

1985) are confident that the hidden mass cannot be in the form of dwarfs, whereas J. N. Bahcall, P. Hut and S. D. Tremaine (*Astrophys. J.* **290**, 15; 1985) believe that brown dwarfs are the best candidate.

It seems possible that some of these questions will be answered now that brown dwarfs have been observed. For some time infrared observations have provided candidate objects (see, for example, T. O. Boroson, M. S. Giampapa and J. Liebert, *Astrophys. J.* **283**, 758; 1984) but no definite identifications. Now there seems to have been a definite detection in Van Biesbroeck 8B, the companion to another very low-mass nearby star Van Biesbroeck 8A. The identification has been made using infrared speckle interferometry by D. W. McCarthy Jr, R. G. Probst and F. J. Low (*Astrophys. J.* **290**, L9-13; 1985). Now Nelson and his colleagues describe detailed models of the structure and evolution of very low mass

stars, and show that the observed luminosity and surface temperature of Van Biesbroeck 8B are consistent with its having a mass of about 0.06 solar masses and an age of about 2×10^8 years, comfortably less than the age of the Galaxy. They also suggest that the mass of Van Biesbroeck 8A is very close to the hydrogen-burning limit.

It is obviously of great interest to know that brown dwarfs do exist and to have the opportunity to check the models of low-mass degenerate stars against observations. One or two stars do not, however, account for the hidden mass, so observers will be looking for every opportunity to discover further objects to obtain estimates of their space density. As Nelson *et al.* point out, the Hubble Space Telescope and the Space Infrared Telescope Facility may provide such opportunities. □

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Evolutionary biology

Costs of reproduction

from Linda Partridge and Paul H. Harvey

Most genetic models for the evolution of life-history patterns assume that an organism's reproduction early in life has a negative effect on its later reproduction. Therefore, reproductive rates at all ages cannot be simultaneously maximized by natural selection^{1,4}. One physiological basis for this effect may be that early reproduction diverts resources away from growth and repair, so that survival rates and fertility are subsequently lowered. Different life-history patterns can evolve as a consequence of reproductive trade-offs. For instance, if growth rates are reduced when an organism's resources are channelled into reproduction, but fertility increases with an individual's size, natural selection may favour delayed maturity and hence higher reproductive success at maturity. Conversely, if larger individuals attract the attention of predators, then early reproduction may be favoured.

These notions of reproductive costs and trade-offs provide an evolutionary explanation for the observed diversity of age-specific reproductive patterns, but until recently there has been little empirical testing of the hypothesis. Attempts to demonstrate and measure the costs of reproduction are producing what at first sight seem to be mixed results.

One major category of study examines correlations between early and late reproduction among different individuals (or clones, populations or species) living in the wild or in captivity. Both negative and positive correlations have been found. For example, the overwinter survival rates of female song sparrows (*Melospiza melody*) that have reared broods of different sizes are positively correlated with brood size⁵.

Similarly, early and late fertility are positively correlated with survival both in and among clones of a planktonic rotifer (*Platylabus patulus*)⁶. In contrast, female red deer (*Cervus elaphus*) calving in one breeding season have a reduced probability of survival to the next breeding season and, if they do survive, of then calving⁷. Only 22 of 33 such studies cited in a recent review⁸ suggest that reproductive costs do occur. But correlation is not causation, and the other studies can be interpreted on the basis of a cost of reproduction if a third variable acts simultaneously on early and late reproductive rates. For instance, individuals may differ in size, nutritional status or their fit to the habitats they occupy, particularly in the laboratory. Under such circumstances, rates of early and late reproduction may be positively correlated, because of their common correlation, with a third variable.

Therefore, when investigating costs of reproduction, it is essential to perform manipulative experiments in which other confounding variables are kept constant⁸⁻¹¹. Laboratory studies with male fruitflies (*Drosophila sp.*) provide an example of manipulations that can demonstrate costs to reproduction when the correlational evidence seems to point in the other direction. The natural correlation between longevity and age-specific reproductive activity in males is positive, because both variables are strongly correlated with body size¹². When reproductive activity is manipulated by allowing males access to an excess of sexually receptive females, rates of survival are reduced¹³. Similarly, female *Drosophila* that lay few eggs because they are kept virgin¹⁴,

or are made sterile by high temperatures¹⁵ or radiation¹⁶ have higher survival rates than females reproducing normally. Similar experiments have manipulated clutch sizes of birds in the field and hence the effort expended on parental care. One study on blue tits (*Parus caeruleus*), outstanding for its careful experimental design and large sample sizes, showed that large clutches result in weight loss and increased mortality in female but not male parents, possibly because although both sexes feed the nestlings, only the female incubates¹⁷.

Genetic manipulations of reproduction have also revealed costs. *Drosophila* females selected for high fertility late in life show increased longevity and lowered early fertility^{18,19}, and females with high fertility early in life have low longevity²⁰.

The general conclusion from properly conducted experiments is that reproduction does have costs; genetic variation has been found in the few cases where it has been looked for, thus providing the raw material for the evolution of reproductive trade-offs. Nevertheless, adequate tests of the importance of reproductive trade-offs in life-history evolution will entail experimental work under field conditions. Laboratory studies probably tend to underestimate reproductive costs, because many important features of field conditions, such as competition for food, predators and competitors are usually absent. However, making the relevant manipulations under field conditions can be extremely difficult. For instance, it is relatively easy to alter clutch and brood size in birds by addition or removal of eggs or nestlings, and hence to measure costs of parental care, but manipulation of the rate of egg laying to assess costs of egg production would be more difficult. Although there are few field studies of reproductive costs, only this type of information will allow adequate tests of some fundamental assumptions of life-history theory. □

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