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Signal detection theory has influenced the behavioural sciences for over 50 years. The theory provides a simple equation that indicates numerous ‘intuitive’ results; e.g. prey should be more prone to take evasive action (in response to an ambiguous cue) if predators are more common. Here, we use analytical and computational models to show that, in numerous biological scenarios, the standard results of signal detection theory do not apply; more predators can result in prey being less responsive to such cues. The standard results need not apply when the probability of danger pertains not just to the present, but also to future decisions. We identify how responses to risk should depend on background mortality and autocorrelation, and that predictions in relation to animal welfare can also be reversed from the standard theory.

For every complex problem there is an answer that is clear, simple and wrong.

—H. L. Mencken

## 1. Introduction

Signal detection theory formalizes the intuition that an individual facing a high probability of danger (e.g. through predation) should be more wary than another individual that is at less risk. The theory assumes that sensory inputs (signals) are uncertain, so which of two possible situations actually applies cannot be perfectly discriminated. With two actions to choose between, each being best in one of the situations, an individual chooses the action that seems most appropriate, given the signal that they have received. Two types of error are possible: ignoring true dangers and responding to ‘false alarms’; the optimal decision depends on the expected payoffs of each action. Signal detection theory has been used to explain a diverse range of behaviours, including mate choice decisions [1], immune function [2], the behaviours of predators choosing between models and mimics [3], the evolution of plant defences [4], and mental illnesses [5]. The theory has spawned shorthand terms for some effects, such as the ‘smoke detector principle’ [2,6] and, in an evolutionary context, is sometimes now referred to as ‘error management theory’ [7]. We describe standard signal detection theory and its key predictions in the next section.

The apparent simplicity and power of the standard theory can be misleading. An implicit assumption of the standard theory is that only a single decision will be made, but decisions are rarely taken in isolation. In a more realistic model, modifying the value of a parameter may often correspond to modifying the parameter for multiple decisions. The change is important because multi-step, knock-on effects can produce counterintuitive effects.

Our recent work made the use of signal detection theory more realistic by incorporating it into a larger framework of state-dependent modelling [8]. State-dependent detection theory (SDDT) can be used to analyse numerous behavioural decisions where the consequences of a decision at one time (e.g. whether to forage or flee) influences decisions by altering the reserves of the decision-maker. Our earlier work [8] used SDDT to address behavioural responses to novel situations that are safe but appear dangerous (e.g. presence of ecotourists). Here, we use SDDT to examine the critically important issue of behavioural responses to actual danger (e.g. predation risk) and how the

responses should alter with the level of danger. We describe the theory in greater detail in §3. We then show that the results of the more realistic theory conflict with those of standard signal detection theory; predicted trends are often reversed.

## 2. Standard signal detection theory

Signal detection theory [9] has been applied to many scenarios; here we illustrate the principles in a foraging scenario. We assume that the real situation is either safe (no predator present) or dangerous (predator present, with probability  $p$ ). If safe, then it is best to forage, and if dangerous then it is better to flee. Prey evaluate the situation and take action after receiving a signal (of strength  $x$ ) that tends to be larger when the situation is dangerous, e.g. predators typically being larger or louder. Because the two signal distributions overlap, prey are somewhat uncertain about whether the environment is safe or not. This uncertainty means that an individual faces a trade-off; a more wary individual (more easily induced to flee) will less often err by continuing to forage under dangerous conditions, but will more often flee unnecessarily in safe conditions. Being more wary thus results in lower predation risk in the short-term, but higher risk of energy shortfalls (and if energy reserves are low, higher risk of starvation or needing to take greater risks to obtain food). The conflict between foraging and fleeing is, of course, a central trade-off that has been the subject of numerous models (e.g. [10,11]); the signal detection framework emphasizes, in particular, the role of cues and their uncertainty in balancing this trade-off.

Signal detection theory identifies the optimal threshold,  $x_T$ , for action, whereby receiving a signal larger than the threshold indicates that it is better to flee; otherwise it is better to forage. The optimal threshold depends on the payoff values,  $V$ , associated with each combination of situation and action (table 1) and is given by:

$$\frac{P(x_T|D)}{P(x_T|N)} = \frac{(1-p)(V_{NF} - V_{NR})}{p(V_{DR} - V_{DF})} \quad (2.1)$$

([12], or see electronic supplementary material), where  $p$  is the background probability (prior to receiving any signal) that the situation is dangerous.

