

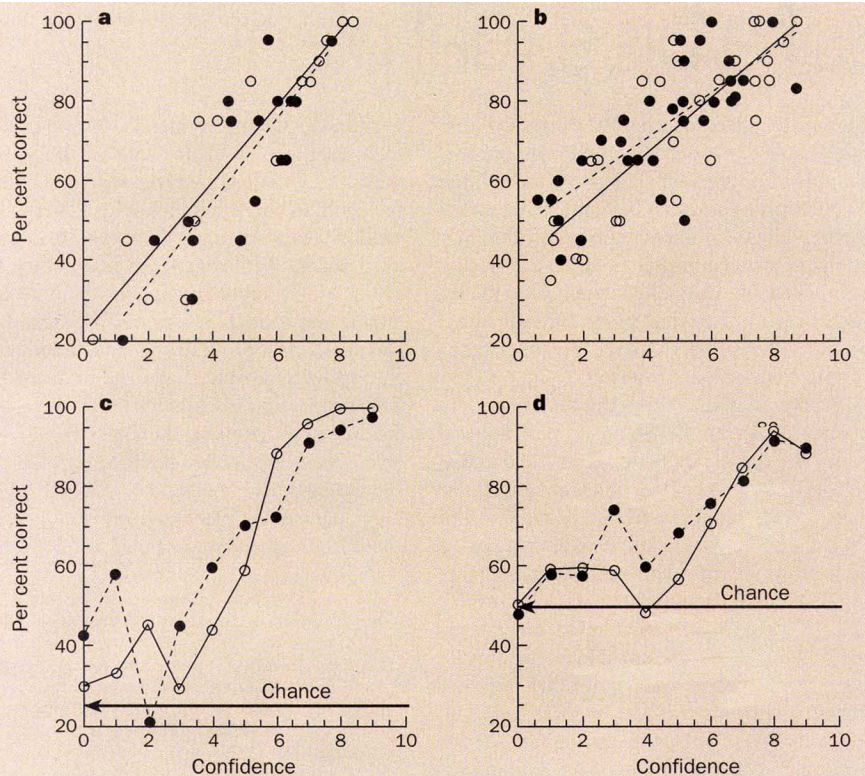
## Heritabilities and paradigm shifts

In his influential book *The Structure of Scientific Revolutions*, Kuhn<sup>1</sup> described scientific endeavour in terms of occasional revolutionary shifts from one favoured paradigm to another. Although research is not totally uncritical between revolutions, currently popular explanations can be accepted too readily. Here, we provide a quantitative example from evolutionary biology.

Female choice of ornamented males has been hotly debated over the past 20 years<sup>2</sup>. The 'good genes' school claims that ornaments are honest indicators of male viability, allowing choosy females to gain through enhanced offspring viability<sup>3</sup>. The 'fisherian' school argues that male ornaments evolve in a runaway fashion once females have started to favour ornamented males, and the ornaments convey no fitness benefits to the offspring. Between 1981 and 1986, orthodox theoretical models<sup>4</sup> excluded the possibility of any additive genetic variance allowing females to 'shop for good genes'. However, new models that appeared between 1986 and 1988 indicated that ornaments can evolve as honest viability indicators<sup>5</sup>, and the previously suppressed good-genes theory was no longer considered naive.

Pomiankowski and Møller<sup>6</sup> found high heritability estimates from a survey of the available data, which supported the underlying assumptions of good-gene models. But we have found a remarkable change in the data since 1988 (Fig. 1). The average heritability for ornaments reported before 1988 was 0.37 (s.d. = 0.14,  $n = 10$ ), but subsequently rose to 0.67 (s.d. = 0.34,  $n = 24$ ; Mann-Whitney rank test,  $z = 2.29$ ,  $P < 0.05$ ). The higher mean reflects a simultaneous increase in the variance of the estimates (for the increase in variance  $F = 5.56$ ,  $P < 0.01$ ). There were no significant changes in the mean heritability estimates for nonsexual traits (until 1987, mean = 0.40, s.d. = 0.19,  $n = 9$ ; since 1988, mean = 0.53, s.d. = 0.20,  $n = 9$ ;  $z = 1.41$ ,  $P > 0.10$ ). Additionally, there was no increase in the coefficient of additive genetic variance for the sexual traits ( $z = 0.66$ ,  $P > 0.10$ ). This index has been advocated as a preferred index<sup>6</sup> only recently. It seems possible, therefore, that the changing heritabilities reflect publication biases rather than any changes in the features of the organisms.

