The circle shown in Fig. 3 shows an area where all three phases have been identified in different runs. The centre of this circle is in excellent agreement with the γ−β−perovskite+MgO triple point reported[29] at 22.9 GPa and 2,260 K.

The present data strongly support earlier estimates of the phase-boundary temperature between ringwoodite and perovskite of about 1,900 K at 24 GPa, the pressure at a depth of 660 km in the Earth's mantle. The measurements also show that phase relations in simple systems can be measured more reliably in laser-heated diamond cells than by using multi-anvil methods; this is because measurements of pressure and temperature are more accurate, and the method provides the capability to use an inert and nearly hydrostatic pressure environment. Moreover, phase boundaries can be measured over much larger temperature ranges. Additional constraints on the phase diagram will have to come from calori-metric and spectroscopic measurements—as shown for the $MgSiO_3$ high-pressure polymorphs[11]. Larger samples and multi-anvil devices will be required for more complex systems, but pressure estimates will need to be improved by the systematic investigation of high-temperature equations of state of inert pressure calibrants such as gold. These could be provided by synchrotron X-ray measurements in laser-heated diamond cells. □

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Ecological and evolutionary processes at expanding range margins

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Many animals are regarded as relatively sedentary and specialized in marginal parts of their geographical distributions[1,2]. They are expected to be slow at colonizing new habitats. Despite this, the cool margins of many species' distributions have expanded rapidly in association with recent climate warming[3–10]. We examined four insect species that have expanded their geographical ranges in Britain over the past 20 years. Here we report that two butterfly species have increased the variety of habitat types that they can colonize, and that two bush cricket species show increased fractions of longer-winged (dispersive) individuals in recently founded populations. Both ecological and evolutionary processes are probably responsible for these changes. Increased habitat breadth and dispersal tendencies have resulted in about 3- to 15-fold increases in expansion rates, allowing these insects to cross habitat disjunctions that would have represented major or complete barriers to dispersal before the expansions started. The emergence of dispersive phenotypes will increase the speed at which species invade new environments, and probably underlies the responses of many species to both past[11] and future climate change.

Our first example concerns the silver-spotted skipper butterfly *Hesperia comma* in southern England. Near the coldest edges of their geographical ranges, ectothermic animals are often restricted to unusually warm habitats, such as areas of short vegetation on sheltered, south-facing (in the northern temperate zone) hillsides[1,2]. If they are limited by temperature, such populations should respond to climate warming by expanding into nearby habitats that were previously too cool. In 1982, *H. comma* was largely restricted to south- and south-west facing chalk grassland fragments in south-east England[12]. By 2000, however, it had colonized a wider range of aspects, including east-, west- and north-facing hillsides (Kuiper's test, $n = 82$, $m = 228$, $k = 5,478$, $P < 0.001$, where n is the number of habitat units occupied in 1982, m is the number colonized between 1982 and 2000, and k is the test statistic; Fig. 1a, b). High population densities were found on all aspects in 2000. Using these and additional habitat criteria[12] (see Methods), we were able to estimate the distributions of habitat in the eastern half of the South Downs hills (about 400 km^2 of south-east England), corresponding to 1982 and 2000 definitions of habitat. We estimated that 105 thermally

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Table 1 Latitudinal patterns of distribution of A. agestis

Latitudinal band (OS 10-km grid)	Number of squares occupied by A. agestis		Proportion of A. agestis squares within H. chamaecistus distribution*		Proportion (number) of UK squares occupied by H. chamaecistus
	1970–1982	1995–1999	1970–1982	1995–1999	
1–10 (south)	46	56	0.43	0.41	0.23 (27)
11–20	188	278	0.65	0.59	0.47 (171)
21–30	80	254	0.66	0.39	0.28 (119)
31–40	19	93	0.74	0.41	0.22 (79)
41–50 (north)	0	10	na	0.30	0.33 (68)

* The association between A. agestis and H. chamaecistus distributions (at 10-km grid resolution) becomes weaker between 1970–1982 and 1995–1999, but more so in northern (latitude 21–40N) than in southern (1–20N) Britain (four-way interaction term of log-linear model: latitude × year × butterfly presence × H. chamaecistus presence; $\chi^2 = 14.01$, d.f. = 1, $P = 0.0002$).

suitable habitat patches (total habitat area $2.00\,km^2$) would be available with the 1982 definition of habitat, compared with 175 patches ($3.92\,km^2$) with the 2000 definition of the same type of vegetation on any aspect.

