behaviour of the various complexes is the same, but they exhibit profoundly different emission properties, we conclude that the specific nature of the bridge is the key to the colour switching phenomenon. It is well known that electron conduction, stabilization and delocalization on such bridging ligands depend on the geometry, energetics and structural features of the molecules[19-21]. Furthermore, use of different polymers with a higher-energy LUMO level (the HOMO level is chosen to be the same)—so that electron transfer mediated by the Ru complex cannot populate their excited state—did not result in green emission at reverse bias.

Symmetric devices with Au as anode and cathode have symmetric emission properties (that is, they show red emission at both forward and reverse bias), clearly indicating that an asymmetry in the device's charge injection behaviour is needed for the differentiation of the two possible mechanisms of light emission in the $[Ru(ph)_4-Ru]^{4+}$ PPV system. As the work functions of the ITO and Au contacts are energetically comparable, and the red/green switching behaviour is also seen when Au is replaced by Al, influences other than simple energetics must also have a role in allowing the stepwise electron transfer at reverse bias; we intend to study these influences in greater detail in the near future. □

1. Baldo, M. A. et al. Highly efficient phosphorescent emission from organic electroluminescent devices. Nature 395, 151–154 (1998).
2. Buda, M., Kalyuzhny, G. & Bard, A. J. Thin-film solid-state electroluminescent devices based on tris(2,2'-bipyridine)ruthenium(II) complexes. J. Am. Chem. Soc. 124, 6090–6098 (2002).
3. Wu, A., Yoo, D., Lee, J.-K. & Rubner, M. F. Solid-state light emitting devices based on the tris-chelated ruthenium(II) complex. 3. High efficiency devices via a layer-by-layer molecular-level blending approach. J. Am. Chem. Soc. 121, 4883–4891 (1999).
4. Faulkner, L. R. & Bard, A. J. Electroanalytical Chemistry (ed. Bard, A. J.) 1–95 (Marcel Dekker, New York, 1977).
5. Rudmann, H., Shimada, S. & Rubner, M. F. Solid-state light emitting devices based on the tris-chelated ruthenium(II) complex. 4. High-efficiency light-emitting devices based on derivatives of the tris(2,2'-bipyridyl) ruthenium(II) complex. J. Am. Chem. Soc. 124, 4918–4921 (2002).
6. Handy, E. S., Pal, A. J. & Rubner, M. F. Solid-state light emitting devices based on the tris-chelated ruthenium(II) complex. 2. Tris(bipyridyl)ruthenium(II) as a high-brightness emitter. J. Am. Chem. Soc. 121, 3525–3528 (1999).
7. Elliott, C. M., Pichot, F., Bloom, C. J. & Rider, L. S. Highly efficient solid-state electrochemically generated chemiluminescence from ester-substituted trisbipyridineruthenium(II)-based polymers. J. Am. Chem. Soc. 120, 6781–6784 (1998).
8. Juris, A. et al. Ru(II) polypyridine complexes: photophysics, photochemistry, and chemiluminescence. Coord. Chem. Rev. 84, 85–277 (1988).
9. Pei, Q., Yu, G., Zhang, C., Yang, Y. & Heeger, A. J. Polymer light-emitting electrochemical cells. Science 269, 1086–1088 (1995).
10. De Cola, L. & Belser, P. Photoinduced energy and electron transfer processes in rigidly bridged dinuclear Ru/Os complexes. Coord. Chem. Rev. 177, 301–346 (1998).
11. Maness, K. M., Terrill, R. H., Meyer, T. J., Murray, R. W. & Wightman, R. M. Solid-state diode-like chemiluminescence based on serial, immobilized concentration gradients in mixed-valent poly[Ru(vbpy)₃](PF₆)₂ films. J. Am. Chem. Soc. 118, 10609–10616 (1996).
12. Luttmer, J. D. & Bard, A. J. Electrogenerated chemiluminescence. 38. Emission intensity-time transients in the tris(2,2'-bipyridine)ruthenium(II) system. J. Phys. Chem. 85, 1155–1159 (1981).
13. deMello, J. C., Tessler, N., Graham, S. C. & Friend, R. H. Ionic space-charge effects in polymer light-emitting diodes. Phys. Rev. B 57, 12951–12963 (1998).
14. Brédas, J. L., Chance, R. R. & Silbey, R. Comparative theoretical study of the doping of conjugated polymers: polarons in polyacetylene and polyparaphenylene. Phys. Rev. B 26, 5843–5854 (1982).
15. Berggren, M. et al. Light-emitting diodes with variable colours from polymer blends. Nature 372, 444–446 (1994).
16. Yang, Y. & Pei, Q. Voltage controlled two colour light-emitting electrochemical cells. Appl. Phys. Lett. 68, 2708–2710 (1996).
17. Hamaguchi, M. & Yoshino, K. Color-variable electroluminescence from multilayer polymer films. Appl. Phys. Lett. 69, 143–145 (1996).
18. Tasch, S. & Brandstätter, C. Red-green-blue light emission from a thin film electroluminescence device based on parahexaphenyl. Adv. Mater. 9, 33–36 (1997).
19. DeCola, L. & Belser, P. Electron Transfer in Chemistry (ed. Balzani, V.) 97–136 (Wiley-VCH, Weinheim, 2001).
20. Yaliraki, S. N., Kemp, M. & Ratner, M. A. Conductance of molecular wires: influence of molecule-electrode binding. J. Am. Chem. Soc. 121, 3428–3434 (1999).
21. Pourtois, G., Beljonne, D., Cornil, J., Ratner, M. A. & Brédas, J. L. Photoinduced electron-transfer processes along molecular wires based on phenylenevinylene oligomers: a quantum-chemical insight. J. Am. Chem. Soc. 124, 4436–4447 (2002).

