

Pushing Up The Daisies

J. G. Dyke & I. R. Harvey
Evolutionary and Adaptive Systems Group
University of Sussex
j.g.dyke@sussex.ac.uk

Abstract

When components of an interacting dynamical system (such as organs within an organism, or daisies within the Daisyworld model) have a limited range of viability to changes in some essential variable, intuition suggests that increasing any individual range of viability will also increase viability in the context of the whole system. We show circumstances in which the reverse is true.

Introduction

An organism may be defined as an open physico-chemical system existing in steady state with its external environment. It is this ability to maintain a steady state within a constantly changing environment that contributes towards the success of both real and artificial living systems. Homeostasis in this context describes the mechanisms and processes that organisms employ in order to minimise the impact of external perturbations on their internal states. Increased robustness to external perturbations can be achieved in two main ways: 1, increase in the efficacy of homeostatic mechanisms to minimise the impact of external perturbations on internal variables; 2, increase in the range of values that the internal variables can take without endangering the viability of the organism. In this paper we present results from a radically simplified version of the Daisyworld model in which the second approach is adopted. We investigate the effects of increasing the viability range, and detail circumstances in which, counter-intuitively, doing this actually decreases the systems robustness to external perturbations.

The 'parable' of Daisyworld (Lovelock 1983, Watson & Lovelock 1983) is a simple mathematical model designed to demonstrate global homeostasis in which despite large changes in heat input from the sun, the ambient planetary temperature is regulated by the biota to within the range most favourable for life. The original results have been replicated many times and many extensions and developments of the original zero-dimensional model have been produced. In this paper we develop a radically simplified 'two box' Daisyworld model introduced in (Harvey 2004) and recently extended as a two dimensional cellular automata version (Williams & Noble 2005). Lovelock's motivation for the original Daisyworld model was to borrow ideas of homeostasis at the organism level and then apply them to the operation of a hypothetical planetary homeostatic system. Another motivation is to take the principles of Daisyworld-type homeostasis and

consider it as a model of homeostasis employed by both real and artificial systems. Therefore Daisyworld-type homeostasis need not be limited to daisies, or global regulation, but can be seen operating within diverse areas such as a simple agent that performs phototaxis (Dyke & Harvey 2005), or the regulation of blood glucose in humans (Saunders et al 2000).

The results presented and discussed here may apply to other formulations of the Daisyworld model. Preliminary results indicate that the results and analysis presented here do not apply specifically to the original Watson and Lovelock model, but the fact that they do apply to the even simpler variant model presented here suggests that these possibilities could exist with many other similar versions.

Daisyworld

Using realistic constants and modelling assumptions, a number of equations sketch out the Daisyworld planet. The model consists of a star that emits short wave energy which is received on the surface of a grey planet that is home to two daisy species: a black species and a white species. Albedo is a measure of the reflectivity of an object. In Daisyworld the black daisies have a low albedo (0.25), the grey planet intermediate albedo (0.5) and the white daisies a high albedo (0.75). The white daisies having the highest albedo in the model will reflect more of the short wave energy from the star and so have a lower temperature than either the grey planet or the black daisies. The same applies, but in reverse to the black daisies. The black and white daisies share a viability range of temperature. They are only able to grow when the local ambient temperature is within 5–40 degrees Celsius. Within this range growth rates of the daisies vary, with optimum growth being achieved when the temperature is 22.5 degrees.

Simulations begin when the luminosity is low (brightness of the star is dim) and the ambient temperature of the planet is below 5 degrees. As luminosity increases the ambient temperature reaches 5 degrees and black daisies begin to grow. The increase in the number of black daisies initiates a feedback loop that increases their temperature and a population explosion of black daisies; the greater the coverage of black daisies, the lower the albedo and so the warmer the planet which increases the growth rate of the black daisies. This feedback loop is regulated by the parabolic growth rate of the daisies. As the ambient temperature increases past 22.5 degrees, the daisy growth rate decreases. At steady state the ambient temperature, growth rate and constant death rate are at equilibrium.