Expansion rates are likely to increase with habitat availability. For *H. comma* at its northern limit, there are now more patches to colonize, shorter distances between them, and more populations generating emigrants. We used Hanski's spatially realistic incidence function (metapopulation) model[13–15] to simulate expansion away from the only two patches of habitat occupied by *H. comma* in the South Downs in 1982. This simulation was done in two ways, using patch networks on the basis of the 1982 and 2000 definitions of habitat suitability. Distance expanded was estimated as the mean distance from the main patch occupied in 1982 to the ten furthest populations (Fig. 1c; distances to the nearby, extremely small 1982 population were very similar). We first estimated parameters for the model in a different patch network (Surrey) occupied by *H. comma*, elsewhere in southern England, before using these parameter estimates to make independent predictions of expansion in the South Downs network. In 18 years (generations), the observed distribution of *H. comma* reached 16.37 km (Fig. 1c), corresponding well to the mean 14.35 km (s.d. 1.79) modelled expansion using the 2000 habitat network (Fig. 1e). In contrast, the observed expansion fell well outside the 99.9% confidence limit of simulations using the 1982 network (Fig. 1d; mean 4.98 km, s.d. 0.80). An approximate doubling of habitat availability led to an approximate trebling in expansion rate.

The second example considers the brown argus butterfly (*Aricia agestis*), which has also expanded both its habitat and geographical range over the past 20 years. Between 1970–1982 (ref. 16) and 1995–1999 (ref. 6), this butterfly increased 1.2-fold in the south of England, and 4.9-fold further north, in central England (Table 1). In 1970–1982, the northern part of the butterfly's distribution was mainly restricted to the distribution of one host plant *Helianthemum chamaecistus* (Cistaceae), a plant itself restricted to fragmented chalk and limestone grasslands[16,17]. Further south, there was a greater tendency for *A. agestis* populations to use *Geranium* and *Erodium* species (Geraniaceae) (Table 1). These plants are more widespread than *H. chamaecistus* and occur in both chalk and non-chalk habitats[17]. Between 1970–1982 and 1995–1999, *A. agestis*

expanded disproportionately into Geraniaceae-containing areas—especially *Geranium*—in the northern half of its distribution (Table 1; $P = 0.0002$). *H. chamaecistus* often grows on sheltered or southerly facing hillsides that are likely to be warmer than most *Geranium*-containing habitats: we propose that most northern *Geranium* habitats were too cool to achieve population growth in the 1960s and 1970s, but warm enough in the 1980s and 1990s.

The disproportionate expansion of habitat breadth in the northern half of the distribution could be explained completely by ecological processes. However, once habitat range has begun to expand for ecological reasons, phenotypes able to use either a wide range of habitats or the commonest type of habitat available in marginal areas may show relatively fast rates of range expansion. In *A. agestis*, expanding and non-expanding marginal populations differed in choice of host plant, and thereby habitat. We carried out choice experiments in the field, during which wild butterflies were experimentally exposed to four potential host plant species. Long-established and non-expanding marginal populations of *A. agestis* from limestone and sand dune habitats chose to lay eggs on host plants appropriate to their natural habitats (Table 2; 92% of eggs on *Geranium molle* and *Erodium cicutarium* at Gwithian and Mexico Towans sand dunes in Cornwall; 74% of eggs on *H. chamaecistus* plants on limestone in the Creuddyn Peninsula, north Wales). In contrast, females from populations that had been established recently chose to lay two-thirds of their eggs on *G. molle*, irrespective of whether they came from limestone (Barnack, north Cambridgeshire, colonized in 1994; C. Gardener, personal communication) or sand dune habitats (Gibraltar Point, Lincolnshire, colonized in 1994; K. Wilson, personal communication) (Table 2). Females in these populations chose to lay eggs on the most widespread host plant used during range expansion (*G. molle*), rather than on the host plant that was used naturally in the habitats where the populations occurred (*H. chamaecistus* at Barnack; *E. cicutarium* at Gibraltar Point). Nonetheless, both populations retained the ability to lay on *H. chamaecistus* (Table 2).

