reproducing individuals remain. Therefore, an interdependence between time to reproduction and at least one of longevity or fecundity is required to maintain diversity. The form of the trade-off determines the shape of the distribution of abundance of coexisting individuals across the trait space and the stability of that distribution (Box 1).

These results confirm the main features of the individual-based model—that the trade-off between time to reproduction and fecundity sustains the diversity in the community, and governs the form of the resulting abundance distribution. The trade-off is a simple but fundamental example of the link between individual- and community-scale features of the system. Its central role suggests that an explanation of community dynamics must incorporate an account of individual behaviour. Furthermore, by integrating more complex mechanisms encompassing uptake, competition and the effect of the nutritional status of an individual on its fecundity, the trade-off is also more amenable to measurement than the plethora of underlying finer-scale mechanisms. Although the differential equation model reproduced the qualitative results of the individual-based model, the predicted abundance distribution is not log-normal (except for very special choices of the form of the trade-off). An explicit account of space, as in the individual-based model, seems to be required to produce the log-normal form of the abundance distribution at equilibrium. Neither geneflow nor mutation are essential processes in the generation or maintenance of the log-normal form, although they are likely to modify the associated parameters (Box 1).

We have shown that significant diversity in traits can be sustained on small spatial domains, and that this diversity possesses the observed forms of community-scale patterns. This suggests that progress can be made using relatively small systems which are amenable to experimentation, and replacing species with individuals as the fundamental ecological accounting unit. ☐

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Sustainability of three apple production systems

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Escalating production costs, heavy reliance on non-renewable resources, reduced biodiversity, water contamination, chemical residues in food, soil degradation and health risks to farm workers handling pesticides all bring into question the sustainability of conventional farming systems[1–4]. It has been claimed[5,6], however, that organic farming systems are less efficient, pose greater health risks and produce half the yields of conventional farming systems. Nevertheless, organic farming became one of the fastest growing segments of US and European agriculture during the 1990s[7,8]. Integrated farming, using a combination of organic and conventional techniques, has been successfully adopted on a wide scale in Europe[9]. Here we report the sustainability of organic, conventional and integrated apple production systems in Washington State from 1994 to 1999. All three systems gave similar apple yields. The organic and integrated systems had higher soil quality and potentially lower negative environmental impact than the conventional system. When compared with the conventional and integrated systems, the organic system produced sweeter and less tart apples, higher profitability and greater energy efficiency. Our data indicate that the organic system ranked first in environmental and economic sustainability, the integrated system second and the conventional system last.

Organic management practices combine traditional conservation-minded farming methods with modern farming technologies but exclude such conventional inputs as synthetic pesticides and fertilizers, instead putting the emphasis on building up the soil with compost additions and animal and green manures, controlling pests naturally, rotating crops and diversifying crops and livestock[10]. Organic farming systems in the US range from strict closed-cycle systems that go beyond organic certification guidelines by limiting, as much as possible, external inputs to more standard systems that simply follow organic certification guidelines. Integrated farming systems reduce the use of chemicals by integrating organic and conventional production methods.

Just because a system is organic or integrated does not ensure its sustainability; nor does sustainability, an inherently complex

Table 1 Soil quality ratings of three apple production systems

Soil quality functions	Year	Organic	Conventional	Integrated
Accommodate water entry	1998	0.21a	0.16b	0.23a
	1999	0.21a	0.16b	0.20ab
Facilitate water movement and availability	1998	0.21a	0.21a	0.24b
	1999	0.19a	0.18a	0.20a
Resist surface structure degradation	1998	0.23ab	0.19a	0.24b
	1999	0.21a	0.15b	0.21a
Sustain fruit quality and productivity	1998	0.24a	0.23ab	0.21b
	1999	0.22a	0.21a	0.21a
Total soil quality rating	1998	0.88a	0.78b	0.92a
	1999	0.83a	0.70b	0.81a

Soil quality functions (each with a maximum value of 0.25) were assigned values on the basis of soil properties analysed and then added to determine soil quality ratings for each system. A total soil quality rating of 1.0 represents soil conditions optimal for both fruit production and environmental quality. Differences between values in a year followed by different letters are significant at the 0.05 level (least significant difference).