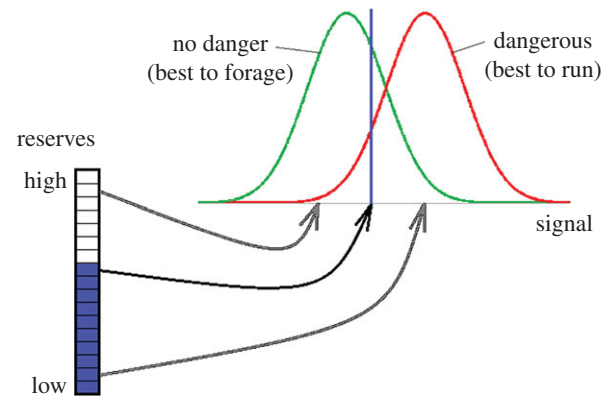
Assuming that none of the payoff values depend on  $p$ , the right-hand side of equation (2.1) decreases monotonically as  $p$  increases, so the optimal threshold for action,  $x_T$ , decreases. In other words, if there is a high perceived probability of danger, then the individual should be more prone to fleeing, as [9, p.23] point out.

A key difficulty with signal detection theory is that the expected reproductive success (the reproductive values in the payoff matrix) should depend on the reserve state of the individual [10,13]. For instance, the cost of fleeing may be very high if the individual is near starvation [14–16]. This has led to signal detection theory being incorporated into a wider framework of state-dependent modelling [8], as we now describe.

## 3. State-dependent detection theory

Following the scenario outlined above, SDDT identifies the optimal response thresholds for action, depending on the individual's reserve level, as illustrated in figure 1.

Time is discretized into a series of independent units with signal detection theory being used to make a decision in each time step. With SDDT, the expected payoff values associated



**Figure 1.** SDDT sets an optimal detection threshold for each level of reserves. The individual can be killed by predation or starvation, so at high reserves, the individual is more willing to respond to a perceived danger than when reserves are low and it needs food to avoid starvation.

**Table 1.** The generic payoff matrix of signal detection theory.

		situation	
		dangerous, D	no danger, N
action	flee (run & hide), R	$V_{DR}$	$V_{NR}$
	forage, F	$V_{DF}$	$V_{NF}$

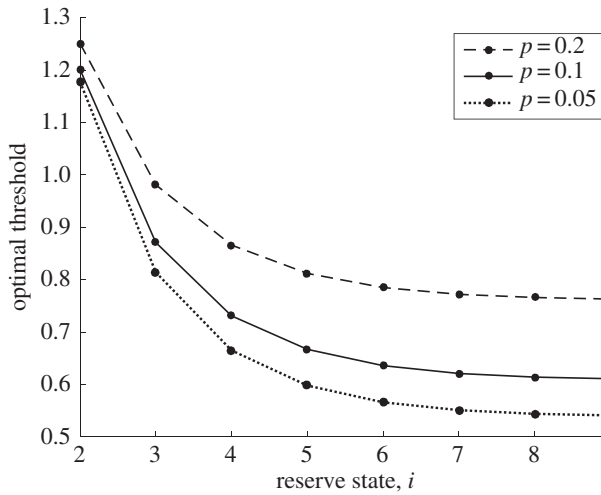
with each combination of situation and action (cf. table 1) emerge from the analysis as part of the process [8].

We model the specific, simple scenario where a unit of reserves is lost in each time step but two units of energy are obtained when foraging (resulting in a net gain of a unit of energy while foraging). The individual dies if it forages when a predator is present or if reserves reach zero. The aim of the individual is to reach a reproductive reserve level,  $L$  (we have set  $L = 10$ , except where specified). The thresholds at each reserve level are optimized to maximize the probability of reaching this reserve level.

## 4. State-dependent detection theory results

In complete contrast to standard signal detection theory, increasing the probability of danger,  $p$ , increases thresholds (figure 2). In other words, the SDDT model suggests that as the perceived probability of danger increases, individuals should require a higher signal (of danger) in order to flee.

