The Traill island model, how it compares to previous work and a proposed low-dimensional simplification

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The Gilg, Hanski & Sittler (2003) model for Arctic lemmings

The predator-prey community in Gilg *et al.* (2003) is constituted of one prey species, the collared lemming, and its four predators: the stoat, the Arctic fox, the long-tailed skua and the snowy owl. The basic structure of the model is that of a coupled system of nonlinear differential equations for the lemming and stoat populations (present year-round and all years), with time-varying terms. The time-varying part of the model results largely from avian and fox predation on lemmings, which happens only in the summer, in addition to a heightened intrinsic population growth of lemmings in winter. Finally, another forcing term comes from the stoat reproduction, which is modelled as a discontinuous burst, the stoat population being multiplied by $(1 + v)$ every year in the spring. The model here is slightly reformulated to make its mathematical structure more apparent. The lemming population dynamics are described by

$$\frac{dN}{dt} = \underbrace{r(t)N}_{\text{exp. growth}} - \underbrace{\Gamma(N, N', t)}_{\text{generalist predation}} - \underbrace{\frac{cN^2 P}{D^2 + N^2}}_{\text{specialist predation}} . \tag{1}$$

For convenience, we will count time in unit of years, and define the variable $t_{mod} = t \equiv 1$, hence t_{mod} is time of year between 0 and 1. A key variable is N', the lemming density at snowmelt:

$$t_{mod} < t_{\text{snowmelt}}, \qquad N' = N(t) \,\&\, r(t) = r_w$$
$$t_{mod} > t_{\text{snowmelt}}, \quad N' = N(t_{\text{snowmelt}}) \,\&\, r(t) = r_s \tag{2}$$

N' can be thought of as a perceived lemming density by generalist and nomadic predators upon their seasonal arrival to the system, that introduces a short time delay in summer in the model (decisions made by the predators are conditional to N'). The generalist predation term $\Gamma(N, N', t)$ is exactly zero in winter, and changes during the summer as a function of settlement and reproduction schedules of the various predators. The stoat density P has dynamics of the form

$$\frac{dP}{dt} = -(d_h + \Delta(N)(d_l - d_h))P \tag{3}$$

with d_h the maximum stoat death rate and d_l the minimum death rate, and $\Delta(N)$ a sigmoid function between 0 and 1, that makes the dynamics switch between the two mortality rates according to the formula $\Delta(N) = 1/2 + \arctan(b(N - D))/\pi$. In other words, there is more predator death when there is no food. The stoat compartment is submitted to an external forcing, i.e. each year at time t_{stoat} the integration stops and the predator density switches from P to $P(1+v)$ where v is the number of offsprings (the youngs are assumed to be equivalents to adults).

The generalist predation rate can be decomposed into 3 separate terms corresponding to the different predators (both for adults and juveniles, the latter being counted in "adult equivalents"). It is a function of time through the predator densities:

$$\Gamma(N, N', t) = \underbrace{\frac{W_f N^2(P_f(t) + P_{yf}(t))}{D_f^2 + N(t)^2}}_{\text{fox}} + \underbrace{\frac{W_o N(t)^2(P_o(t) + P_{yo}(t))}{D_o^2 + N(t)^2}}_{\text{owl}} + \underbrace{\frac{W_l N(t)^4(P_l(t) + P_{yl}(t))}{D_l^4 + N(t)^4}}_{\text{skua}}. \tag{4}$$

The numerical response of the predators (and hence, the seasonal variation in the generalist predation pressure) is fully described in Table 1.

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Predator	Adults (when present)	Youngs x Growth youngs	Arrival date	Leaving date	Birth date
Fox	$P_f = \frac{b_f N'^2}{Y_f^2 + N'^2}$	$P_{yf}(t) = \frac{b'_f N'^2}{Y_f'^2 + N'^2} \times \frac{1}{1+e^{-0.36(365 t_{mod}-9)}}$	$t_{ofa} = 0.52$	$t_{fall} = 1.0$	$t_{\text{snowmelt}} = 0.65$
Owl	$P_o = \frac{b_o(N'-2)}{Y_o + N'-4}$	$P_{yo}(t) = \frac{b'_o(N'-2)}{Y'_o + N'-4} \times \frac{1}{1+e^{-0.36(365 t_{mod}-9)}}$	$t_{ofa} = 0.52$	$t_{fl} = 0.94$	$t_{\text{birth owl}} = 0.67$
LT skua	$P_l = 0.02$	$P_{yl}(t) = \frac{b'_l N'^2}{Y_l'^2 + N'^2} \times \frac{1}{1+e^{-0.464(365 t_{mod}-4.55)}}$	$t_{la} = 0.62$	$t_{ll} = 0.81$	$t_{\text{birth skua}} = 0.72$

