the experiment, participants were asked to discard a piece of paper featuring an organization diagram. An easily accessed waste bin and a less conveniently placed recycling bin were available. Participants who had been primed with the environmental benefits recycled the sheet of paper significantly more often than the control group, whereas those that had been exposed to the economic benefits did not. In the second experiment, a fourth condition was added: a group of participants was prompted with both environmental and economic benefits. Again, the group that was given just the environmental benefits recycled significantly more often than the others.

The results of both experiments confirm the hypothesis of a spillover effect — from car-sharing to paper recycling in this case — when participants are made to think of the environmental benefits of the initial activity. It seems that using the environmental benefits of an activity as an incentive triggers people's desire to protect the environment, which then leads to the spillover effect. Promoting the self-interested (economic) motives associated with car-sharing did not increase the likelihood of people recycling paper because the economic reasons for car-sharing are irrelevant to the broad goal of protecting the environment, and therefore they do not activate that goal. When participants were prompted with self-interest right after self-transcendent motives had been used, any effect from the environmental stimulus was "crowded out"[8] or neutralized, and no spillover effect was detected.

The work by Evans *et al.*[6] shows that thinking about the benefits of a specific pro-environmental behaviour, as a person would do if he or she were seriously contemplating the behaviour, or had already adopted it, can spill over into other behaviours and in this way potentially promote a broader range of changes towards a more sustainable lifestyle. However, for this effect to occur, people need to be prompted with the benefits for the environment rather than self-interested reasons. Hence, the study suggests that campaigns can promote a broad sustainable lifestyle by focusing on a single behaviour at a time as long as their messages address the right set of motivations to change behaviour.

Evans and colleagues[6] leave important questions for future research, however. They focused on the spillover effect in the case of perhaps the most common green behaviour of all: recycling. Logically, prompting people with environmental incentives is unlikely to induce spillover onto actions that they do not think of as green. This raises questions both about the range of behaviours that could potentially benefit from a pro-environmental spillover effect, and about what else can be done to increase these effects on behaviours that are deemed especially important to change[9], such as buying a more fuel-efficient car or installing attic insulation. Future study is also needed to probe the effects occurring in the case of prompting many different values (value importance, order of stimuli).

Campaigners have long believed that successfully promoting a specific pro-environmental behaviour can have a 'knock-on' effect on other pro-environmental actions for a wider change[10]. The experiments conducted by Evans *et al.*[6] are the first to empirically test one of the most likely ways such a spillover effect can happen[7]: by prompting people with values or reasons common to all green behaviours. They have convincingly shown that a campaign focused on the self-transcendent (that is, pro-environmental) rationale for engaging in car-sharing not only has the potential to promote the specific, targeted behaviour, but it can also induce people to recycle paper, another pro-environmental action. Their research warns against the widespread tendency to include self-interested justifications in campaigns promoting green behaviour. When self-interested justifications are included, campaigns miss the opportunity to induce environmental actions beyond the specifically targeted behaviour. ❐

John Thøgersen is in the Department of Business Administration, School of Business and Social Sciences, Aarhus University, Bartholins Allé 10, Building 1327–124, 8000 Aarhus C, Denmark.
e-mail: jbt@asb.dk

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ENVIRONMENTAL EPIDEMIOLOGY

Fluctuating temperature effects

Relationships between hosts, parasites and pathogens may be strongly affected by changing patterns of temperature variation.

Ross A. Alford

Interactions among and between microbes and their hosts often depend on environmental context[1]. Averages of environmental variables such as temperature and moisture are often used to characterize that context, and to model how it affects organisms and their relationships[1,2]. However, conditions in most environments fluctuate, with varying amplitude, length and predictability[1,3]. Understanding how this variability affects particular systems may be essential for anticipating and responding to the effects of environmental change[1,3]. Writing in *Nature Climate Change*, Raffel *et al.*[3] provide a framework for understanding how most organisms and their pathogens interact in fluctuating environments. Their ideas may help to predict responses to environmental change, including the emergence of pathogens.

Figure 1 | The critically endangered golden frog of Panama *(Atelopus zeteki)* has been driven close to extinction by outbreaks of chytridiomycosis, which Raffel *et al*. show can be facilitated by short-term temperature fluctuations.

As with many good ideas, those of Raffel *et al.* seem simple and obvious in retrospect. They are based on the underlying fact that rates of many biochemical reactions are temperature sensitive[3]. The body temperatures of most organisms fluctuate substantially with changes in environmental temperatures. Many organisms can compensate for changes in body temperature by adjusting the rates of metabolic processes[3] — these adjustments are referred to as acclimation responses.