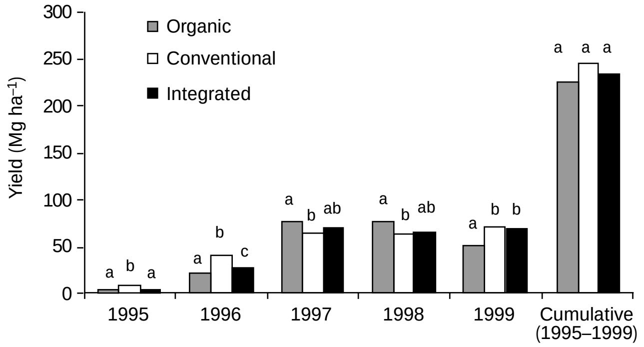

Figure 1 Fruit yields of three apple production systems. Differences between values in a year followed by different letters are significant at the 0.05 level (least significant difference).

concept[11], readily lend itself to quantification. To be sustainable, a farm must produce adequate yields of high quality, be profitable, protect the environment, conserve resources and be socially responsible in the long term[12]. But under conventional economic systems, market and social forces can change the viability of a production system independent of its environmental sustainability[13]. It has been proposed that ecological and economic systems should be linked so that ecosystem services are accounted for in commercial markets, thereby making sustainable land management a prerequisite for economic sustainability[14,15].

A crucial step in developing such ecological–economic links is to assess the effects of agricultural systems on specific, measurable properties that are important indicators of sustainability. We measured the effects of an organic, a conventional and an integrated apple production system on the sustainability indicators of soil quality, horticultural performance, orchard profitability, environmental quality and energy efficiency. Perennial food crops such as apples may prove to be more sustainable to produce over the long term than annual crops[16], and they currently comprise a significant portion of the world's agricultural production. For example, globally, nearly 5.6 million hectares of apples were harvested in 2000 (ref. 17). In the USA alone, apples and other high-value perennial food crops constituted 16% of the total value of food crops in 1998 (ref. 18).

We measured soil quality by analysing physical, chemical and biological soil properties and incorporating the data into a soil quality index[19]. Soil quality is the capacity of a soil to sustain biological productivity, maintain environmental quality and promote plant and animal health[20]. We evaluated soil quality in terms of four soil functions: accommodating water entry; accommodating water movement and availability; resisting surface structure degradation; and supporting fruit quality and productivity. Soil quality ratings in 1998 and 1999 for the organic and integrated systems were significantly higher than those for the conventional system (Table 1), largely owing to the addition of compost and mulch in 1994 and 1995. Organic matter has a profound impact on soil quality, enhancing soil structure and fertility and increasing water infiltration and storage[21]. Because of poorer ability to accommodate water entry and to resist surface structure degradation, the conventional system (no organic amendments added) scored lowest overall in soil quality.

We assessed horticultural performance by measuring fruit yields, size and grade; tree growth; leaf and fruit mineral contents; fruit maturity; and consumer taste preference. There were no observable differences in pests, disease or physiological disorders among plots during each growing season. Differences in annual fruit yields were inconsistent among the three systems (Fig. 1). Cumulative yields were similar for all three systems. In 1995–1997, fruit size was similar across systems, except in 1996 when apples were larger in the integrated system (see Fig. A1 in Supplementary Information). In 1998 and 1999, the organic system produced smaller fruit (see Figs A1 and A2 in Supplementary Information). In 1995–1997, all marketed fruit produced from the three systems was sold for processing because it was downgraded primarily owing to skin russetting, a physiological skin disorder that reduces the fruit's visual appeal but not its taste or other attributes. (Although russetted Golden Delicious apples are not sold as fresh fruit in the US marketplace, Italy domestically markets a fully russetted Golden Delicious apple, and in the world market fully russetted Bosc pears are preferred to non-russetted ones.) The low landscape position of the experimental site in the orchard resulted in early season cool, humid conditions that contributed to the unusually high level of russetting. Fruit damage due to other physiological disorders, pests and diseases were minimal and equal for each of the three systems. In 1998 and 1999, marketable fruit not graded as Washington Extra Fancy or Fancy was sold for processing (see Table A1 in Supplementary Information).