The data are compatible with a genetic contribution to host plant choice, but breeding experiments are required to confirm this. Butterflies from the Cornish and North Wales populations that had been reared in a common environment (laboratory) were released in a field containing experimental *H. chamaecistus* and

Table 2 Percentage of eggs laid on plants by four A. agestis populations in choice experiments

Population	Natural hosts	Expansion*	Helianthemum chamaecistus	Geranium molle	Geranium dissectum	Erodium cicutarium	n (eggs)
North Wales	H. chamaecistus	40%	74.1	14.8	7.4	3.7	27
Cornwall	Geraniaceae	0%	2.0	56.0	6.0	36.0	50
Barnack	H. chamaecistus	1,600%	12.9	70.2	14.0	2.9	183
Gibraltar Point	E. cicutarium†	250%	14.1	63.7	14.3	7.9	1,360

Schreirer–Ray–Hare tests: overall population × host plant interaction: SS/MS$_{total}$ = 23.0, d.f. = 9, $P = 0.006$. Population × host plant interactions were significant for all pairwise comparisons between populations except Barnack versus Gibraltar Point ($P = 0.688$) and Cornwall versus Gibraltar point ($P = 0.093$). χ^2 tests: four populations and four host plants, $\chi^2 = 143.8$, d.f. = 9, $P < 0.0001$. All pairwise comparisons between populations were significant at $P < 0.0001$, except Barnack versus Gibraltar Point ($P = 0.042$).
* Per cent increase between 1970–1982 and 1995–1999 in 10-km grid squares occupied in 50-km squares centred on each site.
† Some Geranium species may also be used, but this has not yet been observed.

G. molle plants. The released females differed in choice of host plant species in the expected direction, consistent with a genetic interpretation (140 eggs from the Cornish butterflies on *G. molle*, 25 on *H. chamaecistus*; 168 eggs from the north Wales butterflies on *G. molle*, 189 on *H. chamaecistus*; $\chi^2 = 66.6$, degrees of freedom (d.f.) = 1, $P < 0.001$). Females reared in the laboratory from the same populations showed no detectable effects of larval environment (host plant species or temperature) on subsequent egg-laying preferences (E.J.B., unpublished observations). Phenotypic carry-over (maternal) effects could affect these single-generation results, but could not plausibly explain the results of the choice experiments at Barnack and Gibraltar Point. Virtually all Barnack butterflies developed as larvae on *H. chamaecistus* and virtually all Gibraltar Point butterflies developed on *E. cicutarium*, and must have done so for the previous 9–10 generations. However, given a choice, both populations laid eggs disproportionately on *G. molle*. Similarly, learning by adults (or conditioning on emergence) could not be responsible for the observed patterns of host choice. Butterflies with similar adult experiences of habitat and host plants differed strongly

in choice of plants (for example, north Wales and Barnack), whereas adults exposed to dissimilar habitats and host plants exhibited similar host choice characteristics (Table 2; Barnack and Gibraltar Point).

Host choice phenotypes in the expanding region may have arisen from selection within each population ancestry during range expansion, or the entire range expansion may have been initiated from populations that already possessed the host choice characteristics of Barnack and Gibraltar Point. Whatever the origin, expansion into *Geranium*-containing habitats in the north enabled the butterfly repeatedly to bridge gaps of greater than 14 km in the fragmented *H. chamaecistus* distribution[6,16,17]. This is a distance that *A. agestis*[18,19] and comparable butterflies[20,21] would be extremely unlikely to cross in one step, without the availability of stepping-stones of other types of habitat.

