

moderate, inter-annual variations and measurement errors. This conclusion is supported by the much smaller r.m.s. deviation of only 2.5 m yr^{-1} for the InSAR/GPS velocity differences of the points located in the stagnant part of the glacier, where the contribution to the uncertainty from flow variability is negligible.

The absolute accuracy of the elevations is of the order of 10 m, compared to the GPS measurements. Because the GPS points lie in fairly flat areas and the local r.m.s. noise in the radar DEM is of the order of a metre, the observed elevation errors are primarily caused by low-frequency errors.

Observed accuracies are consistent with errors expected from atmospheric artefacts, the constant velocity, and the surface parallel flow assumptions (discussed below). A 0.5-cm atmospheric delay perturbation (one-way) will, with baselines and time separations of this study, lead to a 10-m elevation error if applied to one of the ascending interferograms and a 5 m yr^{-1} horizontal velocity error if applied to the ascending or descending interferograms with the smallest topographic sensitivity. In polar regions, typical dynamic atmospheric one-way delay perturbations are expected to be $<0.5 \text{ cm}$. Perturbations of similar magnitude can be caused by dry uneven snow layers. When a pair of baselines used to determine both elevation and velocity differ significantly, the velocity estimated is approximately that of the shorter spatial baseline. Here the descending velocity is that of 2–3 December 1995, the ascending velocity is that of 10–11 April 1996; both are winter velocities, expected to vary little over the period. For comparison, thermal noise is of the order of 1–2 mm differential range on each interferogram, equivalent to height accuracies of the order of 1–2 m. Observed correlations were generally high on the glacier, with average values of 0.8–0.9. An uncertainty in the slope of 1° translates into a relative velocity uncertainty of $\sim 4\%$.

The discrepancies between the InSAR and GPS measurements are of the order of the variability observed in the GPS data. However, there are several possibilities for improving the InSAR technique. The technique used here relies on an assumption of surface-parallel flow which even for stationary glaciers is not completely valid, because the ice particles at the surface move downwards in the accumulation zone, and upwards in the ablation zone. As the Storstrømmen glacier is not stationary, an additional vertical flow component is present. For Storstrømmen, the total vertical motion not accounted for by the assumption of surface-parallel flow should be less than $3\text{--}4 \text{ m yr}^{-1}$, causing a maximum error on the horizontal velocity of $\sim 10 \text{ m yr}^{-1}$. However, if the ice thickness was known, the surface-parallel-flow approximation could be replaced by the correct condition derived by using the principle of mass conservation (the continuity equation). Using redundant data to minimize the influence of atmospheric perturbations would further improve the accuracy, and three-dimensional flow velocities with an absolute accuracy of $1\text{--}2 \text{ m yr}^{-1}$ seem within reach.

The InSAR measurements give new important information about the surge and post-surge phases of Storstrømmen. Comparing the GPS measurements of surface elevations with elevations obtained from aerial photographs from 1978 (that is, before the surge) shows that ice has been transferred from the central to the lower part of the glacier⁸. The InSAR area-covering measurements enable us to calculate the ice volumes involved in this mass transfer. At present, the lower part of the glacier is almost stagnant and is therefore thinning due to summer melting. The InSAR maps also reveal that Kofoed-Hansen Brae, the northeastern branch of Storstrømmen (Fig. 2) for which no other measurements are available, is at present a stagnant ice body. Two stagnant ice plugs thus prevent ice from the central part of Storstrømmen from being removed, and summer melting cannot balance the upward movement. This part of the glacier is therefore building up. Today, InSAR height measurements are not accurate enough to directly detect this process, but combining detailed InSAR velocity measurements with ice thickness and ablation data, by means of the continuity equation, will allow

calculation of surface elevation (ice volume) changes. The availability of one more 'look' direction would allow direct measurement of vertical velocities. The application of simultaneous measurements of heights and three-dimensional velocities is not restricted to surging glaciers like Storstrømmen. It is a new and powerful method for assessing volume changes of land-ice masses. □