....

Fingerprints of global warming on wild animals and plants

Terry L. Root*, Jeff T. Price†, Kimberly R. Hall‡, Stephen H. Schneider§, Cynthia Rosenzweig‖ & J. Alan Pounds¶

* Center for Environmental Science and Policy, Institute for International Studies, Stanford University, Stanford, California 94305, USA
† American Bird Conservancy, 6525 Gunpark Drive, Suite 150-146, Boulder, Colorado 80301, USA
‡ Department of Fisheries and Wildlife, 13 Natural Resources Building, Michigan State University, East Lansing, Michigan 48824-1222, USA
§ Department of Biological Sciences & Institute for International Studies, Stanford University, Stanford, California 94305, USA
‖ National Aeronautics and Space Administration, Goddard Institute for Space Studies, 2880 Broadway, Suite 750, New York, New York 10025, USA
¶ Golden Toad Laboratory for Conservation, Monteverde Cloud Forest Preserve and Tropical Science Center, Santa Elena, Puntarenas 5655, Box 73, Costa Rica

....

Over the past 100 years, the global average temperature has increased by approximately 0.6 °C and is projected to continue to rise at a rapid rate[1]. Although species have responded to climatic changes throughout their evolutionary history[2], a primary concern for wild species and their ecosystems is this rapid rate of change[3]. We gathered information on species and global warming from 143 studies for our meta-analyses. These analyses reveal a consistent temperature-related shift, or 'fingerprint', in species ranging from molluscs to mammals and from grasses to trees. Indeed, more than 80% of the species that show changes are shifting in the direction expected on the basis of known physiological constraints of species. Consequently, the balance of evidence from these studies strongly suggests that a significant impact of global warming is already discernible in animal and plant populations. The synergism of rapid temperature rise and other stresses, in particular habitat destruction, could easily disrupt the connectedness among species and lead to a reformulation of species communities, reflecting differential changes in species, and to numerous extirpations and possibly extinctions.

Many studies have examined biological changes in relation to climatic change[4,5], but generally they are concentrated in particular regions or examine a limited set of taxa. To test whether or not a coherent pattern exists across regions and taxa that is consistent with predictions of expected change, we used two types of meta-analyses on these studies: vote counting and the regression-slope model (see Methods). One advantage of meta-analyses is that a broad spectrum of findings can be combined, including those for which statistical significance has not been shown. We examined thousands of articles, including those assembled by Working Group II of the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC TAR WGII)[6]. Of these, we included in our analyses only those that (1) examined a span of at least 10 years, (2) found that a trait of at least one species shows change over time, and (3) found either a temporal change in temperature at the study site or a strong association between the species trait and site-specific temperature. Because we were looking for trends, we also excluded studies examining climatic cycles, such as North Atlantic Oscillation and El Niño/Southern Oscillation. We divided 143 studies that met our criteria into two 'tiers': those demonstrating a statistically significant trend for at least one species examined (tier 1, most of which were used as the methodological basis for conclusions in the IPCC TAR WGII[6,7]) and those in which statistical significance was not shown by the study's authors (tier 2), usually because no statistical tests were applied. We performed our analyses for each tier taken separately and for the two combined. Appendices 1 and 2 of the Supplementary Information provide the data and citations