Although this SDDT result may seem surprising, there is a clear logic to it. When  $p$  is higher, the organism's expected future reproductive success must decrease and thus the payoff values associated with each outcome in standard signal detection theory should change. Standard signal detection theory overlooks this long-term effect. The SDDT model takes into account the change in the probability of danger across time; an increase applies across all time steps. Thus, postponing foraging in order to remain safe simply shifts that risk of facing danger to a subsequent time. And as fleeing decreases the reserves of the animal, the individual will need to be willing to take larger risks (i.e. less prone to flee) at subsequent time steps. This effect is taken into account at all reserve levels where there is a choice to be made. Put another way, if predators



**Figure 2.** Optimal thresholds as a function of reserve level. Receiving a signal above the threshold results in fleeing; lesser signals produce foraging behaviour. As the probability of danger,  $p$ , increases, the minimum signal required to respond to danger increases. Thus, individuals are less prone to react to a signal indicating a possible predator despite knowing that the world is more dangerous. (We assume normal distributions with unit variance. Parameters: mean signal from non-dangerous,  $\mu_N = 0$ , mean signal from dangerous,  $\mu_D = 2$ , reserves required for reproduction,  $L = 10$ .)

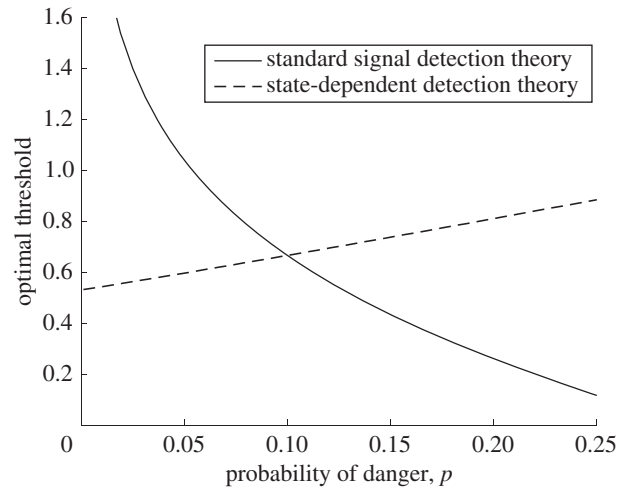
are rare, when an organism receives a signal of possible danger, it can afford to flee because it should have plenty of opportunity to make up for lost energy at a later time. In contrast, if predators are very common, the organism cannot afford to flee every time it receives a signal of possible danger.

To illustrate the difference between results of the two models, we make use of the payoff values from the optimized SDDT model to assess the expected value of gaining or losing a unit of food, at mid-reserve levels of 5. With baseline parameter values, and changing  $p$  in both models, we obtain figure 3. While boldness *decreases* with  $p$  according to the standard theory, boldness *increases* with  $p$  in the SDDT paradigm.

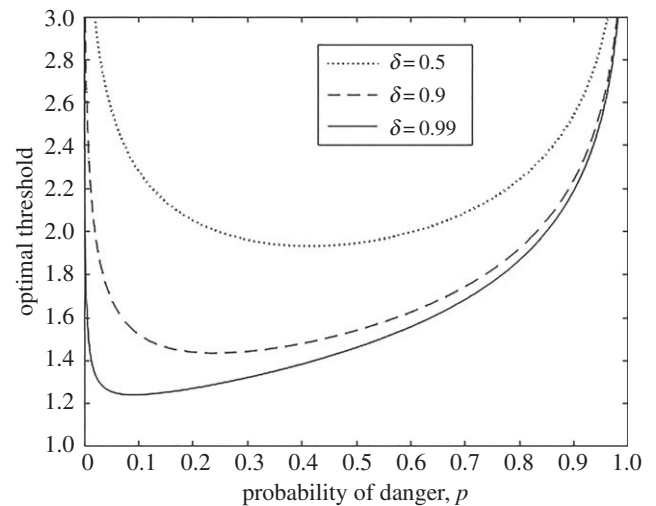
In the electronic supplementary material, we show analytically that the threshold increases (i.e. becomes more risk prone) monotonically with  $p$  in a particular case. We also show that the effect of food availability has the opposite effect in SDDT than in standard signal detection theory; rather than individuals becoming more inclined to forage when food is more abundant, they should be less inclined to forage.

