A fitness based analysis of Daisyworld

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Abstract

The Gaia hypothesis [1], that the earth functions as a self-regulating system, has never sat particularly comfortably with ideas in mainstream biology [2]. A lack of any clear role for evolution in the model has led to claims of teleology – that self-regulation emerges because it is pre-ordained to do so [3,4]. The Daisyworld parable [5], a simple mathematical illustration of Gaia, went some way to addressing these critiques but, despite recent success in incorporating natural selection [6–9], it remains a widely held view that the ideas are inconsistent with biological principles. We show that standard methodology from population genetics can be used to predict the stationary states and dynamic behaviour of Daisyworlds. The system regulates its temperature due to the low-level evolutionary dynamics of competition between the thermally coupled daisies, no higher level principle is invoked. A reconciliation of Gaia with evolutionary theory may allow further development of evolutionary arguments for the existence of global self-regulatory systems.

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1 Introduction

The Gaia hypothesis as initially proposed by James Lovelock asserted that the living planet is maintained in homoeostasis "by and for the biosphere" [1]. Homoeostasis conventionally refers to the manner in which the human body maintains its internal condition and the term is adopted here to describe how

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the abiotic properties of planetary systems are kept at constant or near constant values by the action of strong, life-induced feedback loops. Lovelock's work as an atmospheric chemist led him to this hypothesis; he observed that the presence of life on Earth had significantly altered the atmospheric composition from the expected chemical equilibrium [10]. The hypothesis has been refined over the years but its central message has remained the same: that life is unconsciously regulating the biosphere to the advantage of living organisms. Only through stressing the unconscious nature of this regulation – particular with reference to Daisyworld – has the Gaia hypothesis been able to refute claims of teleology [7,11].

In this article we shall first describe the original Daisyworld model and an extended one, which permits continuous albedo types originally due to Stocker [6]. This model is important in the development of Daisyworld as more recently developed spatial models [12] make use of continuous albedo phenotypes. Simplifying the analysis of this system allows us to relate it to previous work in mathematical biology. We show how a fitness based approach, originally used in the context of quantitative genetics, may used to both interpret and solve the same model of Daisyworld. We justify our conclusions with reference to simulation studies that exhibit the dynamical and steady state behaviour of our model.

2 Model Definition

Daisyworld is a simplified model ecology conceived by Lovelock [5,13,14] in order to illustrate the self-regulation of a biosphere [1]. Two types of daisies inhabit a ficticious planet, each of which absorbs a different amount of incident sunlight according to its colour or *albedo* – white daisies are totally reflecting (albedo 1), black daisies totally absorbing (albedo 0). The daisies are thermally coupled with one another and with the bare ground on the planet which is assigned an albedo of $a_g = 0.5$. Thermal coupling is not so complete that all daisies are at the same temperature, but strong enough that the temperature of a daisy is not solely determined by its own albedo [5]. There is no explicit spatial structure in this model: all daises are in equivalent thermal contact with one another and with the bare ground. The incident sunlight shines uniformly across the planet; at thermal equilibrium the energy emitted by the planet, given to good enough accuracy by a linearised Stefan-Boltzmann law [1], is equal to the amount of incident solar energy. The daisies' growth is optimised at a particular temperature T_{opt} above or below which the birth rate $\beta(T)$ is

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[1] This approximation is used widely in the literature, beginning with the original paper [5]. We are sufficiently far from the repeated minima of the quartic (at zero) that the linear law is acceptably accurate.

reduced; this dependence is approximated by a quadratic law [5]. The daisies die at a constant rate γ which is wholly independent of the temperature. The Daisyworld model, as just defined, has been solved exactly [15,21].