Range expansion by flying insects may also select for increased flight ability[22–24]. Our third example concerns two species of bush crickets that exhibit adult wing polymorphisms. Both species have been spreading northwards and inland from distributions formerly confined to specific habitats in southern, coastal areas (Fig. 2)[7–9]. The long-winged cone-head *Conocephalus discolor* has two forms: long-winged and extra-long-winged (macropterous). Many populations established in the past 20 years show higher frequencies of extra-long-winged individuals, with a low (and fairly constant) frequency of this form in populations established greater than 20 years ago (Fig. 2c). Roesel's bush cricket *Metrioptera roeselii* has a short-winged form that cannot fly and a long-winged form that can. This species also shows increased frequencies of the more dispersive form in populations that have recently been established (Fig. 2d).

Environmental variables, such as temperature, population density and photoperiod, are known to affect whether cricket nymphs will mature to become long- or short-winged adults[25]. Thus, increased frequencies of longer wing morphologies in recently founded populations could represent (1) purely plastic responses to these new environments; or (2) genetic differences affecting, for example, the population density or temperature that a nymph must experience before it will develop into a longer-winged adult. We have not established the genetic basis for the observed differences among populations; however, plastic responses to new environments are unlikely to provide the whole explanation. Sites that have been colonized recently tend to have relatively low population densities and would therefore be expected to possess low frequencies of longer-winged forms[25], the opposite of the pattern observed. Variation in temperature (longer-winged morphologies expected in hotter regions) and latitude (equivalent to photoperiod) are also unlikely to explain the differences, given comparable results for the two species that have different spatial patterns of invasion (Fig. 2). The observed patterns may reflect the increasing number of colonization bottlenecks experienced by younger populations, and/or selection against dispersal in populations once they have been established. The latter is probable if there is a trade-off between investment in flight-related and reproductive structures[25].

Regardless of the proportional contributions of plastic versus genetic change to the observed patterns, the implications for range expansion are profound. If we assume that virtually all long-distance movements are achieved by the longer-winged morphologies (certainly the case for *M. roeselii*), this represents approximately 4-fold and 14-fold increases in long-distance dispersal for *C. discolor* and *M. roeselii*, respectively (based on fractions of longer-winged individuals, pooled across populations established less than 10 versus more than 20 years ago).