Table 1: Numerical responses of generalists. The density of adults in the first column apply only during the period between the arrival and leaving dates mentioned in the 4th and 5th columns. The density of youngs is conditional on that of the adults being positive, and will be non-zero after the birth date. $P_o = 0$ whenever $N' < 2$. Note, for comparison, that the time of stoat reproduction is $t_{stoat} = 0.69$.
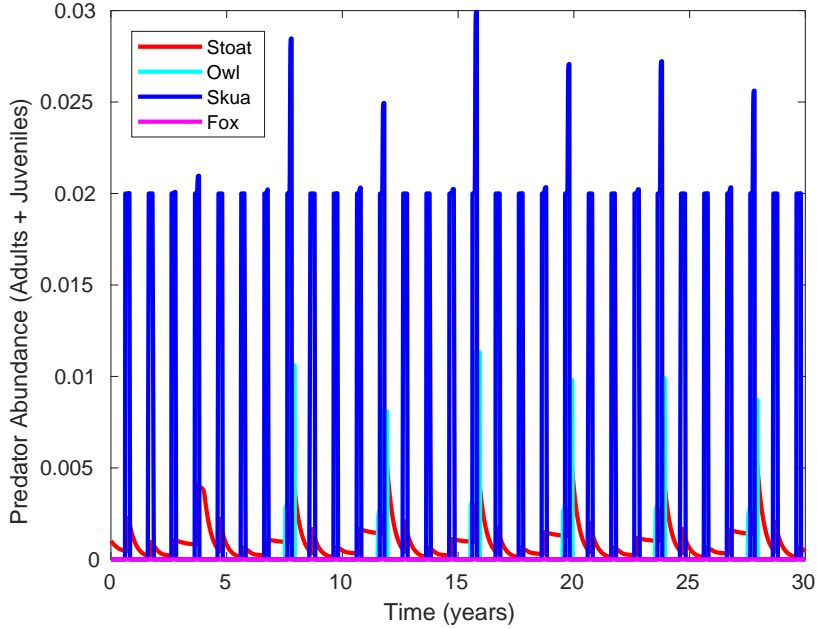

Figure 1: Predator abundances over time in the Gilg et al. (2003) model for the reference parameter set with all predators present.

This seasonal and large mortality (≈ 80 to 90% of lemming individuals are eaten by skuas and owls over the summer in peak years[1]) is in effect *equivalent to a very large seasonal perturbation*, mirroring theoretical results that show the oscillation-generating effects of such seasonal perturbations (Rinaldi *et al.*, 1993; King & Schaffer, 2001; Taylor *et al.*, 2012). Simulations of another, simplified Lemming-Stoat-Skua (LSS) model[2] adapting the framework of Turchin & Hanski (1997) to reduce the model complexity of the Gilg et al. (2003) model, show that the 95% upper quantile of lemming values can be increased by a factor of about 1.3 in case of seasonal rather than constant generalist predation. Hence seasonal generalist predation, together with other sources of seasonality (e.g., in birth rates,