Table 1 **Summary statistics for meta-analyses**

	Significant species	Nonsignificant species	Combined species
Number of species changing	586	882	1,468
Number changing in expected direction	482	708	1,190
Percentage in expected direction	82.3%	80.4%	81.1%
90% confidence interval for percentage in expected direction	73.4–88.6%	70.5–87.4%	74.2–86.5%
Effect size (δ)	−0.09	−0.23	−0.23
90% confidence interval for δ	−0.12 to −0.06	−0.30 to −0.14	−0.29 to −0.17
Standard error for δ	0.0004	0.0023	0.0014
Correlation coefficient (r)	−0.05	−0.12	−0.12
90% confidence interval for r	−0.06 to −0.03	−0.16 to −0.07	−0.15 to −0.09
Standard error for r	0.0002	0.0012	0.0007

A breakdown of values for those species or groups of species that were found, in the studies examined, to have statistically significant trends for various traits and for those that were not statistically significant. In addition, values are listed for the combination of these two categories of species or species groups.

for all of the studies used in our meta-analyses.

We focused on temperature change and ignored other climatic changes, such as precipitation, because the biological effects of temperature are often better understood for most of the organisms examined. Explicitly considering drought in our analyses would have allowed us to include many more studies, particularly from the Southern Hemisphere, but attributing local droughts to globally coherent patterns of climatic changes can often be difficult. We do, however, recognize that factors influencing populations interact in complex ways: temperature can exert its influence, for example, by affecting moisture availability.

Four types of change in species' traits due to warming may be possible. First, the density of species may change at given locations, and the ranges of species may shift either poleward or up in elevation as species move to occupy areas within their metabolic temperature tolerances. Second, because many natural history traits of species are triggered by temperature-related cues, changes could occur in the timing of events (phenology), such as migration, flowering or egg laying. Third, changes in morphology, such as body size, and behaviour may occur. Fourth, genetic frequencies may shift.

Attributing observed changes in populations of plants and animals to climatic change, specifically temperature increases, is possible because we expect the trends created by the large-scale pressure of global warming to show widespread, predictable and concordant patterns of change. In addition, we expect these changes to be concentrated in areas where temperature changes are largest (that is, at higher latitudes and altitudes) and for changes to be less evident elsewhere. Climate change is only one of a long list of pressures that influence the distributions and health of populations, as well as traits such as timing of activities and processes. These other pressures (for example, habitat modification, pollinator loss and exotic species introductions) often result in localized (often around centres of human populations) or multidirectional patterns of alterations to populations of species. To document a strong role for climate change in explaining many of the observed changes in

animal and plant populations, we looked for repeated examples occurring over long temporal and broad spatial scales that showed unidirectional changes predicted by our understanding of the physiological tolerances of species to temperature. The predicted result, or fingerprint, of an underlying consistent shift in a large-scale pattern shown by many species around the globe, coupled with an understanding of the possible causal mechanisms, provides confidence in attributing observed species changes to climatic change. The 85 tier 1 studies and 58 tier 2 studies found strong changes occurring around the globe in various types (taxa) of animals and plants (see Supplementary Information). The meta-analyses we used to analyse the findings of these studies were the vote-counting method[8] and the regression-slope model[9]. We applied the vote-counting method to three different categories of data: 1) the 587+ species or groups of species ('+' because some studies do not provide numbers) in tier 1 (see Methods) that show statistically significant change; 2 the 886+ species or groups of species in both tier 1 and tier 2 that show statistically nonsignificant change or where the significance was unknown; and 3) the combined species (1,473+) showing change. For all three categories, the percentage of species changing in the expected direction was around 81% with a 90% confidence interval ranging from 71% to 89% (Table 1). The meta-analysis results of effect sizes and correlation coefficients were statistically different from zero ($P < 0.05$), which means that we can reject the null hypothesis of equal change in both the expected and opposite directions. Consequently, even this fairly low-powered vote-counting meta-analysis indicates that most changes are consistent with our understanding of how temperature change influences various traits of a variety of species and populations from around the globe. Hence, we can safely state that there has probably been a discernible impact of recent global warming on animals and plants.