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Male eye span in stalk-eyed flies indicates genetic quality by meiotic drive suppression

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In some species, females choose mates possessing ornaments that predict offspring survival^{1–5}. However, sexual selection by female preference for male genetic quality^{6–8} remains controversial because conventional genetic mechanisms maintain insufficient variation in male quality to account for costly preference and ornament evolution^{9,10}. Here we show that females prefer ornaments that indicate genetic quality generated by transmission conflict between the sex chromosomes. By comparing sex-ratio distributions in stalk-eyed fly (*Cyrtodiopsis*) progeny we found that female-biased sex ratios occur in species exhibiting eye-stalk sexual dimorphism^{11,12} and female preferences for long eye span^{13,14}. Female-biased sex ratios result from meiotic drive¹⁵,

the preferential transmission of a 'selfish' X-chromosome. Artificial selection for 22 generations on male eye-stalk length in sexually dimorphic *C. dalmanni* produced longer eye-stalks and male-biased progeny sex ratios in replicate lines. Because male-biased progeny sex ratios occur when a drive-resistant Y chromosome pairs with a driving X chromosome¹⁵, long eye span is genetically linked to meiotic drive suppression. Male eye span therefore signals genetic quality by influencing the reproductive value of offspring¹⁶.

In Malaysia, two closely related species, *C. dalmanni* and *C. whitei*, exhibit biased sex ratios with 33–35% males¹⁷ and form nocturnal aggregations in which male mating success increases with male eye span^{13,14}. Although females possess eye-stalks, the slope of the regression of eye-stalk on body length in males is greater than in females, causing extreme sexual dimorphism for eye span in both species (Fig. 1a, b). Field observations at night indicate that females move further (1.16 ± 0.23 m) between aggregation sites on successive nights than males (0.47 ± 0.20 m; analysis of variance (ANOVA): $F_{1,50} = 5.16$, $P = 0.028$), and males often return to the same site on successive nights. Female-choice experiments using pairs of males differing only in eye span, resulting from artificial selection in *C. dalmanni*¹⁴ or physical manipulation in *C. whitei*¹³, confirm that females prefer to roost and mate¹⁸ with males with long eye-stalks. In contrast, *C. quinqueguttata* did not exhibit sexual dimorphism in eye span (Fig. 1c) or sex-ratio bias (53% males, $n = 197$). *C. quinqueguttata* do not aggregate at night¹¹, and in mate-choice experiments females show no preference for males with larger eye span or body size (G.S.W. and H. Kahler, unpublished data).

To determine whether variation in sex ratio between these congeneric species is consistent with a driving X chromosome, X^d , we compared sex ratios in progeny obtained from individual males.

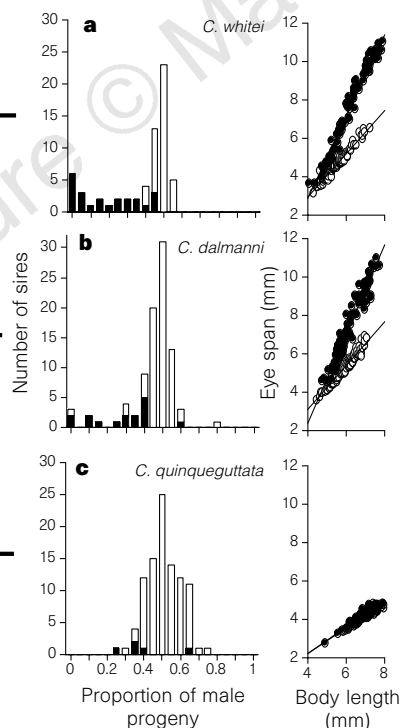


Figure 1 Sex-ratio distribution of male stalk-eyed flies, individuals were of the species: **a**, *Cyrtodiopsis whitei*; **b**, *C. dalmanni*; **c**, *C. quinqueguttata*. Shaded bars indicate males with progeny sex ratios that deviated (χ^2 test, adjusted for continuity; $P < 0.05$) from 0.5. Phylogenetic relationships are indicated on the left. Right, eye span on body length least-squares regressions for field-captured flies of each species. Filled circles, males; open circles, females.