Improving environmental conditions at existing margins, in this instance regional warming at cool margins, are likely to initiate range extensions purely on the basis of ecological, physiological and population-dynamic processes—requiring no evolutionary change. Once an expansion is initiated, individuals and populations that expand most rapidly are likely to be favoured, and expanding range
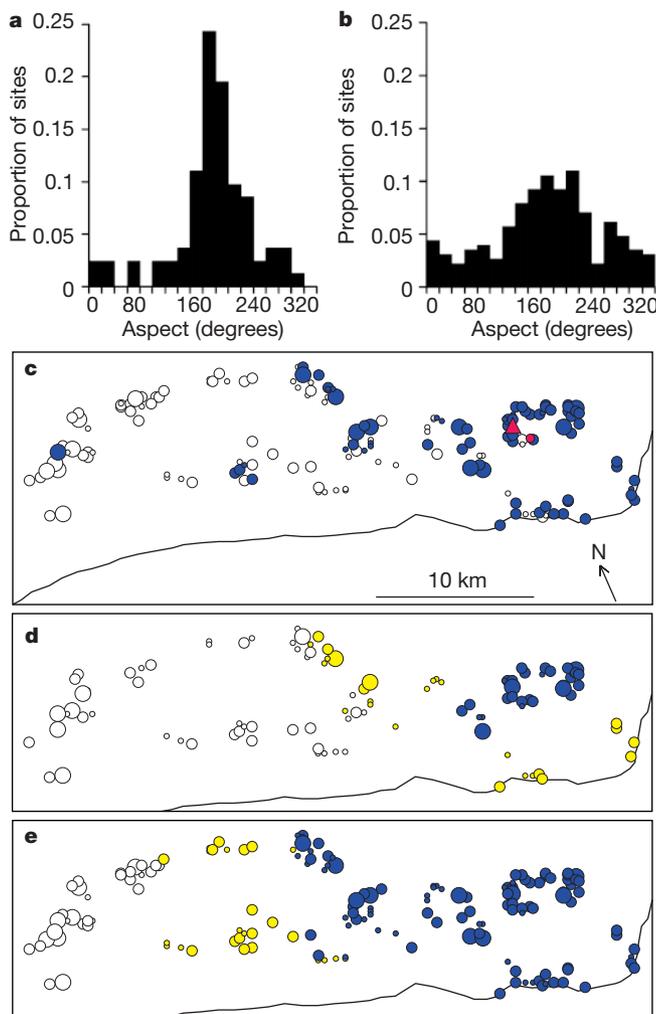
Figure 1 Habitat and range expansion by *H. comma*. **a**, **b**, Aspects of populated *H. comma* habitats in 1982 (**a**), and colonized habitats between 1983–2000 (**b**). **c**, Range of *H. comma* in the South Downs in 1982 (red; triangle contains > 95% of 1982 individuals) and in 2000 (blue and red). Unoccupied habitat (open circles) in 2000 is for the 2000 habitat network. **d**, Range of *H. comma* simulated with 1982 habitat network (blue circles, populated in 2000 in ≥ 50% of simulation runs; yellow circles, < 50% of simulation runs; and open circles, never colonized). **e**, Range of *H. comma* simulated with 2000 habitat network. Symbol sizes exaggerate patch areas (ha); small < 0.5, medium 0.5 to < 5, large ≥ 5. Line shows south coast of England; Beachy Head is at the south-eastern point.
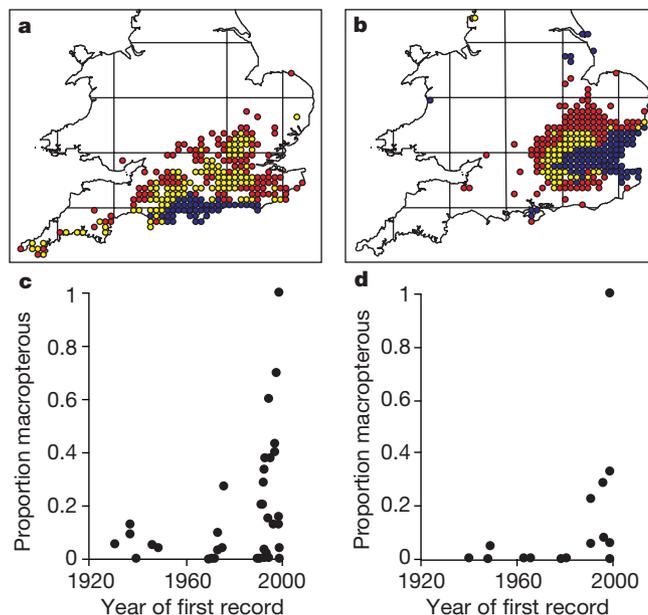
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Figure 2 Expanding distributions of *C. discolor* (**a**) and *M. roeselii*[7-9] (**b**). Lines show national 100-km grid squares. Circles show 10-km records: blue, recorded between 1961–1987; yellow, first recorded between 1988–1996; red, first recorded between 1997–1999. **c**, **d**, Proportions of macropterous individuals in populations sampled in 2000, according to date of first record for *C. discolor* (**c**) (proportion extra-long-winged; Spearman correlation $r = 0.349$, $n = 40$, $P = 0.027$), and *M. roeselii* (**d**) (proportion long-winged; Spearman correlation $r = 0.698$, $n = 17$, $P = 0.002$).

fronts may become characterized by dispersive generalists or by specialists on habitats common in the area of expansion. Once most habitats in a region have been colonized, specialists (in different habitats) and less dispersive forms may be favoured again, especially if there is a trade-off between dispersal and reproduction[25,26]. Evolutionary stasis during range changes has been emphasized[27,28], but transient evolutionary changes in habitat choice, flight behaviour and wing morphology require specific and detailed studies to detect. Such changes may be typical of expanding range fronts. Putative examples include increased frequencies of long-winged forms of ground beetles invading Canada[22], increased thorax sizes (containing flight muscles) of butterfly species expanding their ranges in Europe[23,24], biased orientation of Africanized honey bee swarms invading Mexico[29], and the development of increasingly dispersive seeds during the post-glacial expansion of lodgepole pine in North America[11]. These changes may dramatically increase rates of range expansion.