The actual amount of change shown can be determined for those studies that examined shifts in spring phenologies. The 61 studies that investigated the change in timing of events occurring within the
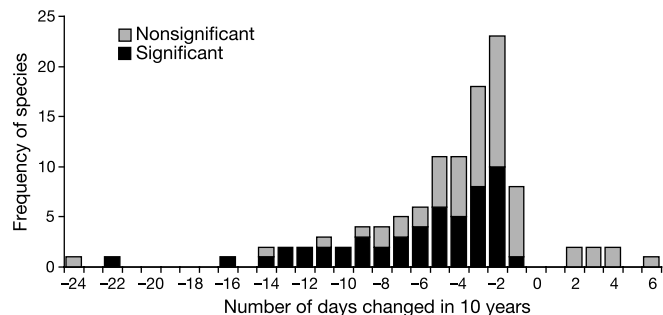

Figure 1 Frequency distribution of species and groups of species (see text) with a temperature-related trait changing by number of days in 10 years. No data were tabulated for species showing zero days changing in ten years (see Methods).
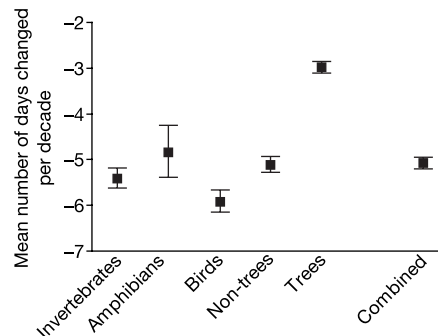

Figure 2 Means ± s.e.m. of days changed for the given groups of species. The 'Combined' category includes only those species tallied in the groups of species (that is, data for the one mammal, two fish and zooplankton are not included).

past 50 years examined a total of 694 species or groups of species. Our meta-analyses of these species indicate that over an average decade within the past 50 years, a statistically significant change towards earlier timing of spring events has occurred. The number of days changed per decade for a given species or species group ranges from 24 days earlier per decade for the breeding of North American common murre (*Uria aalge*) to 6.3 days per decade later for the breeding of North American Fowler's toad (*Bufo fowlen*) (Fig. 1). Using the regression-slope model[9] (see Methods), we found that the estimated mean number of days changed per decade for all species showing change in spring phenology is 5.1 days earlier (s.e.m. ± 0.1; Fig. 1). When the data are grouped by statistical significance, the estimated mean of the species with nonsignificant findings is closer to zero than that for species with significant findings (−3.4 ± 0.1; −6.9 ± 0.1, respectively; negative numbers indicate an earlier shift). The latter mean is understandably earlier than the former, given that regression analysis is more powerful at discriminating steeper slopes than shallower ones. However, all three estimated averages are statistically significantly different from zero, which means that these species are all showing a marked shift towards earlier spring events.

Given that higher latitudes have warmed more than the lower latitudes in the past half century (see Fig. 3d of ref. 1), we expect phenological responses to be larger nearer the poles and not as pronounced closer to the equator. (Unfortunately, our pool of literature did not allow us to test elevational changes.) The latitudes of the spring phenology studies in the Northern Hemisphere extend from 32° N to 72° N, with one study in the Southern Hemisphere at 39°. Because of the unevenness of the location of the data (for example, a preponderance of studies in the United Kingdom), we were able to have large enough sample sizes in each group only by dividing them into two groups along 50° latitude circles. The sample size from 32° to 49.9° was 24 +, which includes the one Southern Hemisphere study. From 50° to 72° N latitude, 85+ species or species groups were examined. As expected, the estimated mean and s.e.m. of the phenological shifts (see Methods) from 32° to 49.9° latitude is smaller (−4.2 ± 0.2) than that between 50° and 72° N latitude band (−5.5 ± 0.1). These two means are statistically significantly different from each other (Kruskal–Wallis test, ($P < 0.0001$), which strongly suggests that species at higher latitudes are indeed reacting more strongly to the more intense change in temperature.