As luminosity continues to rise, coverage in black daisies decreases and white daisies begin to grow. This initiates a feedback loop that decreases their temperature; the greater the white daisies, the higher the albedo and so the cooler the daisies which reduces the growth rate of the daisies. Again, this feedback loop is regulated by the parabolic growth rate of the daisies. Increasing luminosity results in a progressive increase in white daisies (and decrease in black daisies) until the maximum coverage of white daisies is reached. Any further increase in luminosity takes the ambient temperature past the point where growth rates balance death rates and so the coverage of white daisies decreases. This initiates a rapid collapse of white daisies similar in nature to the population explosion of the black daisies. The differential coverage of white and black daisies results in a system that effectively regulates ambient planetary temperature to within the optimum range for daisy growth. Whereas the temperature of a bare lifeless planet would increase in an approximately linear fashion with increases in luminosity, when black and white daisies are present, ambient temperature remains very close to the optimum of 22.5 degrees over a wide range of solar forcings (Fig. 1).

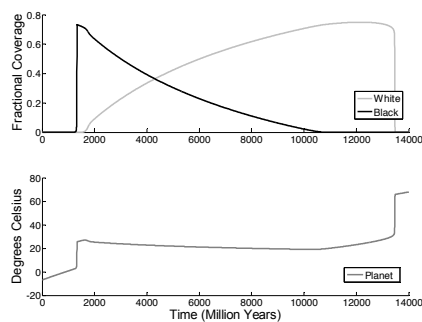


Fig 1. Time is plotted on the horizontal axis on the top and bottom plot. Daisy numbers are plotted on the vertical axis on the top plot. The temperature of the planet is plotted on the vertical axis on the bottom plot. As luminosity increases over time, the temperature on the planet increases initially linearly but then rapidly increases and then stabilises around the optimum growth temperature.

Organisation of Paper

The following sections detail a radically simplified two box Daisyworld model and present results obtained when the viability ranges of the daisies are increased. Contrary to initial intuitions, there are certain circumstances, in this simplified model, where increasing the viability range of the daisies (making them able to survive over a greater range of ambient temperatures) actually decreases the range of solar forcing over which they are able to survive. Analysis is undertaken to understand these results which highlights the role of the feedback effects that the daisies exert on temperature. The results are discussed in more general biological and evolutionary contexts in the discussion and conclusion sections.

Two Box Daisyworld

In order to better understand the effects of changing the viability range, a simplified ‘two box’ variation of Daisyworld first discussed in (Harvey 2004) will be used. Whilst Watson and Lovelock’s Daisyworld was intended as a simple parable of a complex planetary system, it still contains number of features that make analysis a non-trivial exercise. The use of non-linear equations that employ the Stephan-Boltzmann constant for the calculation of heat, space competition between the two different daisy types and the heat transport mechanism produce a number of complex relationships (see (Saunders 1994) for an analytical treatment). The two box model seeks to reduce Daisyworld to the bare minimum in order to highlight the principal interactions and relationships at work. Rather than both black and white daisies competing for space on the same planet, two separate daisy boxes, or daisy beds are seeded with either black or white daisies. These two separate beds are coupled in the form of heat conductance. Heat will flow from the black, warm daisy bed to the white cool daisy bed in proportion to a conducting parameter.

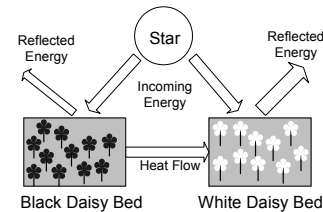


Fig 2. The Two Box Daisyworld which can be regarded as analogous to a simplified two box energy balance climate model. Only black daisies are seeded in the black daisy bed and only white daisies in the white daisy bed. Black daisies, being darker than the grey daisy bed earth will absorb more energy from the star. White daisies, being lighter, absorb less energy. Hence the black daisies are warmer and the white daisies are cooler than the grey bare earth. The two beds are coupled via a heat conducting medium which allows heat to flow from the black to white daisy bed.

The following table lists the differences between the Watson & Lovelock and Two box Daisyworld models:

Watson & Lovelock	Two Box
Variable birth rate and constant death rate used to find total numbers of daisies	Single variable used to find coverage of daisies, no separate birth and death rates
Parabolic growth function	Piece-wise linear coverage function
Space competition between black and white daisies	Black and white daisies occupy separate daisy beds
Temperatures calculated as proportional to fourth power and employ Stephan-Boltzmann constant	Simplified ‘cut-down’ physics employed to calculate temperatures in dimensionless units
Heat flow from black daisies to ambient atmosphere and from ambient atmosphere to white daisies	Heat flow calculated from black daisy bed to white daisy bed

Table 1. A list of the major differences between the original Watson & Lovelock and the two box Daisyworld models.