Tree growth was similar in all three systems (see Fig. A3 in Supplementary Information). Although there were some differences in leaf nutrient contents among the three systems, analyses indicated satisfactory levels of nutrients[22,23] (see Table A2 in Supplementary Information). Fruit tissue nutrient analyses indicated

Table 2 Gross receipts, total costs and net returns of apple production systems

Year	Enterprise budget	Org ($ ha^{-1})	Con ($ ha^{-1})	Int ($ ha^{-1})	Org ($ ha^{-1})	Con ($ ha^{-1})	Int ($ ha^{-1})
			Measured fruit quality			Non-russetted fruit quality	
1994	Gross receipts	0	0	0	0	0	0
	Total costs	23,486	20,702	23,740	23,486	20,702	23,740
	Net returns	–23,486	–20,702	–23,740	–23,486	–20,702	–23,740
1995	Gross receipts	261a	826b	272a	610a	2,353b	754a
	Total costs	12,242a	9,409b	9,381b	12,242a	9,409b	9,381b
	Net returns	–11,981a	–8,583b	–9,109c	–11,632a	–7,056b	–8,627c
1996	Gross receipts	2,482a	4,559b	3,294c	5,825a	13,001b	9,149c
	Total costs	11,608a	11,917ab	12,074b	11,608a	11,917ab	12,074b
	Net returns	–9,126a	–7,358b	–8,780c	–5,784a	1,084b	–2,925c
1997	Gross receipts	12,406a	7,438b	7,983b	38,162a	21,266b	22,214b
	Total costs	17,788a	15,745b	15,947b	17,756a	15,607b	15,904b
	Net returns	–5,381a	–8,307b	–7,964b	20,405a	5,658b	6,310b
1998	Gross receipts	16,485a	8,967b	9,211b	37,442a	21,691b	21,640b
	Total costs	19,074a	17,863a	17,906a	19,637a	17,682b	18,143ab
	Net returns	–2,589a	–8,896b	–8,695b	17,805a	4,009b	3,497b
1999	Gross receipts	24,503a	21,846a	21,438a	25,821a	23,653a	22,593a
	Total costs	18,714a	20,188b	20,011ab	16,219a	18,219b	18,326b
	Net returns	5,789a	1,658a	1,428a	9,602a	5,434a	4,267a

Measured from organic (Org), conventional (Con) and integrated (Int) apple production systems under measured fruit quality conditions (with excessive skin russetting) and non-russetted fruit quality conditions (with 15% cullage). Differences between values in a year and budget category followed by different letters are significant at the 0.05 level (least significant difference). No statistics were generated for 1994 data because costs were the same for each replicate.

some inconsistent differences (see Table A3 in Supplementary Information).

Mechanical analysis of fruit firmness at harvest and after storage in 1998 and 1999 showed that organic fruit was firmer (a positive consumer attribute for apples) than or as firm as conventional and integrated fruit (see Table A4 in Supplementary Information). Ratios of soluble solids (sugar) content to acidity (tartness), an indication of sweetness, were most often highest in organic fruit. These data were confirmed in taste tests by untrained sensory panels that found the organic apples to be sweeter after six months of storage than conventional apples and less tart at harvest and after six months storage than conventional and integrated apples (see Table A5 in Supplementary Information). The same taste tests, however, could not discern any difference in firmness among apples in the three systems at harvest or after storage. Taste tests also indicated that the integrated apples had a better flavour after six months storage but found no differences among organic, conventional and integrated apples in texture or overall acceptance.

Enterprise budgets were generated each year to calculate net returns from total costs and gross receipts. Receipts for the integrated system were estimated using prices for conventionally produced fruit, as unlike organic fruit there was no price premium for integrated fruit. Receipts for the organic system were estimated using prices for conventionally produced fruit in the first three years (1994–1996), the number of years necessary to convert from conventional to certified organic. The price premium to the grower for each grade of organic fruit in the next three years (1997–1999) averaged 50% above conventional prices.