Our spring phenology data set consists of species and populations from major taxa from molluscs to mammals. We had large enough sample sizes to examine the estimated means of the phenological shifts separately for invertebrates, amphibians and birds, and for trees and other plants (Fig. 2). Four of the five means cluster around an earlier shift of 5 days, which is the estimated mean for all taxa combined. Trees, however, show an estimated mean that is later than the cluster (−3.0 ± 0.1). This estimated mean is statistically different from the other means (Kruskal–Wallis test), and the other four means are not statistically different from one another.

Our study shows that recent temperature change has apparently already had a marked influence on many species. Meta-analyses provide a way to combine results, whether significant or not, from various studies, and to find an underlying consistent shift, or fingerprint, among species from different taxa examined at disparate locations. The findings for the nonsignificant species, when aggregated, show nearly as much significant change as the group of species showing statistical significance (Table 1 and Fig. 1). Hence, for the studies we examined, the balance of evidence suggests that a significant impact of recent climatic warming is discernible in the form of long-term, large-scale alterations of animal and plant populations. For example, the average shift in spring phenology (timing) of events, such as breeding or blooming, for temperate-zone species is 5.1 ± 0.1 days earlier in a decade. The observed consistent broad-scale patterns of changes in the expected direc-

tions (80% of species showing change) strongly suggest that recent temperature trends are the most likely explanation for these observed phenomena. Clearly, if such climatic and ecological changes are now being detected when the globe has warmed by an estimated average of only 0.6 °C, many more far-reaching effects on species and ecosystems will probably occur in response to changes in temperature to levels predicted by IPCC[1], which run as high as 6 °C by 2100.

Projected future rapid climate change could soon become a more looming concern, especially when occurring together with other already well-established stressors, particularly habitat destruction. During rapid climatic changes in the past, species showed differential movements[10], rather than shifting together as suggested by many authors, including Darwin[11]. Such differential movement could result in a disruption of the connectedness among many species in current ecosystems (for example, a tearing apart of communities[7]). Research and conservation attention needs to be focused not only on global warming and each of the other stressors by themselves, but also on the synergism of several pressures that together are likely to prove to be the greatest challenge to animal and plant conservation in the twenty-first century[3,12]. Because anticipation of changes improves the capacity to manage—by acting proactively rather than reactively—it behoves us to increase our understanding about the responses of plants and animals to a changing climate. This understanding, coupled with further documentation of change, may well indicate a need for actions to modify conservation efforts and future planning to account for climate change, and to slow the projected rate of warming. □

Methods

We used results from 143 studies, each of which found some trait of a species showing a trend over a span of at least 10 years. The geometric mean of the time span for all studies was 30.3 years and the average was 34.5 years. Gaps between years were allowed. Several studies investigated more than one species and some species showed no change. The relative number of species exhibiting change compared with all species reported in the literature sources we examined is not the relevant metric we consider, because we are not trying to determine what percentage of species is responding to current climatic changes. Given that all species examined in this study (and indeed by the entire scientific community) represents only a small proportion of the total number of species that exist in the world (itself unknown), such percentage claims are untenable by any analysis. Rather, a relevant metric to detect a discernible influence of global warming on plants and animals is the fraction of those species exhibiting change that have changed in the direction expected given a temperature trend at their location. For those studies finding change in more than one species and reporting the change as an average for several species, only one entry is used in the various tests performed. For example, Fleming and Tatchell[13] reported the change in flight period of five aphids as 2.6 days earlier per decade. To be conservative, for all our analyses, this group of aphids (and all similarly grouped species) is considered as one entry, rather than as five.

Meta-analyses used

We used two types of meta-analysis, vote counting and regression slope, to determine whether changes observed are consistent with the possibility that one force, global warming, is instigating a noticeable change in species. The vote-counting method is explained in detail in ref. 8. This method is biased towards finding zero or no effect[14]—of global warming, in our case. The various studies have different sampling lengths (K_i) and so we use a geometric mean of these numbers to determine K, the mean length of years the studies examined traits of species or populations. In all three vote-counting analyses that we used—species showing statistically significant change, species showing nonsignificant change, and the combined species that showed change—the value of K is 30.