The frequency of biased sex ratio was 36% in *C. whitei* ($n = 75$ sires, 10,395 progeny; Fig. 1a) after about five generations in culture and 16% in *C. dalmanni* ($n = 93$ sires, 10,695 progeny; Fig. 1a) after approximately 30 generations in culture. These X^d frequencies do not differ from estimates¹⁵ obtained for field-captured flies (contingency tests: *C. dalmanni*, $\chi^2 = 0.14$, $P = 0.71$; *C. whitei*, $\chi^2 = 0.05$, $P = 0.82$). In contrast, *C. quinqueguttata* males showed no consistent progeny sex-ratio bias ($n = 102$ sires, 3,553 progeny; Fig. 1c). Phylogenetic reconstruction based on over 3 kilobases of mitochondrial and nuclear sequences indicates that *C. quinqueguttata* is basal to the other two *Cyrtodiopsis* species and that eye-stalk monomorphism is plesiomorphic in the family Diopsidae (R. Baker and G.S.W., manuscript in preparation). Thus, exaggerated male eye-stalks, female preferences and a stable X-linked meiotic drive polymorphism apparently evolved after divergence from *C. quinqueguttata*.

To establish that there is a genetic relationship between exaggerated male eye span and chromosome drive we measured eye span and sex ratios of *C. dalmanni* flies selected for ratio of eye span to body length in males¹⁹. For each generation we selected 10 of 50 males to mate with 25 unselected females in replicate high, low and control lines. After 22 generations, artificial sexual selection primarily changed eye span (Fig. 2). By ANOVA, 95% of eye-span variation could be explained using sex ($F_{1,438} = 6966.2$, $P < 0.0001$), selection treatment ($F_{2,438} = 385.8$, $P < 0.0001$) and replicate ($F_{1,438} = 7.8$, $P < 0.006$) as factors, but they account for only 37% of body-length variation. For body length, the effect of replicate ($F_{1,438} = 30.4$, $P < 0.001$) was greater than selection ($F_{2,438} = 16.1$, $P < 0.001$).

The distribution of biased progeny sex ratios also differed between selection lines (Kruskal–Wallis test: $H = 47.2$, $P < 0.0001$). Compared to the *C. dalmanni* stock population (Fig. 1a), one line with decreased eye span exhibited no change in median sex ratio ($n = 107$ sires, 7,801 flies, Mann–Whitney U test: $Z = 0.44$, $p = 0.66$; Fig. 3a), whereas males from the other low line produced more female-biased progeny ($n = 110$ sires, 8,327 flies, $Z = 2.91$ sires, $P = 0.0036$; Fig. 3b). In contrast, males from both lines selected for increased eye span produced fewer female-biased and more male-biased progeny than stock population males ($n = 111$ sires, 10,652 flies, $Z = 2.90$, $P = 0.0016$, Fig. 3c; $n = 101$ sires, 8,721 flies, $Z = 3.16$, $P = 0.0013$, Fig. 3d). We have

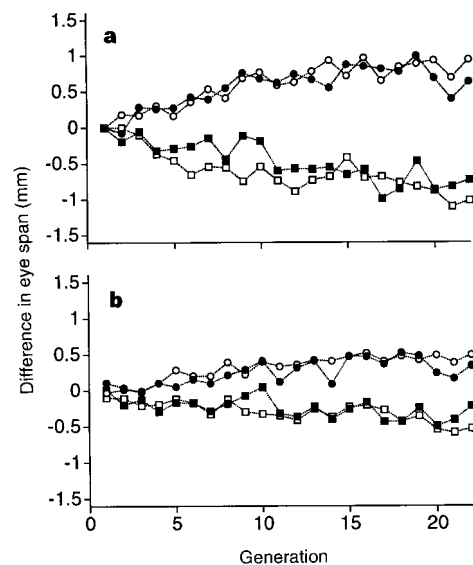


Figure 2 Replicate bidirectional response to selection on male eye-span to body-length ratio plotted against generation for eye span expressed as differences from control line averages. **a**, Males; **b**, females.