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[1] computed for a few peaks with the model
[2] which assumes that all generalist predators behave like skuas
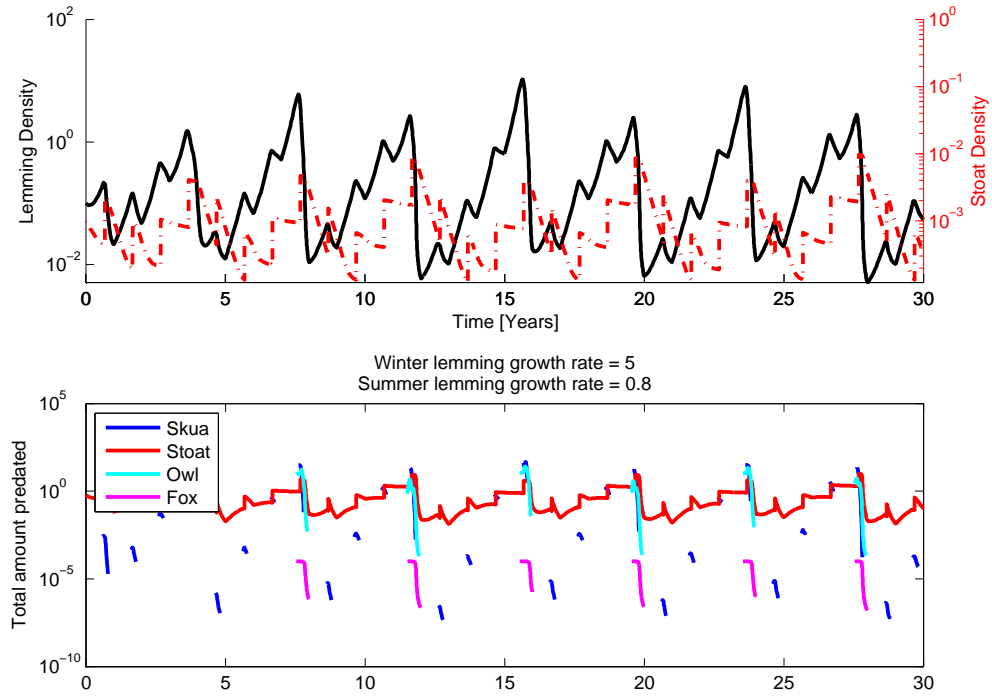
Figure 2: **Population cycles and predation rates in the Gilg et al. (2003) model, in logarithmic scale.** Parameters for lemming and stoats: $r_W = 5$, $r_S = 0.8$, $v = 4.0$, $c = 1000$, $D = 0.08$, $N_{crit} = D$, $d_l = 0.1$, $d_h = 4$, $b = 25$. Lemming density is given in individuals per ha.
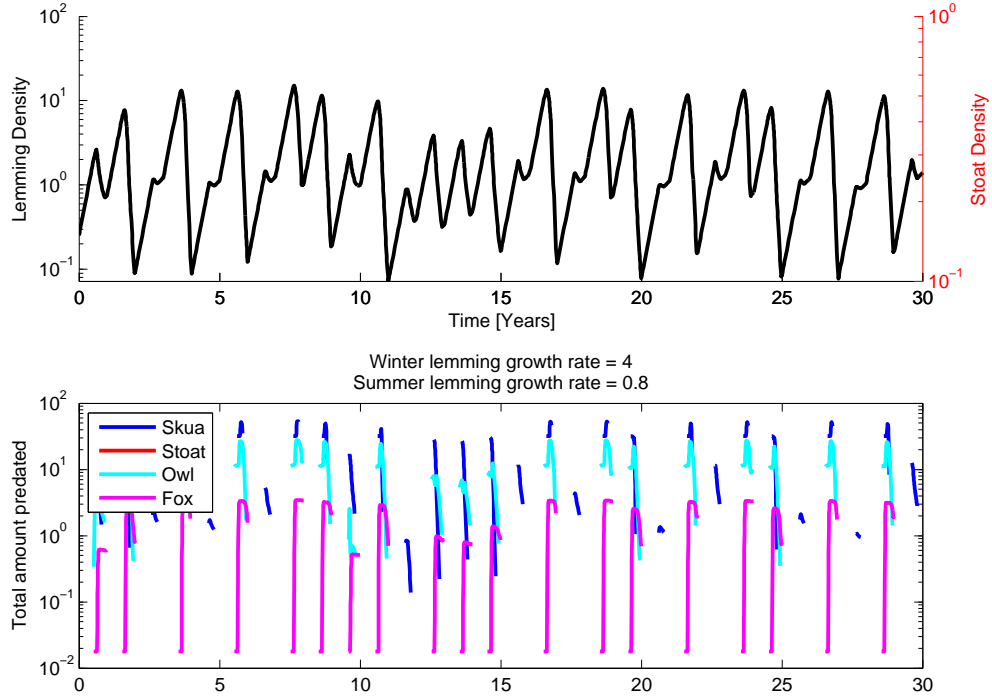
Figure 3: **2-year population cycles (and transients) in the Gilg et al. (2003) without mustelids.** Parameters for lemming growth: $r_W = 4$, $r_S = 0.8$, $v = 4.0$, $c = 1000$, $D = 0.1$, $N_{crit} = D$, $d_l = 0.1$, $d_h = 4$, $b = 25$. The max. number of owls has been multiplied by two.