These chronological changes in heritability estimates may reflect a kuhnian paradigm shift, characterized by relatively conservative attitudes during the normal phase and a more cavalier approach during the revolutionary phase. Heritability estimates derived from small sample sizes are



**Figure 1** Correlation between success and confidence of success. Each point in a and b represents the performance of an individual subject at a particular exposure duration, in either the masked (solid symbols) or the unmasked (open symbols) condition. Linear regressions are shown (masked condition, broken lines; unmasked condition, solid lines). All correlation coefficients are high (a, 0.84, 0.92; b, 0.77, 0.92; masked, unmasked). In experiment 1 (a) the subjects were the three authors and masked and unmasked trials were randomly interleaved. In experiment 2 (b) the two conditions were presented separately and the subjects included three naive observers. Further observations were made of one other experienced subject (D. I. A. M.) in the masked condition alone (see Table 1). Details of the methods are available upon request from M. J. M. c, d, Replotting of the data from a and b, respectively. Each point represents the mean for all of the subjects, collapsed across exposure duration. Irrespective of duration, confidence is still a good predictor of success rate in both unmasked and masked conditions.

identify the target after similar exposures in the masked condition. They reported that the target did not appear to differ in orientation from the background (inconsistent with the explanation that suppression of one eye might be the cause) but that it did seem to differ in brightness or depth (possibly resulting from false stereo matching).

The other subjects required longer exposures to see the target in the masked condition. J. A. S. also saw the target as being defined by brightness or depth, whereas M. J. M. and D. I. A. M. saw a line surrounding the target. We presume that these verbal reports are post hoc rationalizations

for the segmentation of the image without an orientational cue. Clearly, the experience, although vague, is not unconscious.

Kolb and Braun's subjects were instructed to use the full confidence scale, irrespective of their absolute sense of certainty. If they were reluctant to use the vague cues in the masked condition as evidence for a high-confidence judgement, they may have decided to produce ratings randomly, with the result that Kolb and Braun observed. It is otherwise difficult to understand why they claimed to be highly confident: the opposite of blindsight. We conclude that blindsight in dichoptic displays is difficult to replicate. The motion transparency display used by Kolb and Braun may be more robust.

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Subject	Unmasked	Masked
M. C.	0.99	0.77
F. F.	0.76	0.97
M. J. M.	0.90 (0.96)	0.99 (0.92)
A. J. S. M.	0.95 (0.98)	0.99 (0.94)
J. A. S.	0.87 (0.90)	0.91 (0.85)
J. L.	0.89	0.73
D. I. A. M.	—	0.95

Correlation between the per cent correct scores and the mean confidence rating. Figures in parentheses show results from experiment 1.

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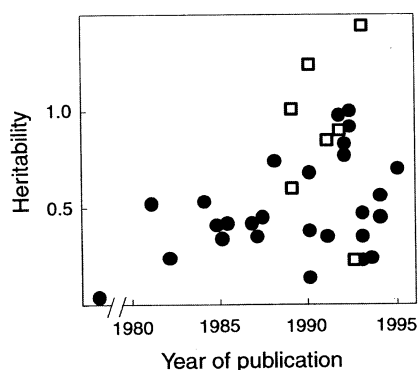


Figure 1 Heritabilities of secondary sexual characters listed in ref. 6 plotted against the year of publication. Open squares, studies with relatively small sample sizes, are based on the offspring of fewer than 20 males. Because the choice of the cutting year (1988) is not unambiguous we ran a series of simulations in which we randomized 1,000 times the 34 heritabilities to 34 publication years and checked all the cutting points (ensuring that the smaller data set had at least 10 observations) and took the largest difference in means and largest ratio in variances. This procedure was repeated 100 times to obtain error estimates, and both the observed differences in means ( $P = 0.0260$ , s.e.m. = 0.0004) and in variances ( $P = 0.0052$ , s.e.m. = 0.0003) are larger than their random expectations.

statistically significant only if the estimate is close to unity. Seven parent-offspring studies with fewer than 20 fathers, published between 1989 and 1993, have higher heritability estimates (mean = 0.90, s.d. = 0.40) than those of the remaining studies with larger sample sizes (mean = 0.50, s.d. = 0.25,  $n = 27$ ,  $z = 2.36$ ,  $P < 0.05$ ). Although none of these studies is wrong, they do not represent a random sample of estimated heritabilities. Perhaps people who have obtained estimates from small sample sizes were unwilling or unable to publish their results during the time when the good-genes model was unpopular, whereas such data were more readily published during the 'revolutionary' phase of the acceptance of this model.

Ironically, heritabilities of ornaments do not solve the initial controversy between the fisherian and handicap models<sup>7</sup> because both require some heritability for the ornaments. The essential difference is that female choice for good genes can occur only if ornaments are honest signals reflecting viability genes. These relationships have not been fully explored empirically, but many innovative studies have emerged<sup>12,6</sup>.

Research on sexual selection by female choice appears to have followed Kuhn's paradigm-shift principle, at least to some degree, even if the result has been a synthesis<sup>8-10</sup> rather than a replacement of ideas. Further, our analysis reveals the risks of relying solely on statistically significant results in the decision process of publishing

empirical research. Perhaps we should show more interest in the appropriateness of the study methods, sample sizes, powers of statistical tests and confidence intervals.