The three systems did not show a net annual profit until 1999 under measured fruit quality conditions (with skin russetting) (Table 2). When we adjusted the economic analysis by eliminating the effects of russetting but maintained the estimated crop loss of 15% due to other factors and the measured size, grade and firmness of fresh fruit in this study, the organic system was more profitable than the conventional and integrated systems in 1997 and 1998. Higher production costs for the organic system in 1995 and 1997 (under measured and non-russetted fruit quality conditions) were largely due to differences in weed control practices, fruit thinning and compost applications. Production costs in 1999, however, were significantly lower for the organic system than for the other two systems due to reduced carryover interest costs resulting from faster repayment of the original investment.

The breakeven point, when cumulative net returns equal cumulative costs, can vary depending on several factors, such as fruit prices, input costs, yields and fruit quality. The breakeven point in this study is projected to occur nine years after planting (in 2002) for the organic system under measured fruit quality conditions. The conventional and integrated systems would break even 15 and 17 years after planting, respectively, under measured conditions. Under non-russetted fruit quality conditions, the breakeven point would occur six, eight and nine years after planting for the organic, conventional and integrated systems, respectively. Assuming similar non-russetted fruit quality conditions, estimated breakeven points for conventional apple orchards in central Washington range from 8 to 11 years from planting[24].

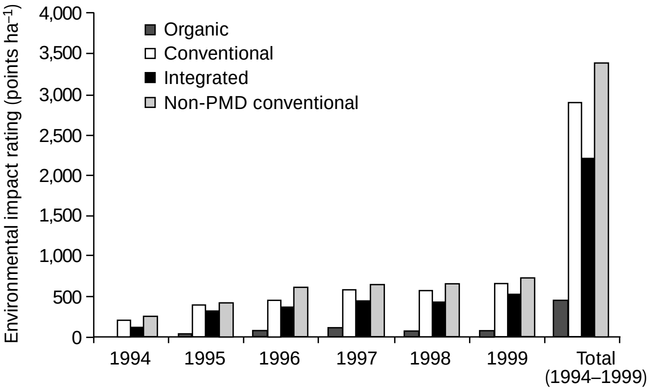

Figure 2 Environmental impact ratings of four apple production systems: Organic, conventional, integrated and non-PMD conventional. Higher ratings indicate greater potential for negative environmental impact. For a listing of chemicals used and their impact ratings for the four production systems, see Table A6 in Supplementary Information.

Without price premiums for organic fruit, the conventional system would break even first, the integrated second and the organic third under measured or non-russetted fruit quality conditions. For breakeven points of the organic and integrated systems to occur in the same year as the conventional system, price premiums of 12% for the organic system and 2% for the integrated system would be necessary under measured fruit quality conditions. Under non-russetted fruit quality conditions, premiums of 14% for the organic system and 6% for the integrated system would be necessary to match the breakeven point of the conventional system.

We assessed the environmental impact of the three production systems by using a rating index[25] employed by scientists and growers to determine the potential adverse impact of pesticides and fruit thinners, including naturally occurring certified organic products. The higher the rating, the greater the negative impact. As only 35% of conventional Washington apple growers use pheromone-mating disruption (PMD), an environmentally benign biological control used in our conventional treatment, we also included a conventional system in which synthetic pesticides were used in place of PMD. The total environmental impact rating of our conventional system was 6.2 times that of the organic system, whereas the integrated system rating was 4.7 times greater and the non-PMD conventional system rating was 7.7 times greater (Fig. 2).

Energy accounting was divided into inputs (labour, fuel, fertilizers and so on), output (yield) and output/input ratios (energy efficiency). Cumulative energy inputs and output for the six-year study period were lower for the organic system than for the conventional and integrated systems (Table 3). The output/input ratio for the organic system during the six-year study period, however, was 7% greater than that for the conventional system and 5% greater than that for the integrated system, making the organic system the most energy efficient.