In the original Daisyworld, defined above, there is no mutation, therefore daisy seeds of both colours are presumed to exist all over the planet. Although the system spontaneously settles to a homoeostatic steady-state for wide ranges of solar driving, there are still teleological concerns as the white and black daisies are present by construction and the appropriate type flourishes when required to maintain homoeostasis [16]. Natural selection is present in the system only as a form of differential survival between the two phenotypes; all variation in the system is present from the outset and the daisies lack the ability to make any further evolutionary change. A model that remedies at least some of these concerns by allowing the daisies to adopt any value of albedo from 0 to 1 (grey-scale daisies) was proposed by Stocker [6], and later Lenton [7]. Mutation is incorporated by allowing the albedo of an offspring to differ from that of its parent by a Gaussian noise term [6] with coefficient m.

3 Direct mathematical approach

This evolvable Daisyworld model may be readily simulated, but an approximate mathematical solution is also possible which follows closely from the analysis by Stocker. It transpires that the governing equations for this Daisyworld are mathematically simpler if, instead of working with the actual occupation distribution, $\alpha(a;t)$, we work instead with the probability distribution of the live daisies, $p(a;t)$. The two are simply related:

$$p(a;t) \equiv \frac{\alpha(a;t)}{1-\alpha_g(t)} \tag{1}$$

where

$$\alpha_g(t) = 1 - \int \alpha(a;t)da \tag{2}$$

We assume here and subsequently that the daisy distribution is sufficiently narrow that the integration range may be extended beyond $[0,1]$ without error (see [6]). This assumption will fail when the limits of regulation are approached and also when the variance of the distribution is large, i.e. when mutation is high; both conditions cause sufficent probabilistic weight to be outside the $[0,1]$ interval. The temporal evolution of this system in terms of the actual occupations by the grey-scale analogues is described by the growth equations used in Daisyworld [5,6,17] modified for this continuous setting

$$\frac{\partial \alpha(a;t)}{\partial t} = \alpha(a;t)\beta(T(a))\alpha_g(t) - \alpha(a;t)\gamma + m\frac{\partial^2 \alpha(a;t)}{\partial a^2} \tag{3}$$

where the final "diffusive" term represents the genetic drift through mutation. The growth function is $\beta(T) = 1 - k(T_{opt} - T(a))^2$ with constant width k and we require that the linear thermal coupling relation between the daisies [5] implies that the local temperature felt by a daisy in the interval $[a, a + \delta a]$ is

$$T(a) = q(A - a) + T_I\frac{(1-A)}{(1-a_g)}, \tag{4}$$

where a_g is the bare ground albedo, A is the overall planetary albedo $(\alpha_g a_g + (1-\alpha_g)\bar{a})$, q is a constant and T_I is the temperature of a dead planet at the same solar driving. From this equation we construct a pair of equations: one representing the temporal behaviour of the amount of bare ground in the system α_g by integrating,

$$\frac{\partial \alpha_g(t)}{\partial t} = (1 - \alpha_g(t))(\gamma - \alpha_g(t)\bar{G}) \tag{5}$$

where $\bar{G} = \int p(a;t)\beta(T(a))da$ and the other, the temporal behaviour of the daisy albedo distribution, $p(a;t)$

$$\frac{\partial p(a;t)}{\partial t} = \alpha_g(t)\left[\beta(T(a)) - \bar{G}\right]p(a;t) + m\frac{\partial^2 p(a;t)}{\partial a^2}. \tag{6}$$

by using the definition (1) and the previous equation (5).

The first equation has two fixed point solutions, one of which is stable and corresponds to the existence of daisies on the planet. The second equation, with the population fixed, has been described by Stocker [6] and also Levins [18,19] in a different setting. A self consistent solution of this equation is a normally distributed phenotype $p(a;t)$, with a constant variance. This may be verified by direct substitution [6] or by integrating for the higher moment equations. Note that the general solution to this equation is in fact a parabolic cylinder function (see appendix), of which the Gaussian is a special case in the limit of constant standard deviation. Our simulation results however (Fig 1) indicate that the Gaussian steady state is indeed the one selected.