Of particular interest are the two different methods used to calculate the differential responses of the daisies to varying temperature. Watson & Lovelock employ the following:

$$\beta_i = \begin{cases} 1 - 0.003265(295.5 - T_i)^2, & 278 < T_i < 313 \\ 0, & \text{otherwise} \end{cases}$$

β_i is the birth or growth rate of the i th daisy type and T_i is the temperature of the i th daisy type. The Two Box model assumes that the coverage D_i of each daisy bed (parameterised from empty (0) to full (1)) varies with the temperature T_i of that daisy bed as in this piecewise linear ‘Witch’s hat’ function:

$$D_i = \text{Max} \left[1 - 2 \left(\frac{T_{opt} - T_i}{\varphi} \right), 0 \right]$$

T_{opt} is the optimum temperature for the daisies (equivalent to 278 Kelvin in the Watson & Lovelock model), and φ is the width of the viability range of the daisies. Both equations produce a viability range over which the daisies are able to grow and survive (Fig. 3).

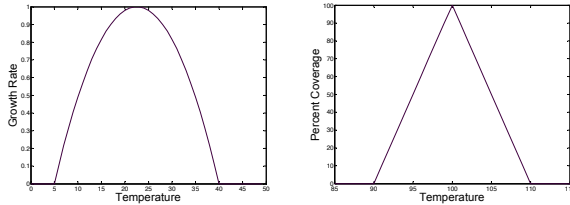


Fig 3. Daisy response functions. The left hand plot shows the differential daisy growth rates in the original Watson & Lovelock model. The right hand plot shows the differential daisy coverage in the two box model.

Operation of Algorithm

Computer simulations were run in which the initial daisy coverage was set at 0.0001. Final steady state values were not allowed below this value thus simulating a constant small daisy population or as in the Watson & Lovelock model, a set of daisy seeds scattered on the surface of the planet. It was assumed that there is sufficient time for the daisy coverage to adjust itself to the current star temperature; hence the star temperature was held constant whilst the daisy coverage algorithm was iterated to find steady state values. Steady state values for a range of star temperatures were found by initialising starting daisy coverage with the previous steady state daisy coverage values. Initial daisy coverage was not reset, unlike (Harvey 2004). In order to find any non-zero stable equilibrium point for any fixed value of star temperature and heat conductance, the following algorithm was iterated:

1. Calculate albedo for the black and white daisy beds from daisy proportions
2. Calculate the temperature from the albedo
3. Adjust bed temperatures via the conductance constant
4. Use the ‘Witch’s hat’ functions to calculate new target daisy proportions D^*

5. Adjust the daisy proportions a little way towards the new values: $D \leftarrow (1 - \delta)D + \delta D^*$
6. Go back to 1

δ values of 0.001 produced effectively vanishingly small changes after 200,000 iterations of the loop; these values were used to obtain the results presented in this paper.

Role of Heat Conductance

The amount of heat conductance is parameterised to vary from 0 (no conductance, perfectly insulated beds, effectively separate planets) to 1 (infinite conductance, isothermal beds, respond as a single bed). The value of the conductance has a significant effect on the operation of the model. This issue has been discussed in more detail in (Harvey 2004) and (Dyke & Harvey 2005). Here we concentrate on the conductance value that maximises the ‘both-daisy range’. Maximum homeostasis is observed in both the Watson & Lovelock and two box Daisyworld models when both daisy types are present. Temperature is regulated most effectively when there are non-zero numbers of both black and white daisies. In Watson & Lovelock’s Daisyworld, planetary temperature actually decreases slightly whilst luminosity increases, but this does not occur in the two box model. In the two box model, the rate of increase of planetary temperature is least when both daisy types are present. Fig. 4 shows daisy coverage and temperatures for increasing values of star temperature when the conductance parameter is set to 0.857, which is the value that maximises the both-daisy range.