Taylor *et al.*, 2013), can increase the potential for high-amplitude oscillations. Our LSS model does confirm, however, that increases in the *average* quantity of generalists (G) such as skuas decreases cycle amplitude and periodicity like shown in Turchin & Hanski (1997).

The Gilg *et al.* (2003) model without mustelids, but with generalist predators, can exhibit 2-year population cycles for some parameter values (Fig. 3), and this is largely due to the recruitment of juveniles foxes at the end of the cycle. We initially spotted this because of a typo in Gilg *et al.* (2003)'s Supplementary Material (which has been corrected in Gilg *et al.*, 2009 and did not affect Gilg *et al.*, 2003's simulations) where the max density of owls b_0 had been multiplied by two. Two-year population cycles do not appear for the standard parameter set of Gilg *et al.* (2003), but it is easy to imagine that for a slightly different predator composition at another study site, such short-term fluctuations might become possible.

On the other hand, removing the skua population in the differential equations model leads to a blow-up (unstable oscillations diverging away from the attractor). Therefore, our interpretation of the cycles in the model of Gilg *et al.* (2003) is that:

1. Long-tailed skuas keep the lemming cycle within bounds through predation during the summer

and generate, together with owls, strong seasonal forcing. Their influence is therefore two-fold: (a) their generalist predation tends to keep lemmings in check but (b) the fact that such predation is seasonal contributes to the population cycling.

2. The slightly delayed reproductive response of foxes can for some parameter sets create a short-period (2-year) cycle in absence of mustelids.

3. Stoats generate an eventually unstable lemming-stoat oscillation, which is transformed into a more sustainable attractor by generalists (skuas in particular).

Our conclusion is therefore that both 'generalists' such as skuas/owls/foxes and specialists such as mustelids contribute to some degree to generating collared lemming fluctuations in the Traill Island model. These considerations open up new challenges in defining the precise role of generalist (or nomadic specialists) versus resident specialist predators.

Comparison to the vole weasel-model of Turchin and Hanski (1997)

The model of Turchin & Hanski (1997) can be written

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \underbrace{\frac{GN^2}{C^2 + N^2}}_{\text{generalists}} - \underbrace{\frac{aNP}{D + N}}_{\text{specialists}} \tag{5}$$

$$\frac{dP}{dt} = sP\left(1 - q\frac{P}{N}\right) \tag{6}$$

Adding seasonality and adimensionalizing, we arrive at

$$\frac{dn}{dt} = r(1 - e\sin(2\pi t))n - rn^2 - \frac{gn^2}{h^2 + n^2} - \frac{an}{n + d} \tag{7}$$

$$\frac{dp}{dt} = s(1 - e\sin(2\pi t))p - sp^2/n \tag{8}$$

with possibly a small noise term on all parameters, so that each parameter Π_t is transformed once a year into $\Pi_t(1 + \sigma\epsilon_t), \epsilon_t \sim N(0, 1)$. This models reproduces the Fennoscandian gradient when G is increased from South to North. We use here the parameters $r = 6$, $e = 1.0$, $K = 150.0$, $s = 1.25$, $C = 600.0; D = 6.0, , Q = 40.0;, G = 60.0, H = 15, \sigma = 0$.