For a Gaussian distribution we may derive the first moment equation for the mean albedo from the probability distribution evolution (6) to obtain

$$\frac{\partial}{\partial t}\bar{a} = \frac{2qk\sigma_a^2}{\bar{G}}\left(T_I - T_{opt} + Q(a_g - \bar{a})\right). \tag{7}$$

where Q (given by $q\alpha_g + T_I(1-\alpha_g)/(1-a_g)$) is a rescaled version of the thermal coupling constant q.

We find the planetary temperature at the stationary state, when the time derivatives are zero, to be

$$T = T_I\left[\frac{T_{opt} + \frac{q\alpha_g(1-a_g)}{(1-\alpha_g)}}{T_I + \frac{q\alpha_g(1-a_g)}{(1-\alpha_g)}}\right] \tag{8}$$

which may be binomially expanded to reach the answer $T \simeq T_{opt}$ when $q\alpha_g$ is small compared to the temperatures T_I and T_{opt}. For an inhabited planet $q\alpha_g$ is constrained to be less than T_I for any physically reasonable approximation of heat transfer; in practice for typical parameter choices ($q = 50$) it will be at least an order of a magnitude smaller. This then gives a concise, theoretically derived, statement of the homoeostatic nature of the Daisyworld system.

4 Fitness approach

Whilst the method above works for the simple Daisyworld system, it is desirable to seek a more general method to enable analysis of more complex models that have sought to extend or criticise the Daisyworld model. We now show that we may also approach the problem in a more biologically appealing way using a frequency-dependent fitness. Considering purely phenotypic evolution, the effect of natural selection on the mean phenotype can be described as a closed equation in terms of the mean phenotype and fitness, given that the phenotype is normally distributed and the variance of this distribution does not change with time. The analysis above as well as our simulations show that both these restrictions are reasonably satisfied (Fig 1).

After selection, the next generation will be a fitness-weighted sample from the current population. The change in mean trait brought about by selection will be given by the difference between the fitness-weighted mean trait, $\bar{z}_w$ and an unweighted mean trait $\bar{z}$ [20].

$$\frac{\partial \bar{z}}{\partial t} = \bar{z}_w - \bar{z}$$

$$= \frac{1}{\bar{W}} \int W(z) z p(z;t) dz - \int z p(z;t) dz \tag{9}$$

where, z is the phenotype and $W(z)$ is the fitness of phenotype. For a population with normally distributed trait of variance σ_z^2

$$\bar{W} = \int W(z) p(z;t) dz \tag{10}$$

$$\frac{\partial \bar{z}}{\partial t} = \frac{\sigma_z^2}{\bar{W}} \left[\frac{\partial \bar{W}}{\partial \bar{z}} - \int p(z;t) \frac{\partial W(z)}{\partial \bar{z}} \mathrm{d}z \right], \tag{11}$$

The first term in brackets describes a population maximising its fitness on a static fitness landscape; the second describes the frequency-dependent effects where interactions between organisms are important.

In Daisyworld we identify fitness $W(z)$ as lifetime reproductive success $(\beta(T(a))/\gamma)$ and albedo a as trait z, thus

$$W(a) = \frac{1}{\gamma} \left[1 - k \left(T_{opt} - 2T_I - qa + (q - 2T_I)(\frac{\alpha_g}{2} + (1 - \alpha_g)\bar{a} \right)^2 \right] . \tag{12}$$

Feedback between the daisies and the mean thermal properties of the planet lead to a frequency-dependent fitness. Substituting this form of the fitness into (11) we obtain an exact expression for the steady state that determines the overall planetary temperature, T, for any solar driving. This steady state is identical to that found in the previous section by the direct approach (7), demonstrating, for this particular system, the equivalence of the two differing approaches. Over a wide range of imposed temperatures Daisyworld maintains itself at, or very close to, the optimal temperature for the daisies; this self-regulatory behaviour is a consequence of natural selection acting upon a particular form of frequency-dependent fitness.

5 Computational Work

To support the analytic conclusions in this article we present three contrasting simulation studies: one is inexact but enables the dynamics to be illustrated whereas the other is a stationary solution of the discrete representation of equation (3). Finally we present a novel simulation, based on the first, to illuminate new conclusions we make about Daisyworld models.