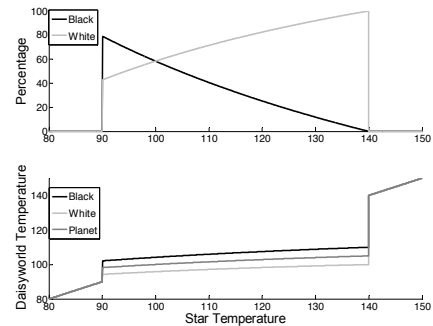


Fig 4. The top plot shows coverage of black and white daisies plotted on the vertical axis. The bottom plot shows daisy and planet temperatures. Star temperature is plotted on the horizontal axis of both plots in dimensionless units. Star temperature is initialised at 80 and increases. When star temperature reaches 90, black and white daisies begin to grow. When star temperature reaches 140, black daisies have gradually decreased to zero and the white daisies have suddenly dropped to zero. Heat conductance was set to 0.857 so maximising the both-daisy range.

Results

The experiments shown here are chosen so as to illustrate the counter-intuitive result that in some circumstances increasing the viability range of the daisies can, in the

context of the coupling between the two daisy beds, actually reduce the range of viability of daisies to perturbations in solar input. The results of four experiments will be presented. The viability range of the daisies will be adjusted when there are only white daisies, only black daisies, both white & black daisies present and finally when both white & black daisies are present for increasing then decreasing star temperatures. Adjusting the viability range of the daisies in the two box model is achieved simply by increasing or decreasing the value for ϕ which dictates the width of the hat-function. Two values for ϕ were used: 'normal' where $\phi = 20$ giving a viability range of 90-110 and 'wide' where $\phi = 30$ giving a viability range of 85-115.

Experiment 1. White daisies only.

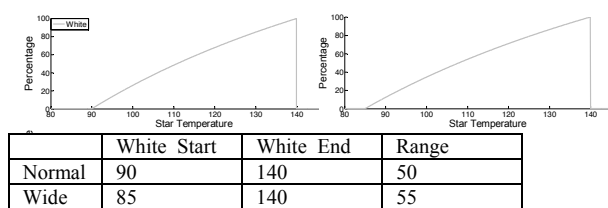


Fig 5. The left (right) plot shows white-only daisy growth with a normal (wide) viability range. When the viability range is increased, the white daisies grow at lower star temperatures but end at the same star temperature.

Experiment 2. Black daisies only.

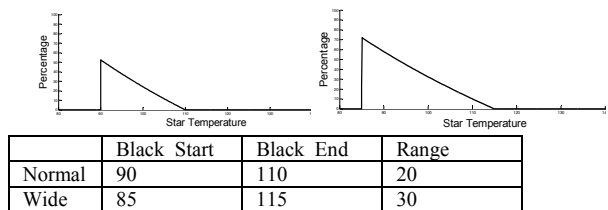


Fig 6. The left (right) plot shows black-only daisy growth with a normal (wide) viability range. When the viability range is increased, the black daisies grow at lower star temperatures and end at higher star temperatures.

Experiment 3. Black & white daisies. Fig 4. (on previous page) plots the values for the normal viability range.

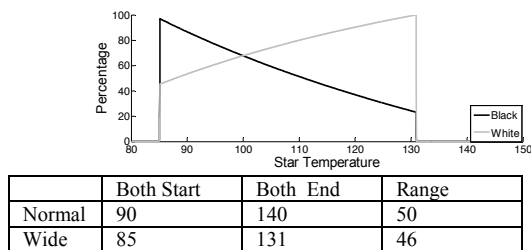


Fig 7. When the viability range is increased, the daisies begin to grow at lower temperatures. However there is a proportionally greater decrease in the maximum temperature that the daisies are able to survive and so the both-daisy range is decreased.

The Core Results

We now come to the core results of the paper, with Figures 8 and 9 illustrating Experiment 4. Increasing the viability range of each daisy species will be shown to decrease the range of viability of the dynamical system as a whole.

Experiment 4. Black & White daisies, increasing then decreasing star temperature. The results presented thus far are produced by computations in which star temperature is initialised below the daisy viability range and then increased past it. It is illustrative if the star temperature is then decreased. Figs 8 & 9 show results when star temperature is increased and then decreased for the normal then wide daisy viability range.