previously shown¹⁵ that a modifying Y chromosome, Y^m , causes 63% male-biased progeny sex ratios when paired with X^d . The form of spermiogenesis disruption in sex-ratio biasing *C. dalmanni* males suggests that male excess occurs because X^d damages some X^d -bearing, but not Y^m -bearing sperm, in X^dY^m males¹⁵. Therefore, we estimate X^d frequency within each line as the fraction of sires producing either female-biased (X^dY) or male-biased (X^dY^m) progenies, and Y^m frequency as the proportion of sex-ratio-biasing males producing male-biased progenies, that is $X^dY^m / (X^dY + X^dY^m)$. Given a stock population frequency estimate of 6.7% and 10 males mating in each of 22 generations, the probability that Y^m should increase in frequency by drift, only in the high lines, is 0.005 (Monte Carlo simulation). Mean male eye span from each line correlates significantly with the frequency of Y^m (Fig. 4b) but not X^d (Fig. 4a), indicating associated Y-linked effects on drive suppression and eye span.

Meiotic drive has been implicated in the evolution of female preferences in at least one other system. Female house mice heterozygous for transmission-distorting t-haplotypes prefer $+/+$ over $+/t$ males and avoid producing inviable t/t offspring²⁰. The benefits of choosing long eye span in stalk-eyed flies differ because sex-chromosome drive distorts the sex ratio. Consequently, choosy females produce more sons in a female-biased population, and those sons carry genes for both long eye-stalks and meiotic drive suppression. Choosy females also enhance the fertility of male offspring because 48% of X^dY , but only 11% of X^dY^m , male sperm degenerate¹⁵. The selective forces maintaining the X^d polymorphism have not yet been identified. However, the low frequency of Y^m

suggests that suppression is costly¹⁵, as expected for a stable polymorphism^{21,22}. Recent studies report drive suppressors on the Y chromosome and every autosome in *Drosophila simulans*²³, as well as polymorphism for Y-linked drive suppression in *D. mediopunctata*²² and *D. paramelanica*²⁴. If sex-chromosome meiotic drive is indeed more widely distributed than suspected^{25,26}, then other cases of sex-linked indicators of drive suppression should occur. For example, some guppy populations exhibit sex-ratio meiotic drive²⁷ and female preferences for males with Y-linked colour patterns^{28,29}. To the extent that X-linked drivers, or other costly selfish genetic elements, continuously coevolve with suppressors³⁰, genetic variation for fitness should persist and allow male ornament exaggeration. □

Methods

Field work. We captured flies near streams 20–32 km north of Kuala Lumpur, Malaysia, in January 1989 and 1996. To estimate daily movements we netted 47 *C. dalmanni* and 55 *C. whitei* along a mountain stream and marked individuals with a unique combination of paint spots on the thorax. Then, in 14 consecutive nights, we recorded location to the nearest 0.05 m for all marked flies roosting along 25 m of stream. We calculated the average distance each fly moved per day between the first and last day sighted.

Sex ratio. For each species and selected line we mated six or more females to each male for a week and then allowed isolated females to oviposit on 50 ml of medium¹⁹ for 2 weeks. We estimated sex ratios for each male by pooling the male and female progeny produced by all of his mates. To obtain sufficient virgin flies for breeding from each selected line we used flies after 22 generations of selection or a succeeding generation in which 25 males and 25 females from each line were arbitrarily selected for mating. We detected no change in mean eye span within each line between these generations.

