinite somatic survival.

The disposable soma theory is named for its analogy with disposable goods, which are manufactured with limited investment in durability, on the principle that they have a short expected duration of use. The theory, as it is outlined above, applies to any species that exhibits an iteroparous (repeatedly reproducing) life-history plan, and that has a clear distinction between soma and germ-line (sensu Weismann; see Kirkwood & Cremer, 1982). [The principle of optimising the trade-off between maintenance and reproduction can be extended, however, to other life-history patterns: see Kirkwood, 1981, 1985].
Central to the disposable soma theory is the idea that maintenance is costly. Although it is not yet possible to quantify the costs of maintenance in detail, there is no doubt that the overall maintenance cost is substantial. Basal metabolism accounts for the major part of the energy budget of a typical organism, and basal metabolism is largely concerned with maintenance of one kind or another. In particular, there is an extensive network of intracellular processes whose operation is essential for maintaining cellular homeostasis. Maintenance of DNA, for example, involves numerous repair systems (SEDGWICK, 1986). The fidelity of DNA replication is maintained by the highly tuned proofreading capacity of DNA polymerases. Proofreading is metabolically expensive, as can be demonstrated by in vitro studies on mutant polymerases with altered proofreading capabilities (GALAS & BRANSCOMB, 1978). Accuracy in protein synthesis is also important for maintaining cell viability, and this too is costly. SAVAGEAU & FRETER (1979) estimated the cost of proofreading the charging of transfer RNA by the aminoacyl-tRNA synthetases to account for 2% of the energy requirement of a cell, and this is just one of several operations that are needed for accurate protein synthesis. Similarly, there are energy-dependent enzymatic processes to degrade abnormal proteins (HIPKISS, 1989) and to protect cells against the highly reactive oxygen radicals that arise as by-products of aerobic metabolism (HALLIWELL & GUTTERIDGE, 1989).

In addition to explaining why ageing occurs, the disposable soma theory also suggests how the genetic control of lifespan is arranged, and how different species have evolved different lifespans.

Natural selection operates on the genes that regulate key aspects of somatic cell maintenance in such a way as to secure the optimum balance between surviving long enough and spending too much on survival. The ‘set point’ of a maintenance function determines the average period of longevity assured. To take a specific example, let us consider DNA repair. If we suppose the exposure of DNA to damaging agents to be constant, but vary the level of DNA repair activities, then we vary the rate at which DNA damage accumulates, for the rate of damage accumulation equals the difference: (Rate of new damage - Rate of repair). The rate of DNA damage accumulation determines the average length of time taken before DNA defects reach harmful levels, and hence, longevity.

Now if we recall that in the disposable soma theory it is the presence of extrinsic, environmental hazard that makes it not worthwhile to invest in better maintenance than is needed to preserve somatic functions through the normal expectation of life in the wild, we can see that it is the level of environmental risk that imposes the selection for a longer or shorter intrinsic lifespan. A species subject to high environ-