## 5. The effect of background mortality

So far, the only possible sources of mortality have been starvation and predation. We now introduce an additional form of mortality that the individual is assumed to have no control over by its choice of behaviour. This background mortality risk could relate to anything from disease to asteroid strikes. The essential point is that only by reaching reproductive size more quickly can the risk of background mortality be reduced. While up to this point, we find that increasing the prevalence of predators makes individuals bolder, in this section, we show that with the addition of background mortality, increasing  $p$  from low to medium to high can first decrease and then increase boldness; i.e. that both the conventional wisdom, that increased  $p$  makes animals more wary, and our new result can both apply, but under different ranges of predator prevalence.



**Figure 3.** Standard signal detection theory and SDDT predict different trends in detection thresholds as  $p$  increases; decreasing for standard theory but increasing according to SDDT. The SDDT line shows the threshold value at mid-level reserves of 5 (this provides payoff values of  $V_{DR} = V_{NR} = RV(4) = 0.8555$ ,  $V_{NF} = RV(6) = 0.9043$ ,  $V_{DF} = 0$ , which we have used for the standard signal detection calculations). The signal detection theory line has been calculated using the payoff matrix when at reserves of 5 with  $p = 0.1$ ; thus the lines have equivalent values at that point. (Parameters:  $\mu_N = 0$ ,  $\mu_D = 2$ ,  $L = 10$ .)



**Figure 4.** Background mortality ( $\delta > 0$ ) produces non-monotonic thresholds with respect to the probability of danger,  $p$ . (Parameters:  $\mu_N = 0$ ,  $\mu_D = 2$ ,  $L = 3$ .)

We assume that background mortality strikes with probability  $\delta$  per time step. The value of  $\delta$  does not affect the trend of the standard signal detection equation: individuals should become less bold as  $p$  increases (see electronic supplementary material). However,  $\delta$  does affect the state-dependent result (figure 4). The electronic supplementary material provides an analytic case to show that the U-shape of the figure 4 results hold across all background mortality levels,  $0 < \delta < 1$ .

This small change in the formulation of equations, introducing a fixed background mortality at each time, therefore results in non-monotonic outcomes with respect to  $p$ . The intuition is that when predators are very rare, the situation is likely to be safe even when a moderately strong signal has been received; prey should only flee when the signal is very strong (fleeing increases the probability of background mortality before reproductive size is reached). If predators are somewhat

more common, prey should be more fearful (have a lower threshold) because moderately strong signals are now more likely to correctly indicate danger, and prey still have plenty of opportunities to recover lost energy. If predators are very common, prey cannot afford to flee continually, so again require a strong signal to stop foraging.

A crucial component of the reversal of the standard result is that when an individual flees, their energy reserves decline, and the individual must thus face the danger more often in the future. Without this effect (if the individual simply remains at the current reserve level when fleeing), the standard result would apply—of being more ready to flee if danger is more prevalent.

## 6. Autocorrelation and other scenarios

Standard signal detection theory assumes that only a single decision will be made, where future prospects are known. In contrast, the state-dependent approach has assumed that the current decision is just one of many such decisions, all with the same independent probability,  $p$ , of danger. These are two extreme possibilities. In many situations, the current probability of danger is only partially predictive of future probabilities and this may influence current behaviour; if  $p$  is currently high but may soon change, then there is good reason to wait before foraging.

The intermediate case can be modelled in a simple way by assuming that there are two possible probabilities of the world being dangerous,  $p_1$  and  $p_2$ , with an action being required at each time step. With probability  $\lambda$ , the world will remain in the current state in the next time step. In the electronic supplementary material, we provide the general formulae and analyse a simple case (assuming that the organism has evolved to respond appropriately to  $p_1$ ,  $p_2$  and  $\lambda$ ). The results confirm that for high autocorrelation ( $\lambda$  close to 1), the thresholds increase as the corresponding probabilities of danger increase (the SDDT result).

Our models so far have assumed that the decision-maker must reach a particular level of reserves in order to reproduce. However, the standard signal detection theory result—of individuals becoming more risk averse as the probability of danger increases—is also reversed when survival probability is maximized over a fixed period (e.g. a small bird in winter; [17]) and when maximizing expected survival time (see electronic supplementary material).

Finally, the models to this point have assumed an internal state variable, but this constraint is not necessary to get different trends from standard signal detection theory. For instance, if an individual must survive transit to a particular location and receives a signal of the current risk, then the individual may become less risk averse as danger increases (electronic supplementary material). This model highlights that there must be a twofold effect of danger for the standard signal detection theory result to be reversed.