The regression-slope meta-analysis provides a way to examine directly the shift in spring phenological changes. For this method to work, the various studies examined must have used the same measurement of change, which in these meta-analyses is the number of days changed per decade. We included only those studies that examined more recent spring shifts, from 1951 to 2001. Details of the methods we used here to derive estimated slopes are given in ref. 9. Our only deviation from this formulation is that we did not include the sampling variance term in the calculation of the variance of the slope parameter. This is because most studies examined do not report some of the data necessary to derive the sampling variance. This term acts to reduce the size of the variance of the regression slope. Consequently, the variances presented here are slight overestimates, making our inferences more conservative.

Potential biases

Apart from the problems inherent in summarizing information from diverse studies of numerous subjects and methods, potential biases in the data are also of concern in analyses like ours. We do not claim that all authors of studies in the literature we cite report all

species they observe, and there may be a bias to report primarily those species that show change. Even if there were such a bias, however, it would have no influence on our claim of a discernible impact of warming on plants and animals, because our metric of investigation is what fraction of those species that exhibit change has changed in the direction expected with local temperature trends, not what fraction of all species has exhibited change. The only way that observer bias could influence our metric would be if there were a systematic bias among the scores of studies we examine for researchers to select as study subjects only species showing changes in the direction preconceived by the authors to reflect temperature change. In addition, these many authors would have to have deliberately and systematically suppressed reporting on those species that changed in directions opposite to that expected. We find this possibility of widespread and systematic biases far-fetched, and thus believe that the metric we use is adequate for examining in an unbiased manner the existence of a discernible climatic signal in the traits of many plants and animals.

1. Houghton, J. T. *et al.* (eds) in *Climate Change 2001: The Science of Climate Change* (Cambridge Univ. Press, New York, 2001).
2. Harris, A. H. Wisconsinan pre-pleniglacial biotic change in southeastern New Mexico. *Quat. Res.* **40**, 127–133 (1993).
3. Schneider, S. H. & Root, T. L. in *Status and Trends of the Nation's Biological Resources Part 1* (eds Mac, M. J., Opler, P. A., Puckett Haecker, N. & Doran, P. D.) 89–116 (US Geological Survey, Reston, Virginia, 1998).
4. Walther, G.-R. *et al.* Ecological responses to recent climate change. *Nature* **416**, 389–395 (2002).
5. Penuelas, J. & Filella, I. Responses to a warming world. *Science* **294**, 793–795 (2001).
6. McCarthy, J. J., Canziani, O. F., Leary, N. A., Dokken, D. J. & White, K. S. (eds) *Climate Change 2001: Impacts, Adaptations, and Vulnerability* (Cambridge Univ. Press, New York, 2001).
7. Root, T. L. & Schneider, S. H. in *Wildlife Responses to Climate Change: North American Case Studies* (eds Schneider, S. H. & Root, T. L.) 1–56 (Island Press, Washington DC, 2002).
8. Hunter, J. E. & Schmidt, F. L. *Methods of Meta-Analysis: Correcting Errors and Bias in Research Findings* (Sage, Thousand Oaks, California, 1995).
9. Raju, N. S., Fralicx, R. & Steinhaus, S. D. Covariance and regression slope models for studying validity generalization. *Appl. Psychol. Meas.* **10**, 195–211 (1986).
10. Overpeck, J. T., Webb, R. S. & Webb, T. III Mapping eastern North American vegetation change over the past 18,000 years: no analogs and the future. *Geology* **20**, 1071–1074 (1992).
11. Darwin, C. *On the Origin of Species: A Facsimile of the First Edition* (Harvard Univ. Press, Cambridge, Massachusetts, 1964).
12. Myers, N. in *Biodiversity II: Understanding and Protecting our Biological Resources* (eds Reaka-Kudla, M. L., Wilson, D. E. & Wilson, E. O.) 125–138 (Joseph Henry, Washington DC, 1997).
13. Fleming, R. A. & Tatchell, G. M. in *Insects in a Changing Environment* (eds Harrington, R. & Stork, N. E.) 505–508 (Academic, San Diego, California, 1995).
14. Hedges, L. V. & Olkin, I. *Statistical Methods for Meta-Analysis* (Academic, New York, 1985).

....

True navigation and magnetic maps in spiny lobsters

**Larry C. Boles & Kenneth J. Lohmann**

Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599, USA

....