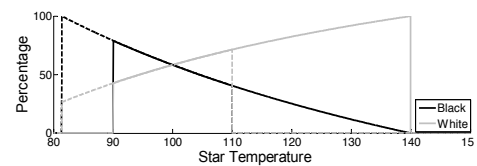


Fig 8. Normal viability range, star temperature increasing (solid line) then decreasing (dashed line). Black and white daisies are able to grow at a minimum star temperature of 81.32 and a maximum star temperature of 140. This gives a both-daisy range of 58.68.

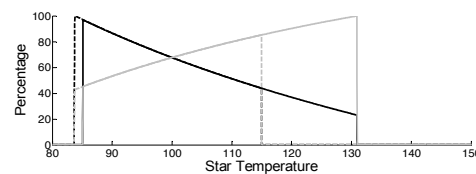


Fig 9. Wide viability range, star temperature increasing (solid line) then decreasing (dashed line). Black and white daisies are able to grow at a minimum star temperature of 83.62 and a maximum star temperature of 130.95. This gives a both-daisy range of 47.33.

The areas of hysteresis can now be observed at the limits of the both-daisy range. For example if star temperature were to increase beyond 140 when the daisy viability range was set to 20, then the white daisies do not begin to grow until star temperature decreases to 110 whereas white daisies will begin to grow sooner at 115 when the daisy viability range is set to 30. Whilst the wide viability range decreases the area of hysteresis, this is accompanied by a decrease in the both-daisy range.

Analysis

Experiment 1. White daisies only. Increasing the viability range extended the range of start temperatures over which the white daisies were able to grow. This was achieved by the white daisies beginning to grow at lower star temperatures. However the right hand side of the any-daisy range remained at 140 when the viability range was increased. The origins of this result are found in that the right hand side of the viability range of the white daisies

does not determine the maximum temperature at which they are able to survive. Rather, it is a function of the 'height' of the viability function and the strength of feedback that the white daisies exert on temperature. White daisies are able to survive increasing energy output from the star, not via their ability to survive increasing temperatures (i.e. by extending their viability range to the right), but by the negative effect that increasing numbers of white daisies exert on temperature.

As star temperature increases, so does the coverage of white daisies, until maximum coverage is obtained (at point B in Fig 10.). The sloping line represents the negative feedback that the white daisies exert on temperature. Any further increase in star temperature moves the sloping line past the centre of the hat function. This produces a rapid population collapse of white daisies and zero coverage at the steady state (e.g. at point C in Fig 10). From the above, it will be clear that increasing the width of the viability function will not increase the viability range to the right, only the left. The white daisies will begin to grow at lower star temperatures (point S will move to the left), but will still peak and collapse at the same point.

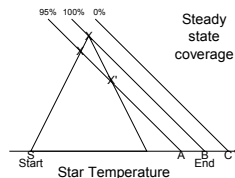


Fig 10. Star temperature increases from left to right on the horizontal axis. Steady state coverage of white daisies increases from bottom to top on the vertical axis. As star temperature increases, white daisies begin to grow at S. The sloping lines represent the negative effect that the white daisies exert on temperature. X characters mark the steady state values for white daisies. X' on line A proves to be an unstable equilibrium point and so the steady state non-zero value would be found at X. The range of star temperatures over which white daisies grow stretches from S to B.

Experiment 2. Black daisies only. When star temperature is increased, increasing the viability range when there are only black daisies present increases the range over which the black daisies are able to survive.

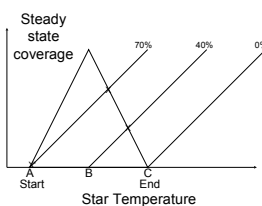


Fig 11. As star temperature increases, black daisies begin to grow at A. X' is an unstable equilibrium point in that any non-zero coverage of daisies increases the temperature of the daisy bed and so increases the coverage of the black daisies. This positive effect takes the temperature of the daisy bed past the centre of the viability range until it comes to rest on the right hand side at point X. As insolation increases black daisy coverage decreases until zero is reached at point C.

The sloping line in Fig. 11 represents the effect that black daisies have on temperature, and has the reverse slope to that in Fig. 10 representing the white daisies.