Raffel *et al.* hypothesize that the speed of thermal acclimation should scale with body size, so that larger, multicellular organisms adjust more slowly than their parasites and pathogens. These differences in rates of acclimation between hosts and their pathogens could lead to changes in the balance between pathogen growth and host defence. A continuum of predictions can be made using these underlying ideas[3]. If fluctuations in environmental temperature are predictable, such as diurnal or seasonal changes, both hosts and pathogens should evolve to acclimate in synchrony with changing temperatures, so that variations produce no net change in the host–pathogen balance. However, unpredictable changes in temperature should generally favour pathogens over hosts, as pathogens can acclimate more rapidly, and neither can adjust its metabolism in anticipation.

The predictions were tested experimentally, using the interaction between the amphibian chytrid skin fungus *Batrachochytrium dendrobatidis* and the Cuban treefrog *Osteopilus septentrionalis*, an introduced tropical species common in Florida. The amphibian chytrid fungus has recently emerged as a serious pathogen in many regions of the world, causing extensive declines in amphibian populations, and both local and global extinctions[4] (Fig. 1). It infects keratinized epidermal cells, and multiplies on the host by releasing infectious zoospores on the host's skin every few days[4]. Interactions between amphibians and the chytrid are strongly affected by environmental context. Under ideal conditions, the population of pathogens can grow exponentially to a threshold density that kills the host[5]. However, *in vitro* the pathogen grows best in a relatively narrow range of temperatures, between 17 and 25 °C. Over 25 °C, growth rapidly slows to a halt, and the pathogen dies at temperatures of 30 °C and higher[6]. Field data show that its prevalence and virulence are strongly affected by average environmental conditions; both tend to be higher in colder seasons and at higher elevations[4]. It has been suggested that the emergence of the pathogen may have been facilitated by changes in weather patterns caused by climate change[7], but this has been challenged on various grounds, including the obvious one that on average temperatures are increasing, and increasing temperatures should in general act against *B. dendrobatidis*, rather than favouring it, at least in tropical areas.

Raffel *et al.* first examined the idea that pathogens may gain an advantage as hosts are adjusting to a change in temperature regime. They acclimated adult and juvenile *O. septentrionalis* to either 15 or 25 °C for four weeks. Half of the individuals in each temperature were then switched to the opposite temperature, simulating a sudden warm or cold spell of a magnitude that could easily occur naturally. All frogs were then inoculated or sham-inoculated with *B. dendrobatidis*. Individuals that had experienced a sudden 10 °C decrease developed more intense infections than those that had been acclimated at 15 °C. These findings support the hypothesis that the metabolisms and immune defenses of frogs that experienced a sudden drop in temperature took some time to adjust through acclimation, while the pathogen was still close to its optimal range and able to adapt more quickly.

A further experiment directly examined the effects of predictability of temperature fluctuations. The growth of *B. dendrobatidis* was compared — in culture and on *O. septentrionalis* — between a thermal regime with regular diurnal fluctuations (between 15 and 25 °C) and one with equal numbers of 12 hour periods at each temperature, occurring in random sequences that varied among replicates. *In vitro*, the pathogen grew faster under the diurnal pattern, indicating that it can adjust its metabolic pathways to a circadian rhythm, however the pathogen grew faster on *O. septentrionalis* when temperature changes occurred in random order. In diurnal conditions, frogs synchronized their defences to a circadian rhythm and slowed the growth of the pathogen. When temperatures fluctuated randomly the frogs' defences could not acclimate rapidly enough, giving the chytrid an advantage.

The results of their experiments are in accord with a previous study finding that the extent of month-to-month variation in temperature was the best climatic predictor for the year that frog populations (genus *Atelopus*) began to decline in Latin America[8]. One of the predicted outcomes of global climate change is an increase in the frequency of extreme climatic events, and if temperatures rise on average, larger temporary decreases may also become more common[3].

Although Raffel *et al.*[3] do not demonstrate that climate change caused the emergence of chytridiomycosis in Latin America or anywhere else, they do show that it could have, following a reasonably simple and obvious mechanism. Their results bring home the fact that models incorporating effects of mean environmental variables on one factor at a time may be too simple to effectively predict the future, or to reconstruct the past. Better models will require us to consider how organisms and their interactions respond to changes in the variability of the physical environment, not just to changes in its average. ❒

Ross A. Alford is in the School of Marine and Tropical Biology, James Cook University, Townsville, Queensland 4811, Australia.
e-mail: ross.alford@jcu.edu.au

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