Our results show that organic and integrated apple production systems in Washington State are not only better for soil and the environment than their conventional counterpart but have comparable yields and, for the organic system, higher profits and greater energy efficiency. Although crop yield and quality are important products of a farming system, the benefits of better soil and environmental quality provided by the organic and integrated

Table 3 Cumulative energy assessment

	Organic	Conventional	Integrated
Labour (h ha^{-1})	2,921	2,008	2,147
Labour (MJ ha^{-1})	2,337	1,607	1,718
Machinery (MJ ha^{-1})	73,974	73,560	73,560
Fuel (MJ ha^{-1})	173,400	182,919	182,919
Electricity (MJ ha^{-1})	10,794	10,794	10,794
Fertilizer (MJ ha^{-1})	311*	16,255	8,901*
Insecticide (MJ ha^{-1})	22,159	42,313	40,375
Fungicide (MJ ha^{-1})	18,023	12,922	12,855
Weed control (MJ ha^{-1})	141	31,931	13,350
Infrastructure (MJ ha^{-1})	144,188	144,188	144,188
Total input (MJ ha^{-1})	445,328	516,489	488,661
Total output (MJ ha^{-1})	526,544	570,745	550,076
Output/input (MJ MJ^{-1})	1.18	1.11	1.13

*This includes composted poultry manure from a local commercial composting facility. The poultry facility from which the raw manure was obtained is assumed to be responsible for the energy charges required for composting the waste; consequently only energy requirements for transporting the compost to the orchard (63 MJ Mg^{-1}) are charged against the organic and integrated systems[30]. For details on fertilizer inputs, see Table A7 in Supplementary Information.

production systems are equally valuable and usually overlooked in the marketplace. Such external benefits come at a financial cost to growers. Currently, growers of more sustainable systems may be unable to maintain profitable enterprises without economic incentives, such as price premiums or subsidies for organic and integrated products, that value these external benefits. Equally important, upon incorporation of external costs into economic assessments of farming systems, we may find that many currently profitable farming systems are uneconomical and therefore unsustainable. The challenge facing policymakers is to incorporate the value of ecosystem processes into the traditional marketplace, thereby supporting food producers in their attempts to employ both economically and environmentally sustainable practices. □

Methods

Study area

In May 1994, we planted four replicate plots for each of the three apple production systems with 'Golden Delicious' apples (*Malus* × *domestica* Borkh.) on EMLA.9 rootstocks on 1.7 ha in a randomized complete block design. The experiment was part of a 20-ha commercial apple orchard in the Yakima Valley, Washington. See Fig. A4 of Supplementary Information for plot layout and orchard system.

Farming systems

In cooperation with the farmers, professional consultants and extension agents, we chose appropriate management practices for the three systems (see Table A7 in Supplementary Information). The organic system included compost and foliar sprays. In the first three years (1994–1996), bark mulch and landscape fabric controlled weeds; thereafter, cultivation and mowing were used for weed control. Organically certified biological controls, including applications of *Bacillus thuringiensis* and PMD to control codling moth (*Cydia pomonella* L.), were used for pest management. Fruit thinning was by hand. The conventional system included synthetic soil fertilizers and foliar sprays, pesticides, chemical fruit thinners and PMD. The integrated system used both compost and synthetic fertilizers and controlled weeds with both bark mulch and herbicides. Pest management and fruit thinning were similar to those of the conventional system. The three systems had similar total soil nitrogen inputs. Pests, diseases and physiological disorders were monitored throughout each growing season by the farmers and professional consultants, who recommended organic, conventional or integrated treatments for their control.

Soil analyses

All soil samples were taken from the inner two rows of each experimental plot to minimize edge effects, excluding the first 20 trees from each end of these sample rows. Samples were collected midway between trees within tree rows. In 1998 and 1999, soil analyses included bulk density, water content, total nitrogen, nitrate-nitrogen, extractable phosphorus, cation-exchange capacity, pH, electrical conductivity, organic carbon content, aggregate stability, microbial biomass carbon and nitrogen, and earthworm populations. Details of analytical procedures are described elsewhere[17].

