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2002 Sewall Wright Award

Linda Partridge

The Sewall Wright Award is the most prestigious award given by the American Society of Naturalists. The award is given annually and honors a senior but active investigator who is making fundamental contributions to the Society's goals, namely, promoting the conceptual unification of the biological sciences. In 2002 the award was presented to Linda Partridge, Natural Environment Research Council Research Professor of Biology at the University College, London. Linda began her career studying the behavioral ecology of birds, but she switched to *Drosophila* so that she could incorporate experimental and genetical approaches into her studies of life-history and related traits.

Linda is an empiricist whose work invariably goes right to the core of fundamental concepts in evolutionary ecology. She is best known for her pioneering work in the genetics, evolution, and physiology of aging, where she has focused on studying trade-offs between reproduction and longevity. However, Linda is also doing breakthrough research on plastic and evolutionary responses to temperature and to parasitoid attack, gene flow and selection along latitudinal clines, and the thermal evolution of body size. She has a rare ability to gather and to integrate information from organismal, physiological, as well as genetic levels. She tailors her experimental approaches to the problem at hand, and she commands an impressive armamentarium of techniques such as artificial selection, laboratory natural selection, physiology, DNA microarrays, and genomics. Linda is freewheeling, energetic, and exhaustingly productive.

Perhaps the best way I can characterize Linda's style is to relate a story about some of her work on aging. One of her first papers in this area showed that mating shortened the life expectancy of male *Drosophila*. In other words, if you are a male fly, any sex is bad for your longevity, and the more sex you have, the sooner you are likely to die. Not surprisingly, this finding raised more than a few eyebrows. Indeed, when Linda presented this paper at a meeting in the United Kingdom, Maynard Smith reputedly stood up at the end of her talk and demanded, "This type of research has to be suppressed!"

Years later I asked Maynard Smith whether this episode had actually occurred. He replied, "Yes, indeed I did say that! I've never been more surprised by a study in my life. After all, sperm is cheap! But even so, females should prefer older males." This last comment provoked an immediate

glance from Sheila, John's wife, who was sitting next to him at the time.

Recognizing an opportunity to have some fun, I immediately wrote to Linda, describing John's assertion, which was basically a good-genes hypothesis. I asked if she knew whether anyone tested to see whether females do indeed prefer older males. If so, I suggested we immortalize this as the "Maynard Smith Effect," otherwise we could call it the "Maynard Smith Fallacy." Linda quickly wrote back, saying that she thought J. M. S. might well be wrong. Because of the trade-off between early reproduction and longevity, she argued that females might well have higher fitness if they chose young—not old—males! In any case, she noted that the idea really needed some hard life-history modeling.

As that anecdote demonstrates, Linda is a critical and independent thinker. Moreover, she is not content merely with describing pattern, but she tries to explore the mechanisms and processes underlying observed patterns. For example, she has found experimentally that elevated male mortality following mating is due in part to increased male activity. Also, she has done parallel studies on the cost of mating in females, following up old work of John Maynard Smith himself, who showed in the 1950s that virgin females lived longer than mated females. Linda found mating per se (as opposed to egg production) does impose a cost on females. Specifically, that cost is caused by proteins in the males' seminal fluid. For females (but not for males), the cost of mating thus reflects a conflict between the sexes.

Linda has also shown that the trade-off between early reproduction and a slowed rate of aging is the key constraint in the evolution of the rate of aging in *Drosophila*. She has recently jumped into the debate over whether caloric restriction slows aging. She found that caloric restriction indeed lowers adult mortality but does so at the cost of daily and lifetime reproductive success. She has even discovered that the insulin IGF-like signaling pathway seems to mediate this association.

A second major area of Linda's work involves adaptation to temperature, especially as regards body size. Here she has studied phenotypic and evolutionary responses to temperature in the laboratory, as well as clinal patterns in nature. Here again, Linda quickly goes beyond merely documenting patterns and tries to uncover the mechanisms underlying observed patterns. For example, it has been known for decades that flies evolving at low temperatures

will be larger than those evolving at high temperatures. But Linda and her colleagues discovered that the evolution of large size by cold flies is a consequence of their having enhanced growth efficiency, which in turn may be a consequence of relatively high efficiency of mitochondria at low temperature.

Much of Linda's work in this general area involves latitudinal clines in body size in *Drosophila melanogaster*. Going well beyond mere pattern description, Linda and colleagues are using neutral molecular markers to test for thermal selection on body size in the field as well as to evaluate asymmetry of gene flow along latitudinal clines (from low to high latitudes). This work is revitalizing an old area of research.

A glance at her curriculum vitae would lead anyone to suspect that Linda is an intense and tireless worker. I can certainly vouch for that, having worked with Linda on a fly project. She counts and sexes flies with a vengeance (though she once told me that she finds fly pushing almost meditative for her!). In any case she picks up useful new techniques almost as fast as she counts flies. Linda is always out in front and leading the edge forward. She is fundamentally irrepressible.

Linda has received impressive awards and honors, including a fellowship in the Royal Society. Since 1994, she has been the Weldon Chair of Biometry at University College, London (note that this was Haldane's Chair!). She has also served on multiple editorial boards of prestigious journals.

In receiving this year's Sewall Wright Award, Linda Partridge joins an extraordinary group who have enriched our science: Russell Lande, Joseph Felsenstein, Richard C. Lewontin, John Maynard Smith, Robert T. Paine, Douglas J. Futuyma, William D. Hamilton, Janis Antonovics, Montgomery Slatkin, and Ilkka A. Hanski. Their fields of research are wide ranging, but all have shared a commitment to our Society's goals of the conceptual integration of the biological sciences and all are having a lasting impact. Linda is especially noteworthy for her ability to pull insights from all levels of biological organization to bear on important conceptual issues.

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