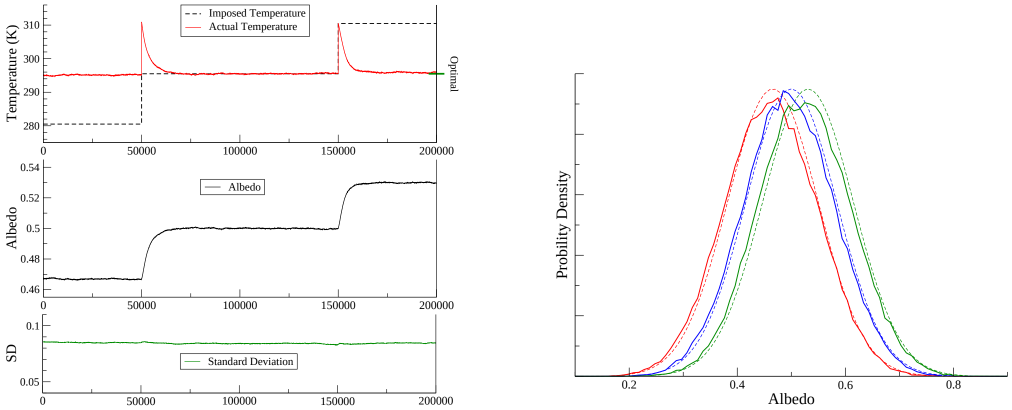

Fig. 1. Simulation Results. On the left figure we illustrate the temperature response of the system (top panel), the albedo response (second panel), invariance of the standard deviation (third panel), the level of site occupation (fourth panel) and the accuracy of the Gaussian approximation on the figure on the right. No error bars are shown as the results are a snapshot run in order for the temporal response of system to be observable. The system was allowed to achieve a steady state with an imposed temperature of $280.5K$ (red distribution). The system was then run for 5×10^4 time-steps before increasing the temperature to $295.5K$. It was then allowed to settle for 5×10^4 time-steps before another distribution snapshot was taken (blue distribution). Finally this process was continued with a further increase to $310.5K$ (green distribution). The Gaussian curve for the given standard deviation and albedo is shown in each case as a dashed line. The optimal temperature of $295.5K$ was preserved throughout in steady state.

5.1 Dynamical Simulation

We create a large number, N, of daisies and vacancies with each daisy taking a random initial value for its albedo in the range $(0, 1)$. An overall average albedo is computed which is then used to calculate the total planetary temperature. At each iteration a random site in the array is selected, if occupied by a daisy it may be killed with probability γ, else if unoccupied a daisy chosen from a random site may spread there with probability $\beta(T_{\text{parent}})$. The parameters used are $N = 10^5$, large enough to suppress finite size effects, $\gamma = 0.2$ to permit sufficiently fast turnover of daisies, $q = 50$ is equivalent to the WL choice and $m = 0.1$ to maintain a narrow distribution of daisies. Other parameters used are taken by convention.

This approach has the advantage that the dynamics of the system can be assessed and consequently we run a stepped simulation in real time in order to demonstrate the relaxation to a Gaussian configuration (Fig 1). This can be seen from (7), where a perturbation from the steady state could be expected to decay exponentially with a relaxation timescale, t_f which is given by

$$t_f = \frac{1}{2\alpha_g qk\sigma_a^2 Q}. \tag{13}$$

A disadvantage of this approach is that it only approximately mimics the analytic equation presented here, indeed this space-free cellular automata (CA) is precisely described by von Bloh et al.[12] in their comparative analysis of Daisyworld CAs. This analysis (equation (22)) shows that the stochastic growth process is incorrect by a factor of $\beta(T)$, but the optimising property of the system means that close to the optimal temperature the two are closely comparable.