Our results should not be interpreted as evidence that all species will be able to change their geographical ranges rapidly in response to recent and predicted climate change. Extremely large numbers of relatively sedentary and specialized species may fail to initiate any expansion across human-modified landscapes, and some expansion is required before the selective pressures described here can result in the evolution of increased habitat range and migration rate. □

Methods

Hesperia comma

Hesperia comma adults and eggs (on the grass *Festuca ovina*) were mapped from July to September 2000. All habitat type was surveyed within 20 km of the 1982 distribution[12], and within 10–15 km of the 2000 distribution, using accepted patch definitions[30]. Comparison of aspects is based on sites (sub-sites where aspects varied) in the Chiltern Hills, North Downs and South Downs. The 1982 network was defined as sparse chalk grassland containing 'ideal' *F. ovina* tufts growing in slight hollows, next to bare ground[12] with aspects 100–300° (containing greater than 90% 1982 populations in south east England). The 2000 network had the same vegetation/*F. ovina* characteristics, but included grassland fragments of all aspects (the weak bias in Fig. 1b arises principally from the relationship between vegetation structure and aspect). For this exercise, we assumed that grazing patterns were the same in 1982 as in 2000.

We applied parameters to Hanski's incidence function model[13] using the 2000 distribution of *H. comma* in Surrey (86 occupied patches; 30 unoccupied). In the model,

extinction probability declines with increasing patch area, and colonization probability increases with proximity to existing populations. The MCMC method (1,000 function evaluations in initiation, 4,000 function evaluations in estimation) was used for parameter estimation[15]. Set parameters were $A_0 = 0.02$ ha, and $B = 0.5$; estimated parameters were $x = 0.278$, $y = 7.261$, $e = 0.337$, $\alpha = 0.445$. A_0, e and x scale the relationship between patch area and extinction, B and α determine migration rates, and y determines the relationship between migration and colonization probability[15]. We assumed no colonization from outside the network and no regional stochasticity[15]. These independent parameter estimates were used to run 100 simulations of 18 generations each for both the 1982 and 2000 habitat models in the South Downs. Eight 1982 network simulations went completely extinct; one had only one surviving population. These were ignored in calculations of 1982 network expansion distances (including them results in an approximately 9% reduction in mean distance colonized).

Aricia agestis

Aricia agestis in Cornwall (Ordnance Survey (OS) grid reference SW5740) has been associated with *Erodium* and *Geranium* species for over 100 generations and is greater than 100 km from *H. chamaecistus*. The north Wales population (SH7683) has an equally long association with *H. chamaecistus*, which receives greater than 99% of eggs (*Erodium* and *Geranium* are present in the region but rare in *H. chamaecistus* habitat)[16,19]. The new Barnack population (TF0704) uses *H. chamaecistus* on limestone (where Geraniaceae are rare). The new Gibraltar Point population (TF5659) uses *E. cicutarium*, and perhaps other Geraniaceae, in sand dunes (*H. chamaecistus* is absent). Barnack and Gibraltar Point are separated by 72 km; other inter-population distances are even greater (less than 5% *A. agestis* individuals are expected to move over 1 km per generation[18,19]. Twenty-four plants each of *E. cicutarium*, *G. molle*, *Geranium dissectum* and *H. chamaecistus* were sunk to ground level in pots in each population in August 2000. We counted eggs over the following month. Numbers of eggs on an individual plant were treated as single observations, considering the effects of host plant, population and host × population interaction in a two-way Schreirer–Ray–Hare test (equivalent to two-way non-parametric analysis of variance). Significant interactions reveal differences between populations in host choice. This test is overly conservative because some plant individuals of each plant species might never have been found by searching females, increasing count variation within each plant species. Therefore, we also used χ^2 tests, treating each egg laid as an independent observation—females can choose where to lay each egg independently.