Horticultural performance

All components of horticultural performance were measured from trees, leaves and fruit sampled in the middle two rows of each plot, excluding the first 20 trees from each end of these sample rows. We recorded yields and size (average mass) of fruit at harvest in 1995–1999. The proportions of fruit suitable only for processing (due to small size or defects) and fruit suitable for fresh market and divided by grade were also recorded. Grading of fresh fruit was based on Washington State's apple industry standards[26]. We used trunk cross-sectional area to estimate unit tree growth. We analysed leaf mineral contents (N, P, K, S, Ca, Mg, B, Zn, Mn, Cu and Fe) in 1994–1999 from pooled samples of mid-shoot leaves taken randomly from each plot in midsummer. We analysed fruit flesh mineral contents (N, P, K, Ca, Mg, B and Zn) in 1995 and 1997–1999 from pooled samples of uniformly sized fruits taken three weeks before harvest. Mineral analyses were carried out according to standard methods[23]. We assessed fruit maturity parameters, including flesh firmness, soluble solids and acidity, according to standard procedures[27] at harvest and after three and six months of controlled atmosphere storage in 1998 and 1999. Untrained sensory panels were used to determine preferences for overall acceptance, texture, flavour, firmness, sweetness and tartness of 1999 fruit from each production system and storage treatment.

Economic analyses

We calculated gross receipts using farmgate prices paid by packing houses to farmers for apples sold at harvest or after storage. Prices for the specific size, grade and firmness of 'Golden Delicious' organic and conventional apples from our study were based on prices from *Washington Growers Clearing House Bulletins* and fruit packing houses in Washington State. Total costs included non-harvest variable costs (fertilizers, pesticides, fuel, labour and water), harvest variable costs (picking, grading, packing and storage) and fixed costs (machinery, interest and taxes). Projected returns for 2000 and beyond were estimated from average fruit sizes (1998–1999) and yields (1997–1999) for each treatment, assuming a 15% cullage rate for all three treatments and a 50% price premium for organic fruit.

Environmental impact assessment

We determined environmental impact ratings for each farming system using an index developed by Stemilt Growers, Inc. of Wenatchee, Washington, as part of their 'Responsible Choice' program[25]. Similar to Cornell University's Environmental Impact Quotient[28] but updated to include fruit thinners and certified organic products, the index takes into account chemical efficacy, potential worker and consumer exposure, leaching potential, soil sorption index, chemical half-life and the effects of chemicals on beneficial organisms, all based on toxicological studies and chemical characteristics of each product. The active ingredient of each pesticide and the dose and frequency of application were used to calculate the environmental impact ratings.

Energy use

Energy use for each production system was calculated from energy data specific to agricultural production[29,30].

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The concepts of 'sameness' and 'difference' in an insect

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Insects process and learn information flexibly to adapt to their environment. The honeybee *Apis mellifera* constitutes a traditional model for studying learning and memory at behavioural, cellular and molecular levels[1]. Earlier studies focused on elementary associative and non-associative forms of learning determined by either olfactory conditioning of the proboscis extension reflex[1] or the learning of visual stimuli[2] in an operant context. However, research has indicated that bees are capable of cognitive performances that were thought to occur only in some vertebrate species. For example, honeybees can interpolate visual information[3], exhibit associative recall[4,5], categorize visual information[6–8] and learn contextual information[9]. Here we show that honeybees can form 'sameness' and 'difference' concepts. They learn to solve 'delayed matching-to-sample' tasks, in which they are required to respond to a matching stimulus, and 'delayed non-matching-to-sample' tasks, in which they are required to respond to a different stimulus; they can also transfer the learned rules to new stimuli of the same or a different sensory modality. Thus, not only can bees learn specific objects and their physical parameters, but they can also master abstract inter-relationships, such as sameness and difference.

An important cognitive capacity is the ability to learn relationships between stimuli. In vertebrates, the capacity to acquire sameness–difference concepts has been studied using two experimental procedures, the matching task and the oddity task. A variation of the former is the 'delayed matching-to-sample' task, in which an animal is presented with a 'sample' and subsequently with two or more secondary stimuli, one of which is identical to the sample. The animal is required to respond to the stimulus just encountered. The 'delayed non-matching-to-sample' task is a variation of the oddity task. The procedure is similar to the matching-to-sample task except that the animal is required to respond to the stimulus that is different from the sample. In both cases, broadly construed sameness and difference concepts are shown only if the animal exhibits positive transfer to a completely new set of stimuli, which it had not experienced during training.