## 7. Discussion

Signal detection theory has been used in many scenarios that involve distinguishing between safe and dangerous situations. As Wickens [18, p. 213] said in the opening line of his paper, 'The signal-detection model [...] is unquestionably one of the most successful models in mathematical psychology'. The

standard result may *seem* obvious: that an individual should be more ready to take evasive action when the probability of danger is higher. While interpreting the signal detection equation, Nesse [2, p. 97], wrote, 'This is consistent with intuition; the defense should be expressed less readily (at a higher criterion) as noise becomes more prevalent than signal' (e.g. when predators are rare). Numerous authors have written similar statements; e.g. Quigley & Barrett [19, p. 444], 'an increase in false alarms is adaptive for individuals living in conditions of high threat'; and Lynn *et al.* [20, p. 727], 'rare targets [...] promote conservative bias'.

Our most striking result is that this conventional wisdom is thoroughly misleading. We consider decision-making not as a single event but as a series of events, and find that as the prevalence of danger increases, individuals should be bolder, not more cautious. The logic is straightforward; animals cannot afford to continually take evasive action when danger is common, because avoidance of danger is costly (e.g. reducing energy reserves); instead they should be more bold. While it has long been recognized that sequential choice models should be better predictors of behaviour in many situations (e.g. [21]), it is perhaps surprising to find such a complete reversal of predictions. We have demonstrated that the standard results of signal detection theory (which apply regardless of what costs and benefits are set) are reversed in numerous biological scenarios (when multiple decisions will be required): risk-sensitive foraging when growing to a particular size before reproducing (either semelparously or iteroparously), maximizing survival over a fixed number of time steps (such as over-winter), maximizing expected survival time, food availability altering and, in some cases, individuals choosing when to alter location.

We have also shown that adding a background probability of mortality, likely an ever-present reality, produces a U-shaped relationship between the prior probability of danger and the organisms' predicted boldness. This occurs because as the probability of danger alters, the risks of predation and starvation, relative to background mortality, are governed by actions and expected future payoffs. Thus the effect of sequential decisions is crucial to understanding this relationship.

The single- and multi-decision models generate very different predictions, so a key issue is whether an empirical situation of interest better fits one scenario or the other. Single-decision models can be suitable for organisms that make a decision that radically alters subsequent trajectories; e.g. whether a juvenile fish should become a hook or a jack [22]. However, many scenarios require individuals to make decisions repeatedly, in which case the SDDT approach may be more applicable. This is often the case even if there will only be one apparent action. For instance, an individual choosing an oviposition site may assess numerous sites (i.e. making multiple decisions) before accepting just once.

In multi-decision scenarios, a key element of the decision-making logic relates to temporal autocorrelation. Our primary SDDT model assumed that the same prior probability of danger would apply to each time step. If the prevalence of predators is high, and it is likely to remain so, prey need to forage despite the persistent risk. However, in an environment with low autocorrelation, foragers should flee readily when the prevalence of danger is high because the risk is likely to reduce soon, allowing the animal to resume feeding in relative safety. Earlier models have identified this effect of autocorrelation (e.g. [23] on vigilance) but not in the context of signal detection theory.

The 'risk allocation hypothesis' [24] predicts that prey in consistently high-risk environments should be less vigilant than prey in consistently low-risk environments. Our SDDT results concur with this prediction, which has empirical support. For instance, Brown *et al.* [25] identified that, 'cichlids previously exposed to [a] high background level of risk exhibited a lower overall intensity response to each alarm cue concentration than those exposed to [a] low background level of risk'. Ferrari *et al.* [26] identify that although empirical support is somewhat mixed, animals that were given more time to evaluate their situations were more likely to behave according to the risk allocation predictions. Higginson *et al.* [27] emphasized that, theoretically, a crucial factor is the expected *duration* of danger. These theoretical and empirical findings concur with our analysis of autocorrelation. How thresholds should shift with expectations remains an interesting question. To address it, we need modelling approaches that take account of how those expectations change (i.e. learning processes), which will often be influenced by past levels of environmental autocorrelation [28].