5.2 Steady-state solution

We can alternatively follow the analytic model and discretise the system in albedo space following the work and notation of Stöcker [6]. The discretised system is divided into Z albedo regions (indexed by i)

$$\frac{\partial x_i}{\partial t} = x_i(\beta_i(1 - \sum_i x_i) - \gamma) + \tilde{m}(x_{i+1} + x_{i-1} - 2x_i) \tag{14}$$

where $\tilde{m}$ is a rescaling of the mutation rate – we adopt $\tilde{m} = m/Z^2$ as an approximation. The variation with mutation rate has already been described in [6], here we perform more detailed simulations that reveal an interesting comparison with the analytic results. We find that the self consistency relation

$$\begin{aligned} \bar{G} = 1 - kq^2\sigma_a^2 = \frac{\gamma}{\alpha_g} \\ \Rightarrow \sigma_a = \frac{1}{\sqrt{kq}}\left(1 - \frac{\gamma}{\alpha_g}\right)^{\frac{1}{2}} \end{aligned} \tag{15}$$

accurately predicts the standard deviation of the distribution (see (Fig 2)) rather than the mutation dependency as this is strongly dependent of details of the choice of $\tilde{m}$.

The clear constant standard deviation as a function of luminosity in the simulations can clearly be seen, as predicted by our analytics. Deviations from this are caused by the assumption regarding the cutting off of the range of integration as the limits of habitability are approached. This result is apparently at odds with the results of von Bloh et al.who report that the standard deviation decreases as the luminosity is increased (or decreased) away from its

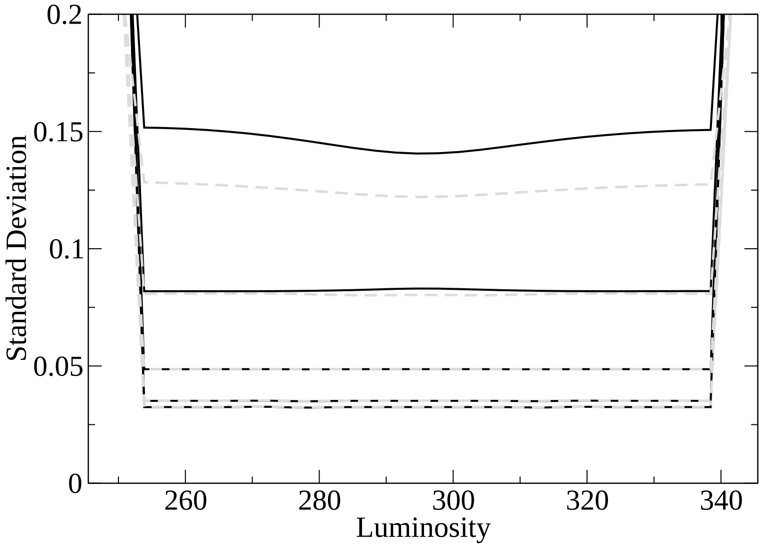

Fig. 2. Results from solving the discretised version of the governing equation using a Runge-Kutta scheme. The plot show 5 different values of m each an order of magnitude large than the next (the top plot has $m = 0.1$). We use 1000 discrete albedo intervals in this solution. The predicted value from the self-consistency relation is shown in dashed grey, the solid black shows our numerically computed solution. The degree of matching is good, with discrepancies caused by the cutting off of the Gaussian tails. This increases with mutation rate as the distribution spreads. The increase in standard deviation asymptotes to a 1/4 power law as m is increased. Crucially the plot shows that the standard deviation of the albedos is constant, independent of L confirming our analytic results when the approximations are valid.

ideal value in their spatial CA simulation. Resolving these two seemingly contradictory results leads to a novel and interesting insight into the Daisyworld system. In the 0-dimensional system described here all the spatial parameters are "integrated out" in order to yield q in an unspecified process that has yet to be described. Importantly this means not only the constants relating to diffusivity (D) and heat capacity (C) but also the spatial configuration of the system, as q is the movement of heat between differing patches. A genuinely spatial system with large patch sizes will express a different q parameter than one with small patches with all else equivalent. The regulatory behaviour of the two system is also different – the spatial system regulates perfectly with only stochastic deviation whereas the "0"-d model has systematic variations (described exactly for the first time in this article). We conclude then that the spatial system is evolving not only its albedo distribution to regulate its temperature it is also evolving its spatial configuration to optimise this regulation. To test this idea we have run a third simulation to examine the validity of this observation which allows q to be a heritable parameter as well as albedo. The results of this are depicted in (Fig 3) which shows how the standard deviation of the albedo distribution varies as a function of temperature. This simulation is run for both the linear and quartic laws for radiative thermal emmision. For both variants of the law, but especially pronouced for the quartic law (as used