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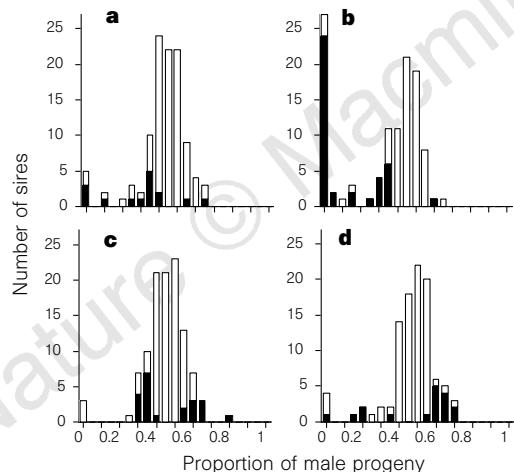


Figure 3 Sex-ratio distributions of male *C. dalmanni* after 22 generations of selection. Selection was replicated for decreased (a, b) or increased (c, d) male relative eye span. Shaded bars denote biased sex ratios, as in Fig. 1.

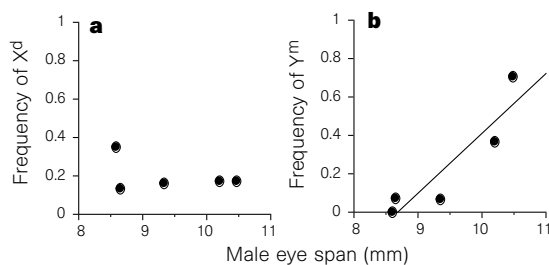


Figure 4 Correlation between mean male eye span and chromosome frequency. **a**, Driving X chromosome, X^d ($r = 0.39$, $P = 0.49$); **b**, drive-resistant Y chromosome, Y^m ($r = 0.91$, $P = 0.02$). Frequency among the stock population and four selected lines after 22 generations of selection is shown.

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Spontaneous sign systems created by deaf children in two cultures

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Deaf children whose access to usable conventional linguistic input, signed or spoken, is severely limited nevertheless use gesture to communicate^{1–3}. These gestures resemble natural language in that they are structured at the level both of sentence⁴ and of word⁵. Although the inclination to use gesture may be traceable to the fact that the deaf children's hearing parents, like all speakers, gesture as they talk⁶, the children themselves are responsible for introducing language-like structure into their gestures⁷. We have explored the robustness of this phenomenon by observing deaf children of hearing parents in two cultures, an American and a Chinese culture, that differ in their child-rearing practices^{8–12} and in the way gesture is used in relation to speech¹³. The spontaneous sign systems developed in these cultures shared a number of structural similarities: patterned production and deletion of semantic elements in the surface structure of a sentence; patterned ordering of those elements within the sentence; and concatenation of propositions within a sentence. These striking similarities offer critical empirical input towards resolving the ongoing debate about the 'innateness' of language in human infants^{14–16}.

We videotaped four deaf children in the USA (one in Philadelphia and three in Chicago) and four in Taiwan, Republic of China (Taipei), interacting with their hearing mothers at home with a standard set of toys. Each child was observed twice between 3 years 8 months and 4 years 11 months. Children were congenitally deaf with no recognized cognitive deficits. Cause of the deafness was unknown. Each child had at least a 70 to 90 dB hearing loss in both ears; even with hearing aids, none was able to acquire speech naturally. Children attended oral schools advocating training in sound sensitivity, lip-reading and speech production. At the time of videotaping, none could do more than produce an occasional spoken word in a highly constrained context.

None of the children had been exposed to a conventional sign system. The children's hearing parents attempted to communicate with them through speech. However, much of their interaction took place in action and gesture, a technique that worked because conversation was about the 'here-and-now'.

Although the number of subjects in the study was small, the number of observations was not. The data contain 6,614 gestural communications (an average of 455 per child, 372 per mother) made up of 10,398 individual gestures (779 per child, 531 per mother).