In Fig. 4 below we illustrate the time series of weasel and vole densities as well as the total amount killed per unit time for specialists or generalists, which shows that specialist predation is superior to generalist predation during vole population declines.
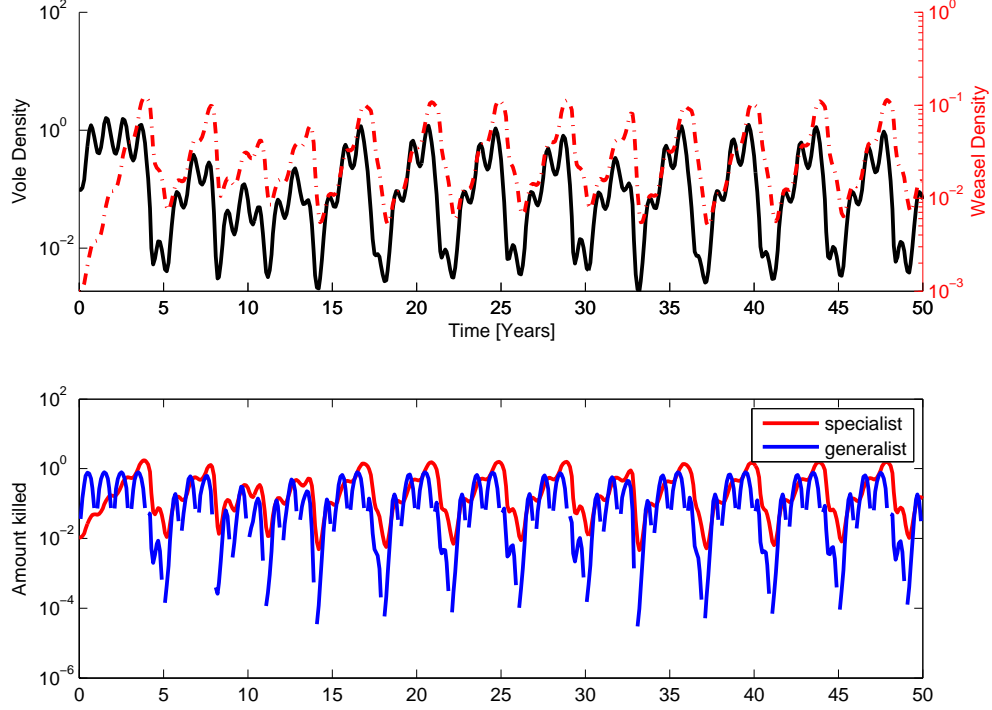

Figure 4: **Densities and predation rates** in the Turchin & Hanski (1997) model.

In contrast, the model we adapted for modelling Greenland lemmings using the same model framework shows a slightly different kind of dynamics.

"Pooled generalists" model (aka Lemming - Stoat - Skua)

Because there are very many parameters in Gilg *et al.* (2003) (≈ 25), we constructed a simplified model to compare its behaviour to Turchin & Hanski (1997). The model assumes that all generalists behave like the skua (the more abundant generalist, with numbers that only depend on the season and not on other species densities). It also assumes that the numerical response has the more simplifed Leslie-type form of Turchin & Hanski (1997), which allows to formulate a smooth model. The LSS model uses a winter indicator variable $W(t) = \frac{1}{2}(1 + \cos(2\pi t))$. The time $t = 0$ is in january, so that $W = 1$ in full winter, 0 in full summer. The full differential equation model then writes

$$\frac{dN}{dt} = r_{min}N + (r_{max} - r_{min})W(t)N - r_{max}\frac{N^2}{K} - \underbrace{\frac{G(1 - W(t))N^4}{H^4 + N^4}}_{\text{generalist = skua}} - \underbrace{\frac{CN^2P}{D^2 + N^2}}_{\text{specialist = stoat}} \qquad (9)$$

$$\frac{dP}{dt} = sP\left(1 - q\frac{P}{N}\right) \qquad (10)$$

Parameters are tailored for the Greenland Traill island case study: $r_{max} = 6$, $r_{min} = 0.5$, $K = 500$, $G = 50$, $H = 2$, $C = 1000$, $D = 0.1$, $s = 1.75$, $Q = 100$. See Taylor *et al.* (2013) for other interesting parameterizations of similar seasonal models. Because the carrying capacity K in absence of predation was absent in the Traill island model, it is here set to a large value, but it is notable that the LSS model can also work without. The functional response exponents have been taken in accordance to Gilg *et al.* (2003) and are all sigmoid (Type III), in contrast to the more classical choice of type II response for specialists and type III for generalists in Turchin & Hanski (1997).