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## Almost airborne

Insect wings appear to have evolved from articulated gills of aquatic ancestors<sup>1,2</sup>. Possible remnants of intermediate stages in this transition occur in modern stoneflies that use non-flying aerodynamic locomotion to move across water surfaces. Such wing-propelled movement is a feasible setting for elaboration of wing size and the development of a powerful flight motor (muscles, neural patterns and wing articulations)<sup>3-5</sup>.

However, the mechanical requirements of surface locomotion are not as strict as those of flying. Flight requires dynamic control of body orientation<sup>6-8</sup> and generation of sufficient lift to achieve full aerodynamic weight support. Given these mechanical challenges, how might surface-skimming insects have made the final transition to true aerial flight? Here we report that stoneflies of the genus *Leuctra* (Leuctrinae; Nemouridea, Plecoptera) use a form of locomotion, mechanically intermediate between skimming and flying, thus demonstrating an advanced stage on the continuum of two-dimensional surface locomotion that may have led to insect flight.

Adult *L. hippopus* and *L. sibleyi* emerge in spring when air temperatures are highly variable. Although otherwise relatively proficient flyers, on contact with the water surface at air temperatures below 13 °C, *Leuctra* stoneflies curve their body into a stereotypical 'S'-shaped posture, raising their fore- and middle legs while they flap their wings and thereby move across water. Maintaining a nearly vertical body orientation permits wing motion over a dramatically increased arc (nearly 180°) compared with surface skimmers that maintain water contact with all six feet and for whom the underlying water restricts wing-beat amplitude to 90-110° (ref. 3). Excessive forward or rearward pitch is controlled by briefly touching the middle feet or tip of the abdomen down on the water such that a stable, upright body position can be maintained over many wing-beat cycles. The risk

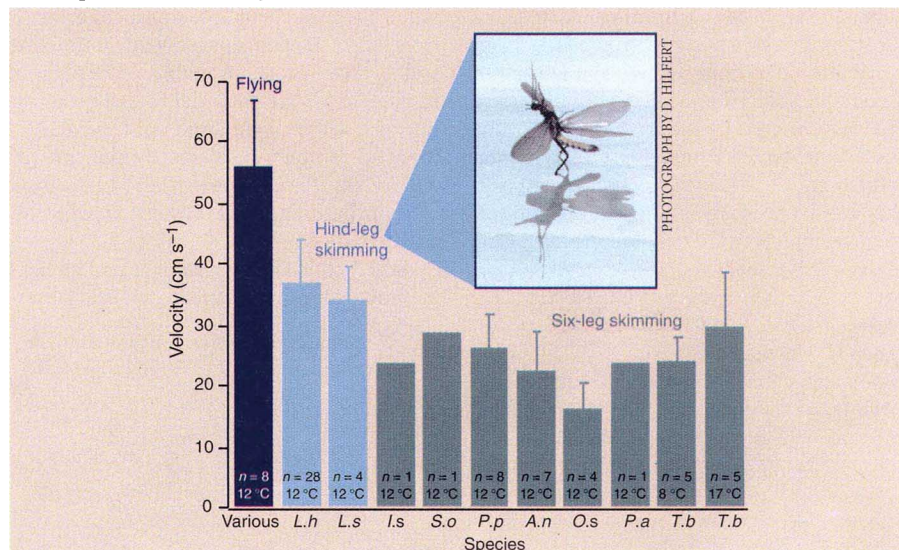


Figure 1 Inset, hind-leg skimming by *L. hippopus*. Photograph has been digitally enhanced. Histogram, velocities ( $\pm 1$  s.d.) attained by stoneflies during flight, hind-leg skimming and conventional skimming (continuous six-legged water contact).  $n$ , number of individuals sampled (see ref. 3 for methods). 'Various' refers to individuals that took off and flew just above the water (*L. sibleyi* ( $n = 3$ ), *Ostrocerca albidipennis* ( $n = 2$ ), *Amphinemura nigritta* ( $n = 2$ ), *Sweltsa onkos* ( $n = 1$ )); *L.h.*, *L. hippopus* (Leuctrinae); *L.s.*, *L. sibleyi* (Leuctrinae); *I.s.*, *Isoperla* sp. (Perlodidae); *S.o.*, *S. onkos* (Chloroperlinae); *P.p.*, *Paranemoura perfecta* (Nemouridae); *A.n.*, *Amphinemura nigritta*; *O.s.*, *Ostrocerca* spp. (Nemouridae); *P.a.*, *Paracapnia angulata* (Capniidae); *T.b.*, *Taeniopteryx burksi* (Taeniopterygidae; data from ref. 3). Note that surface skimming is widespread among the Plecoptera, contrary to previous suggestions<sup>9</sup>. A platform-independent QuickTime movie of hind-leg skimming is available at <http://cac.psu.edu/~jhm10>.