We trained honeybees, *A. mellifera*, in a delayed matching-to-sample paradigm to examine whether they could form a concept of sameness. Training was carried out using a Y-maze placed close to a laboratory window. Each bee entered the maze by flying through a hole in the middle of an entrance wall. At the entrance, the bee encountered the sample stimulus. The sample was one of two different stimuli, A or B, alternated in a pseudo-random sequence. The entrance led to a decision chamber, where the bee could choose one of two arms. Each arm carried either stimulus A or stimulus B as secondary stimulus. The bee was rewarded with sucrose solution only if it chose the stimulus that was identical to the sample. If the bees managed to learn the original discrimination, they were presented with new sample and secondary stimuli in 'transfer tests': the bees had to choose between stimuli C and D, when the sample was either C or D.

Four experiments were carried out, each by training a fresh group of bees. In experiment 1, A and B were colours, whereas C and D were vertical and horizontal black and white gratings. In experiment 2, A and B were gratings, whereas C and D were colours. In experiment 3, A and B were radial and circular gratings, whereas C and D were oriented linear gratings. In experiment 4, A and B were odours, whereas C and D were colours. In all experiments the stimuli chosen were well distinguished by the bees, as indicated by preliminary investigations.

The results for experiments 1 and 2 are shown in Fig. 1. In experiment 1, the bees were trained to match a given colour (blue versus yellow). The acquisition curve showed a significant improvement during training (Fig. 1a: $P < 0.0001$): bees preferred the colour that was identical to the sample, independently of the sample

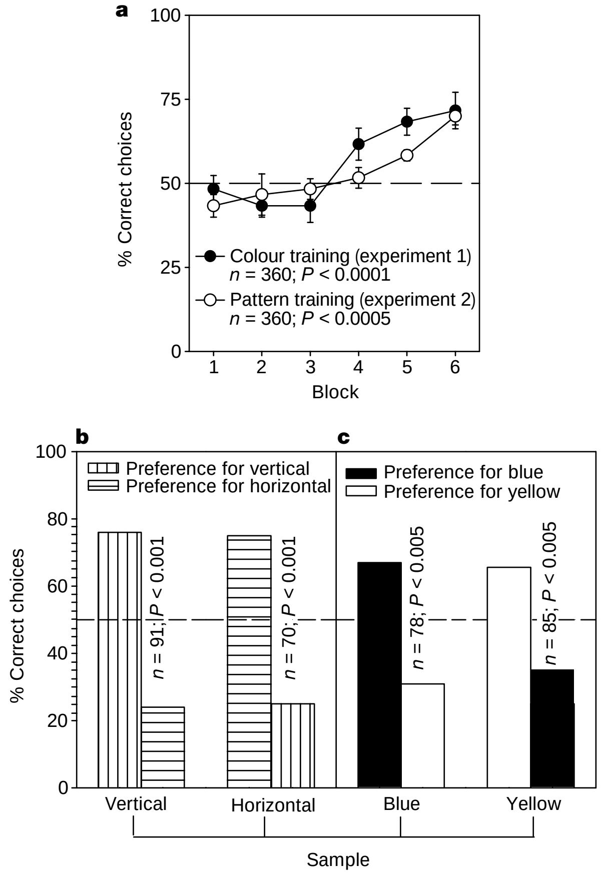

Figure 1 Experiments 1 and 2. **a**, Learning performance of bees during training on colours (experiment 1) and on vertical and horizontal gratings (experiment 2). Data show the results of blocks of ten consecutive training visits for each experiment. **b**, **c**, Results of transfer tests. **b**, Transfer tests with patterns (colour training). In experiment 1, bees trained on the colours were tested on the gratings. **c**, Transfer tests with colours (pattern training). In experiment 2, bees trained on the gratings were tested on the colours. *n*, number of choices evaluated.