Simulating this model, Fig 5 below, we see that the predation by generalists in summer is much higher than that of the specialist (note the logarithmic scale), in constrast to Turchin & Hanski (1997). We also see very clearly that generalists clearly initiate the lemming declines, by "cropping off" the lemming peaks.
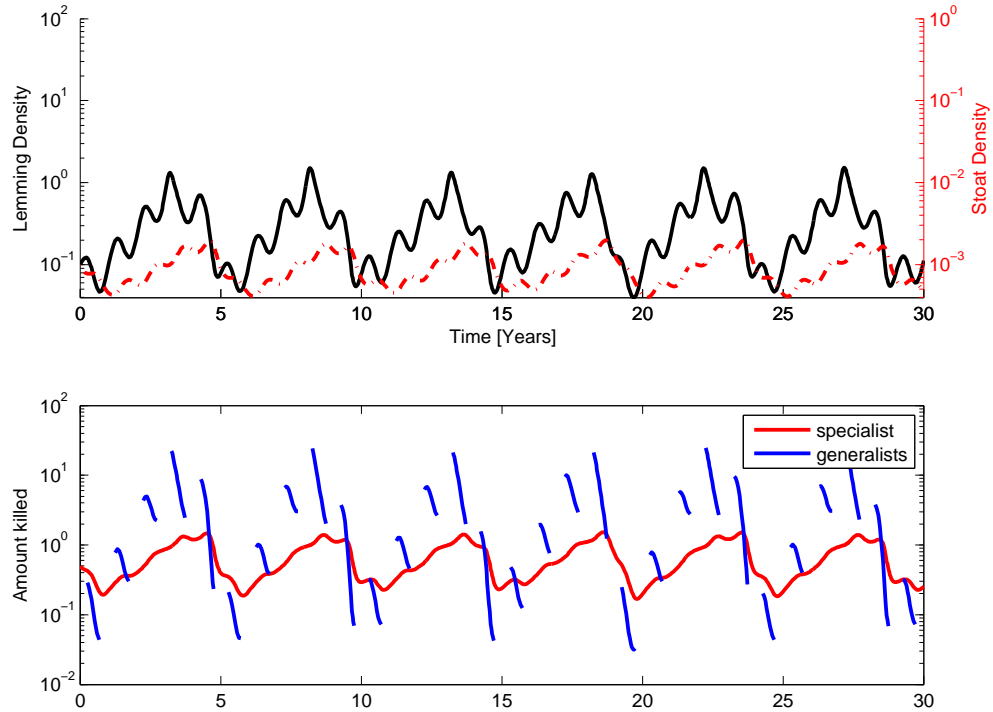

Figure 5: "Pooled generalists" LSS model simulation.

A cautionary tale on cycle shape in mechanistic models

It has been proposed that cycle shape can be a proxy for cycle causation (Turchin *et al.*, 2000). We offer a different view here. A difficulty with the numerous mechanistic mathematical models available to model rodent cycles is that they tend to produce cycles with correct periodicity and amplitude, but with shapes often different from that of the data. In other words, mechanistic models with empirically estimated parameters might not fit all the details of the cycle very well. For example, in Korpimäki *et al.* (2002, Fig. 4) the mechanistic predation model consistently produces cycles that rank in the right side of Royama's triangle, where delayed density-dependence generates the crashes after a plateau at high density (Royama, 1992). However, the data shows often faster crashes, ranking on the left side of the triangle (Fig. 4 in their paper). Conversely, the model in Gilg *et al.* (2003) cited above tends to produce fast crashes in just one year while the data show crashes occurring over one or two years. This is arguably an undesirable property of the model (Oksanen *et al.*, 2008), which incidentally refutes the claims of Turchin *et al.* (2000) that "prey peaks" have a rounded shape. The models by Korpimäki *et al.* (2002) and Gilg *et al.* (2003) therefore seem to be equally good at describing periodicity and amplitude of the time series, but equally limited to reproduce cycle shape[3]. With very rich datasets (>100 data points), it might be possible to find the most likely models just based on cycle shape, but given the limited data available here ($\approx$ 25 years with no spatial replication, which is common in many stuch study sites), such endeavours may be a little premature. Mechanistic mathematical models may be best interpreted as illustrating what is *possible,* rather than what is actually happening in real populations. Although in some cases, it may be possible to at least rank different scenarios based on very contrasted models (Kendall *et al.*, 2005).

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[3]Surely this applies to many other mechanistic models...

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