Our result is also linked with predictions of life-history theory that if organisms have high expected mortality rates (regardless of antipredator defence), then their best strategy can be to exhibit a 'fast' lifestyle [29]. If the juvenile mortality rate (regardless of their behaviour) is high, organisms should forego defence and instead grow rapidly to reach a reproductive size more quickly. If the expected adult mortality rate is high regardless of behaviour, then organisms should put high effort into immediate reproduction since the probability of surviving to have higher fecundity in the future is low. In both life-history theory and in our analysis of antipredator behaviour, key results are driven by expectations about the future, which governs how much emphasis should be placed on short-term versus long-term considerations when choosing a current strategy.

Our findings can easily be translated to other areas. For instance, although the energy cost of activating the immune function is small, the effect on trace minerals is significant [30], so taking action makes any future effort more costly. Consequently, the effect of a change in the background expectation of infection is analogous to our SDDT results vis-à-vis shifting the background probability of danger; if the probability of infection is high, a strong signal of infection may be required to invoke the immune system (and, conversely, if the probability of a signal is perceived to be low, then immune responses may be triggered more easily, e.g. by allergens later in life if few were experienced in childhood). Similarly, the SDDT approach can apply to choosing between toxic and non-toxic foods. If toxic foods are rare (and food is readily available), foragers should be very wary of any foods that appear even slightly dangerous, while if toxic foods are common, foragers may need to be more willing to sample and consume foods of ambiguous quality.

Various authors have used signal detection theory to model moods (how mood may summarize background information to influence behaviour or vice-versa). Nettle & Bateson [5] identify two key aspects: the potential for current actions to affect future state, and the need to model autocorrelation in dealing with moods. However, in following standard theory, they state that, 'If [danger] is very likely under current conditions, then a low threshold should be set; and if [danger] is very unlikely under current conditions, then a high threshold should be set' Nettle & Bateson [5, p. R713]. In the light of

SDDT, we see that whether this statement is true depends on how long current conditions are likely to hold. If conditions are likely to change very soon, then their statement holds; however, if current conditions are expected to last for numerous decisions, their prediction should be reversed.

In animal welfare, a common aim is to use behaviour to infer mental state [31]. Signal detection theory is one candidate for this inferential process, potentially being used to infer an animal's subjective probability of danger. Here too, the possibility of being misled by the standard theory is clear. If animals housed in different conditions were tested for responses to an ambiguous signal (cf. [32]) then standard signal detection theory would suggest that animals exhibiting more apparent fear 'feel' more at risk (higher inferred perception of danger). However, the more advanced theory (SDDT) would lead to the opposite inference: animals that exhibit a more fearful response to a given signal are ones that perceive a lower level of threat in their environment. Those that feel constantly endangered should be inured to the 'risk' and less likely to respond to an ambiguous signal.

Similarly, inferential errors can easily be made in relation to human affect. For instance, in relation to identifying 'targets' (in our case, predators) Lynn & Barrett [33, p. 2] write: 'Rare targets and costly false alarms promote a conservative bias (i.e. a higher threshold, or criterion, for judging that a target is present), whereas common targets and costly misses promote a liberal bias'. In contrast, we have shown that rare predators (what Lynn & Barrett refer to as targets) can promote a *lower* threshold.

One of the attractions of signal detection theory is the relative simplicity of its formulation; it is easy to mistakenly infer that its results therefore hold fairly generally. Considering sequences of actions over time is less simple, so it is less easy to obtain general results (e.g. to show that the trend is always in the other direction). However, as we have seen, the approach is arguably also less prone to such incorrect generalizations. In summary, we see the sequential approach as the more useful route ahead in behavioural ecology, for two reasons:

- (1) The payoffs emerge from the analysis, so are more meaningful than standard signal detection theory, where the payoffs have always been difficult to set (and are now even more difficult in the light of our results).
- (2) Being more grounded in realistic feedback (of reserves affecting behavioural tendencies and vice versa), sequential models (such as SDDT) may produce interesting results and counterintuitive predictions, which have not previously been identified or tested.

Understanding these effects better may be useful in a wide variety of domains, including behavioural decisions, immune function, mental disorders and animal welfare.

**Ethics.** This work is purely theoretical; there are no ethical issues.

**Data accessibility.** This article has no additional data.

**Authors' contributions.** P.C.T. identified the primary result. S.M.E., J.M.M. and A.S. helped with writing the paper and putting the result in context. J.M.M. also supplied one of the backup results in the electronic supplementary material.

**Competing interests.** We declare have no competing interests.

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