For common environment rearing, eggs were obtained from wild-caught females from May to June 2000. Larvae from both populations were reared on the same mix of host plants at 18/6-h light/dark cycle (24 °C light phase; 20 °C dark phase). Emerging adults were released in July 2000, into a roughly 0.25-ha field that contained no natural host plants, into which had been sunk 432 plants each of *H. chamaecistus* and *G. molle*. Eggs could not be identified to population, so Cornish butterflies ($n = 162$ females) were released 10 days before Welsh butterflies ($n = 155$ females). Eggs were counted (and removed) just before release of the Welsh butterflies, and again at the end of the experiment. The first count contained only eggs from the Cornish butterflies, but a few Cornish females still survived when Welsh butterflies were released, so the Welsh result underestimates their true bias towards *H. chamaecistus*.

Bush crickets

Bush cricket wing morphologies were recorded (100% accuracy for *M. roeselii*; 98.25% for *C. discolor*, on the basis of detailed morphological measurements of a sample of 286 *C. discolor* specimens) in the field, from August to October 2000. The sexes did not differ in morphology frequencies. The year of the first record from each bush cricket population was obtained from refs 7–9 (also from J. Widgery, personal communication).

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Honeybee dances communicate distances measured by optic flow

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In honeybees, employed foragers recruit unemployed hive mates to food sources by dances from which a human observer can read the distance and direction of the food source[1]. When foragers collect food in a short, narrow tunnel, they dance as if the food source were much farther away. Dancers gauge distance by retinal image flow on the way to their destination. Their visually driven odometer misreads distance because the close tunnel walls increase optic flow[2]. We examined how hive mates interpret these dances. Here we show that recruited bees search outside in the direction of the tunnel at exaggerated distances and not inside the tunnel where the foragers come from. Thus, dances must convey information about the direction of the food source and the total amount of image motion *en route* to the food source, but they do not convey information about absolute distances. We also found that perceived distances on various outdoor routes from the same hive could be considerably different. Navigational errors are avoided as recruits and dancers tend to fly in the same direction. Reported racial differences in honeybee dances[1] could have arisen merely from differences in the environments in which these bees flew.

We began by setting up an 8-m tunnel pointing southwards, with its entrance 3 m from the hive. A fresh set of ten marked bees was trained to forage from a feeder placed at the far end of the tunnel (feeder distance 11 m). The mean waggle duration of tunnel dancers was 358 ms (Table 1). We then determined which distance corresponds to a waggle duration of 358 ms in bees that fly outdoors, outside the tunnel, to a feeder in the southern direction. Ten marked foragers were trained to fly to a feeder positioned successively at various distances due south, up to a maximum of 450 m. Several hundred dances of marked individuals returning from the feeder were videotaped at each position. The calibration curve relating waggle duration to feeder distance is shown in Fig. 1 (details in Table 1). According to this calibration, tunnel bees that waggle for 358 ms indicate an outdoor feeder 72 m south of the hive.
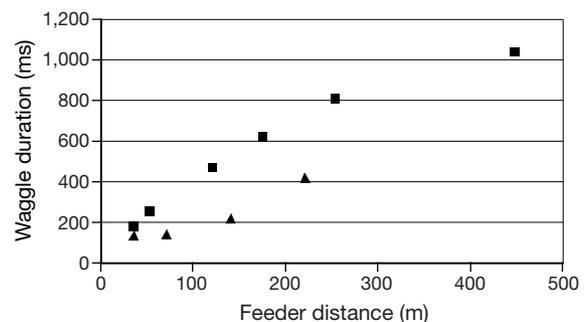

Figure 1 Distance calibration. Variation of waggle duration with feeder distance for an outdoor feeder positioned at various distances from the hive in the southern (squares) and northwestern direction (triangles).