Animals are capable of true navigation if, after displacement to a location where they have never been, they can determine their position relative to a goal without relying on familiar surroundings, cues that emanate from the destination, or information collected during the outward journey[1,2]. So far, only a few animals, all vertebrates, have been shown to possess true navigation[3]. Those few invertebrates that have been carefully studied

return to target areas using path integration, landmark recognition, compass orientation and other mechanisms that cannot compensate for displacements into unfamiliar territory[4,5]. Here we report, however, that the spiny lobster *Panulirus argus* oriented reliably towards a capture site when displaced 12–37 km to unfamiliar locations, even when deprived of all known orientation cues *en route*. Little is known about how lobsters and other animals determine position during true navigation. To test the hypothesis that lobsters derive positional information from the Earth's magnetic field, lobsters were exposed to fields replicating those that exist at specific locations in their environment. Lobsters tested in a field north of the capture site oriented themselves southwards, whereas those tested in a field south of the capture site oriented themselves northwards. These results imply that true navigation in spiny lobsters, and perhaps in other animals, is based on a magnetic map sense.

In the context of homing behaviour, an animal capable of true navigation must possess both a positional sense to determine its location and a directional or compass sense to orient in the appropriate homeward direction[6,7]. Many animals, both vertebrate and invertebrate, possess diverse compasses based on the Earth's magnetic field, the position of the Sun, patterns of skylight polarization and the positions of stars[4,8]. In contrast, few animals are known to possess the ability to determine position relative to a goal after being displaced to unfamiliar areas under conditions in which
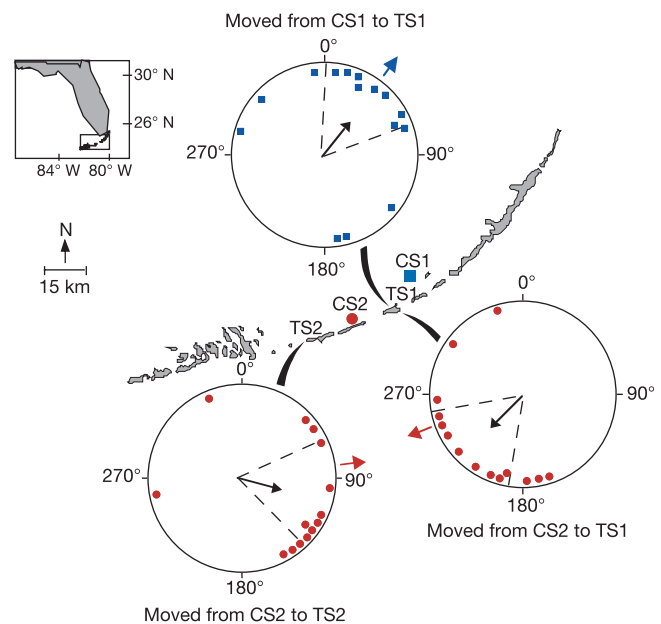
Figure 1 Orientation of displaced lobsters. Lobsters were transported by boat from two capture sites (CS1, CS2) via circuitous routes (see the text) to one of two test sites (TS1, TS2). In the orientation diagrams, each small symbol represents the mean angle of a single lobster. Blue squares indicate lobsters captured at CS1, whereas red circles indicate lobsters captured at CS2. The arrow in the centre of each orientation diagram indicates the mean angle of each group; the arrow length is proportional to the mean vector **r**, with the radius of the circle corresponding to $r = 1$. Lobsters transported from CS1 to TS1 were significantly oriented ($r = 0.51$, $Z = 3.92$, $P < 0.02$, Rayleigh test) with a mean angle of 38°. Lobsters transported from CS2 to TS1 were significantly oriented ($r = 0.65$, $Z = 5.96$, $P < 0.01$) with a mean angle of 222°. Lobsters displaced from CS2 to TS2 were also significantly oriented ($r = 0.51$, $Z = 3.89$, $P < 0.02$) with a mean angle of 105°. In all orientation diagrams, the dashed lines represent the 95% confidence interval for the mean angle. Data are plotted relative to magnetic north. The blue or red arrow outside each orientation diagram indicates the direction from the test site to the capture site. In each case, the mean angle of orientation coincided closely with the direction towards the capture site (see the text) and the 95% confidence interval encompassed this 'homeward' direction.