Unlike hearing children and adults who rarely concatenate their

spontaneous gestures into strings^{17,18}, the deaf children in both cultures often conveyed their message through gesture sentences rather than single gestures. The sentences the Chinese and American children produced conformed closely to a structural analogue of the ergative pattern that predominates in some, but not all, natural languages^{19,20}; importantly, not in English or Mandarin. This observation reduces the likelihood that the grammatical structure noted in the deaf children's gesture systems was somehow derived from the structure of the spoken languages that surrounded them.

The hallmark of an ergative pattern is that the actor in an intransitive sentence (mouse in the proposition 'mouse goes to hole') is distinguished linguistically from the actor in a transitive sentence (mouse in 'mouse eats cheese') and instead is marked like the patient (cheese). In contrast, in English, which is predominantly an accusative language, intransitive actors are treated like transitive actors and not like patients; for example, both actors precede the verb ('the mouse goes to the hole' and 'the mouse eats the cheese') whereas patients follow the verb ('the mouse eats the cheese').

Children in both cultures produced gestures for transitive actors, patients and intransitive actors at different rates (Fig. 1, dark bars; $F(2, 7) = 22.52$, $P < 0.0001$ for the groups combined; proportional data subjected to Freeman–Tukey transform before statistical analysis²¹). Gestures were produced significantly more often for patients (eaten-cheese) and for intransitive actors (moving-mouse) than for transitive actors (eating-mouse; both comparisons $P < 0.01$, Newman–Keuls). There were no significant differences between patients and intransitive actors. This production prob-

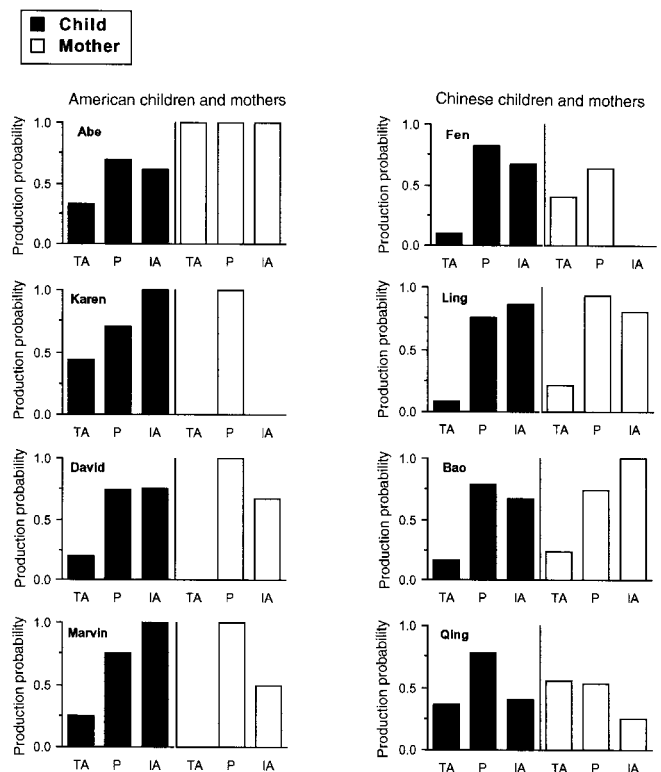


Figure 1 Probability that a gesture will be produced for transitive actors (TA), patients (P), and intransitive actors (IA) in a two-element gesture sentence. Probabilities were calculated using sentences in which three semantic elements could be gestured but only two elements actually were gestured. Deaf children (dark bars) showed significant differences in production patterns across the three elements. Gestures were produced more often for patients than for transitive actors, and more often for intransitive actors than for transitive actors, a structural analogue of the ergative pattern found in certain natural languages. Hearing mothers (white bars) were not consistent in their treatment of intransitive actors and did not display an ergative pattern.