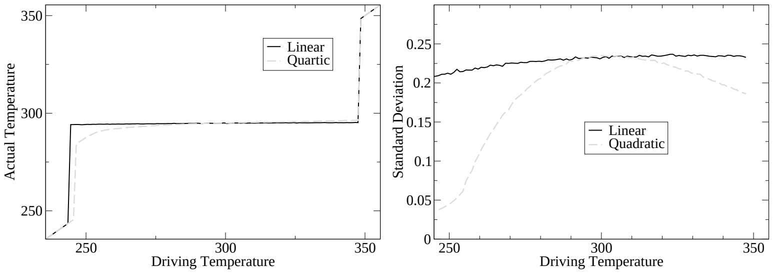

Fig. 3. Results from a new Daisyworld simulation where the q's are heritable. Results from both linear and quadratic are shown as they have differing responses away from the optimal temperature where calibration occurs. The regulatory behaviour is similar (left) and the standard deviation is approximately parabolic in both cases in agreement with the von-Bloh model. This sharply contrasts with the behaviour shown in (Fig 2). This model is a novel Daisyworld simulation and warrants more detailed examination beyond that possible here. We observe that the daisies select very low values of q, indicating their preference to minimise connectivity when subjected to steady driving.

in ref [12]), there is a systematic decrease in diversity when the luminosity is varied in either direction from its optimal value

6 Discussion

We have presented an alternate method for analysing systems with phenotypic variation and environmental feedback. This analytic methodology is well established in quantitative genetics but has not been used before in this context. We have applied a fitness approach to a continuous variants of the original Daisyworld model, presented by James Lovelock [5,13,14], previously a source of some controversy in the biological literature. The method provides analytic foundation to some of the claims in these systems and in the case of the original model an elegant analytic statement of homeostatis $T_{\text{planet}} \approx T_{opt}$. Our simulation studies emphasise the strong regulatory proporties of the system; it is clear that in fully spatial models the underlying structure and connectivity of the model is also being adjusted to assist in maintaining the optimal temperature. It is this feature that distinguishes models that regulate with systematic variations from those that regulate with stochastic variations. This area offers intriguing possibilities for future research.

The technique employed in this paper is predicated on three assumptions: the Gaussian distribution of phenotype; the constant standard deviation of the population; and an appropriate interpretation of the non-overlapping generations and their subsequent selection. We have demonstrated in this article a concise method for solving Daisyworld in which self-regulation is explicitly seen to be an emergent property of competition within the population: what confers reproductive benefit to one daisy (having a higher albedo when the planet is too hot) is also beneficial to the population as a whole (it acts to cool the planet). The generality or otherwise of this emerging state is central to the Gaia Hypothesis and remains an open question.

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Appendix

We provide here a few additional mathematical details as a guide to the derivation of our principle results as well as some extensions. The first step in the analysis is to rewrite the equation for $T(a)$ in what appears to be a non intuitive way, introducing the Q parameter in the process

$$T(a) = T_I + q(\bar{a} - a) + (a_g - \bar{a})Q \tag{16}$$

where $Q = q\alpha_g + T_I(1 - \alpha_g)/(1 - a_g)$ as defined in the main text. We also define a parameter χ via

$$\chi = \frac{1}{q}\left(T_I - T_{opt} + Q(a_q - \bar{a})\right) \tag{17}$$

independent of a, which greatly simplifies the algebra. In particular the quantity $\bar{G}$ can be computed as