Experiment 3. Black & white daisies. Increasing the viability range when increasing insolation has very little effect on the white daisies as maximum coverage is approached. However, there is a significant effect on black daisy coverage and it is this effect which results in the reduction of the both-daisy range. At the limits of the both-daisy range, maximum coverage of white daisies is required to reflect the maximum amount of energy from the star in order to maintain the temperature of the white daisy bed below 100. Any increase in star temperature at this point will move the temperature of the white daisy bed beyond the centre of the viability range and so produce a collapse in the white daisy population. The temperature of the white daisy bed can also be increased by increasing the temperature of the black daisy bed. This can be achieved by increasing the coverage of the black daisies. Such an increase is possible by increasing the viability range of the daisies. Whilst increasing the viability range will not increase the range of star temperatures over which the black daisies are able to grow (in fact as Experiment 3 demonstrates, it decreases it), it does decrease the rate of change of the black daisies with respect to increasing star temperature. The black daisies die off more slowly and so a higher proportion of black daisies are present at the limits of the both-daisy range. This higher black daisy coverage equates to a higher black daisy bed temperature. A proportion of this extra heat is conducted to the white daisy bed. Thus the white daisy bed temperature is higher, maximum coverage is reached at a lower star temperature and so the both-daisy range is decreased. There is a net decrease in the both-daisy range as although the black daisies begin to grow at lower star temperatures, this is offset by the proportionally greater decrease in the range of star temperatures in which the white daisies are able to survive.

Experiment 4. Black & white daisies, increasing then decreasing star temperature. The normal viability range daisies are able to survive at lower and higher star temperatures than the wide viability range daisies. Increasing the viability range of the daisies decreases the area of hysteresis; if star temperature goes beyond the both-daisy range, then the wider the viability range, the sooner the daisies will begin to grow again. However this decrease in the area of hysteresis is accompanied with a decrease in the both-daisy range and so a decrease in the range of solar forcings that the daisies are able to survive.

Discussion

Considering the results in a more general biological context, daisy and planet temperature can be regarded as analogous to an internal variable such as core body temperature that must be maintained to within certain bounds in order for the organism to survive. For example,

in humans, core body temperature must be regulated within 35-41 degrees Celsius. Continued values outside of this range may result in death. Such a corpse would not spontaneously reanimate if body temperature would drop back to 41 degrees or any other temperature. Hysteresis may feature in a lag in the drop of temperature as the body employs mechanisms in order to cool itself, but if the internal variable goes far enough outside of this range for the organism to die, then a reduction in hysteresis will not increase the systems robustness to external perturbations

For the black daisies, we can imagine pressures to increase their viability range. Imagine that viability range is determined by a single allele and that this allele is subject to mutation. As the temperature increases, any mutation that increases the viability range will result in a higher number of phenotypes having that allele being present in the population. There is therefore an evolutionary pressure for viability range of the black daisies to increase. As (Lenton & Lovelock 2000) point out, such evolutionary adaptations are bounded by anatomical, developmental and other physical constraints. However there may be viability ranges well within the maximum possible range that results in a decrease in regulation and so decrease in the range of external forcings that the daisies are able to survive.

It is important to note that these observations do not apply to the original Watson & Lovelock Daisyworld. Preliminary results indicate that increasing the viability range increases the range of solar forcings over which the daisies are able to survive. Therefore these findings do not contradict (Lenton & Lovelock 2001) who conclude that decreasing the viability range of the daisies decreases the amount of life on Daisyworld and the range of solar forcings over which the daisies are able to survive.

Conclusion

For the two box Daisyworld model, it has been shown that when the heat conductance constant is set so as to maximise the both-daisy range, increasing solely the viability range of the daisies, whilst keeping all other parameters fixed actually decreases regulation, decreases the range of external forcing over which the daisies remain viable. Analysis of this result involved understanding the positive and negative feedback that the daisies exert on temperature. When the black and white daisy beds are coupled (via heat conductance) in such a way that maximised the both-daisy range, increasing the viability range increases the strength of both feedback loops which at the limits of the any-daisy range results in the temperature going past the optimum and so produces a collapse in the daisy populations.

The 'parable' of Daisyworld was intended as a simplified model of possible global homeostasis. The two box implementation with its further radical simplifications was designed to distill the essential elements of Daisyworld and aid understanding of such homeostatic systems. Many would argue that homeostasis is central to the very concept

of life. E.g. Autopoiesis is homeostasis of ones identity as an organisation. An understanding of basic mechanisms of homeostasis is therefore crucial both for biology and for Artificial Life.

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