$$\begin{aligned}\bar{G} &= \int p(a;t)\beta(T(a))da \\ &= 1 - kq^2 \int (\bar{a} - a - \chi)^2 p(a;t)da \\ &= 1 - kq^2(\sigma_a^2 + \chi^2)\end{aligned} \tag{18}$$

from which the other results follow. Note that any non-Gaussian effects are picked up in the equation by the appearance of the skew of the distribution in the full time evolution equation for the mean albedo

$$\frac{\partial}{\partial t}\bar{a} = \frac{qk\sigma_a^2}{\bar{G}}\left(2(T_I - T_{opt}) + 2Q(a_g - \bar{a}) - k\sigma_a \text{ Skew}_a\right) \tag{19}$$

The last term drops out if the distribution is indeed Gaussian. Unfortunately we cannot prove the distribution is Gaussian, but we have proved that the Gaussian is a self consistent solution of our equations. A further result can be derived by looking at the time evolution of the second moment which is only dependent on precisely the skew and the kurtosis of the distribution, and not itself. As both these regularised higher moment terms are zero for a Gaussian we can formally derive that for a Gaussian distribution the standard deviation must remain constant.

The definitions above also provide a simple way of demonstrating that the fitness based approach derives an identical distribution. We have identified the fitness $W(a) \equiv \beta(T(a))/\gamma$ and thereby the mean fitness $\bar{W}$ can be identified with $\bar{G}/\gamma$. By taking derivatives we find

$$\frac{\partial \bar{W}}{\partial \bar{a}} = \frac{2kq\chi Q}{\gamma} \tag{20}$$

$$\frac{\partial W(a)}{\partial \bar{a}} = \frac{2kq(q-Q)(a-\bar{a}-\chi)}{\gamma} \tag{21}$$

by integrating (21) and combining with (20) in Lande's relation we immediately find the result (7).

For completeness we also include the complete analysis of equation (6). By writing $x = a - \bar{a}$ we may find a differential equation for $p_{\text{ss}}(a)$ the steady state solution for the probability distribution.

$$\frac{\partial^2 p_{\text{ss}}(x)}{\partial x^2} + \frac{1}{\sigma_a^4}\left[\sigma_a^2 - x^2 + 2\chi x\right] p_{\text{ss}}(x) = 0 \tag{22}$$

where

$$\sigma_a^4 = \frac{m}{\alpha_g k q^2} \tag{23}$$

the standard deviation of a Gaussian when $\chi = 0$. We may also define

$$\chi = \frac{1}{2q}\left(2(T_I - T_{opt}) + Q(1 - 2\bar{a})\right) \tag{24}$$

a quantity whose usefulness will become apparent.

We can now bring equation (22) into a recognisable form by making a further substitution $z = \sqrt{2}(x - \chi)/\sigma_a$ which leads to equation

$$\frac{\partial^2 p_{\rm ss}(z)}{\partial x^2} + \left[\frac{1}{2} + \frac{\chi^2}{2\sigma_a^2} - \frac{z^2}{2}\right] p_{\rm ss}(z) = 0. \tag{25}$$

By comparison with (25) [22] we can now identify $p_{\rm ss}(z) = D_l(z)$. This is Weber's Parabolic Cylinder Function with $l = \frac{\chi^2}{2\sigma_a^2}$. There do not exist expressions for the moments of this distribution but we can immediately observe that in the limit as $l \to 0$ the Weber's function becomes a Gaussian. However this limit is not well defined as there do not exist normalisable analytic continuations for non-integer l for this function, as is known in mathematical physics [23]. The constraint of normalisability implies that the distribution of daisy albedo cannot be skewed in response to any perturbation. The only freedom left to the system is to alter the amount of bare ground, invalidating the form of (25) and the corresponding parabolic cylinder function solution. We observe through simulation that external fluctuations are primarily absorbed by a change in the amount of bare ground in the system rather than a change in the daisy albedo distribution. This is perhaps at odds with the naive expectation that the distribution would skew to accomadate external changes before recentring around a new mean albedo value.

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