The Effects of Predation and Inbreeding Depression on the Viability of a Small Population: Analysis of a Mathematical Model

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The model of Hartt and Haefner (1995) which represents the combined effects of predation and inbreeding depression on a population is re-analysed. It is demonstrated that the system has two trivial equilibria with one or both species extinct and one non-trivial equilibrium with both species present. Conditions on parameter values for the existence of these equilibria are obtained explicitly. The effect of varying parameter values on the size of the two populations at non-trivial equilibrium is also obtained analytically. Local stability analysis is used to obtain an expression for the conditions under which this equilibrium will be stable or oscillatory. Inbreeding depression does not affect the stability of the model predator-prey system. These results are used to speculate on the static and dynamic effects of plausible modifications to the model structure. The principle conclusion is that inbreeding depression decreases the size of the predator population but not that of the prey. The practical implication of this result is that managers should be aware that the effect of inbreeding depression in one species may not be obvious in population changes in that species but may have a major impact in another species within the ecosystem.

Keywords: inbreeding depression, predator-prey, local stability, equilibria.

1. Introduction

Much interest in conservation biology had been devoted to the idea of a threshold population size above which the risk of extinction could be considered low (Soule, 1987). Small populations can be considered at risk for two reasons: demographic and genetic. The stochastic nature of birth and death processes has a more serious effect on small populations and this has been the subject of considerable study (e.g., Pimm, 1991). Small populations are also more at risk from the reduced individual fitness caused by inbreeding. This inbreeding depression has produced another strand of research into minimum viable population sizes (e.g., Hendrick and Miller, 1992). However, it is clear that these two effects will interact with each other and there have been a few studies which investigate this interaction (Lande, 1988; Saloniemi, 1993).

Recently, Hartt and Haefner (1995) presented a model which they used to investigate
the interaction between predation and inbreeding depression on a population’s viability. This model was subjected to a limited investigation by means of numerical simulation for a set of parameter values which the authors considered to be plausible. Here, I re-investigate both the static and dynamic properties of the model using analytic methods already well developed for such systems in the absence of genetic effects. This analysis allows some of Hartt and Haefner’s observations to be confirmed with a great deal more generality and allows further insight about model behaviour to be drawn.

2. The model

Hartl (1988) defines the inbreeding coefficient ($F$) of an isolated population of size ($N$) by the equation

$$\frac{dF}{dt} = \frac{1 - F}{2N}$$

(1)

In the absence of external perturbations, this variable will reach an equilibrium value (unity) which is independent of the population size. However, the size of the population does affect the rate at which equilibrium is reached: the smaller the population the slower the rate of change in $F$.

In the absence of predation, the population ($N$) is assumed to follow a logistic equation:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right)$$

(2)

where $r$ is the intrinsic growth of the population and $K$ is its carrying capacity.

In order to incorporate the effect of inbreeding depression, the intrinsic growth rate ($r$) is separated out into a constant birth rate ($b$), a constant mortality rate ($A$) and a further death rate due to inbreeding depression (a constant ($B$) multiplied by the inbreeding coefficient ($F$)): i.e.

$$r = b - (A + BF)$$

(3)

The population ($N$) is preyed upon by another population ($P$), each member of which is assumed to capture prey individuals at a rate given by the traditional type II functional response (e.g. Ruxton et al., 1992):

$$\frac{cN}{1 + chN}$$

(4)

where $c$ describes the rate at which prey items are encountered and $h$ is the mean time required to process a prey item before being able to capture another.

Adding the effects of inbreeding depression and predation gives the rate of change in the prey populations as

$$\frac{dN}{dt} = \left((b - (A + BF))N \left(1 - \frac{N}{K}\right) - \frac{cNP}{1 + chN}\right)$$

(5)
Assuming that captured prey are converted to predators with constant efficiency \( a \) and predators die at a constant, rate, \( D \), the rate of change in the predator population is given by

\[
\frac{dP}{dt} = \frac{aCN}{1+chN} - DP \tag{6}
\]

3. Population equilibria

At equilibrium, the rates of change in \( F \), \( N \) and \( P \) are all zero. Setting Equation (1) to zero gives

\[
\frac{dF}{dt} = \frac{1-F}{2N} = 0 \tag{7}
\]

Assuming that the prey population is finite, this gives the equilibrium inbreeding coefficient as

\[ \tilde{F} = 1 \tag{8} \]

Setting Equation (6) to zero gives

\[
\frac{ac\tilde{N}\tilde{P}}{1+ch\tilde{N}} = D\tilde{P} \tag{9}
\]

This inequality can be satisfied in two ways, either \( \tilde{P} = 0 \), or \( \tilde{P} \neq 0 \) and

\[
\tilde{N} = \frac{D}{c(a-hD)} \tag{10}
\]

Similarly, the rate of change in the prey population is zero when the following equality is satisfied:

\[
(b-(A+B\tilde{F}))N\left(1-\frac{\tilde{N}}{K}\right) = c\tilde{N}\tilde{P} \tag{11}
\]

This equality can be satisfied in three ways: if \( \tilde{N} = 0 \), if \( \tilde{N} = K \) and \( \tilde{P} = 0 \) or if

\[
\tilde{P} = \frac{(b-(A+B))(K-\tilde{N})(1+ch\tilde{N})}{cK} \tag{12}
\]

where \( N \) is given by Equation (10).

Thus, the system has two trivial equilibria, one where both populations are extinct and the other where the predator population is extinct and the prey population is at its carrying capacity. In addition, there is a non-trivial steady state given by Equations (8), (10) and (12). To be biologically meaningful, we demand that both equilibria values \((\tilde{N}, \tilde{P})\) must be positive; from the equations above, this is satisfied providing the following conditions are met:
These conditions can be interpreted intuitively. If the prey population parameters fail to satisfy condition (i) then the intrinsic rate of growth of the prey population is always negative. Under these circumstances, the prey population will inevitably decline to extinction, closely followed by the predator population. Hence, we predict that integration of the differential Equations (1), (5) and (6) when this condition is not met will result in the extinction of both populations, regardless of the initial values of the three variables.

Notice from Equation (4) that the maximum rate at which a predator can consume prey is $h^{-1}$. This rate occurs when the prey population is infinitely large. This means that the maximum rate (per capita) at which the predator population can grow is $h^{-1}$. Hence, if condition (ii) is not satisfied, then the predator’s rate of growth will always be less than the death rate. When this occurs the predator population will simply decline to zero, allowing the prey population to grow unchecked to its carrying capacity. Hence, failure to satisfy condition (ii) causes the system to revert to the other trivial steady state.

Substituting for $N_A$ in condition (iii) and rearranging gives

$$D < \frac{caK}{1 + chK}$$

(16)

Condition (ii) is not sufficiently strict. In practice, the maximum rate at which a predator can catch prey is less than $h^{-1}$. This occurs because the prey population cannot become infinite, it is bounded above by $K$. The maximum (per capita) rate of increase of the predators in this system is given by the right-hand side of Equation (16). Conventionally, Equation (16) is rearranged to the form

$$K > \frac{D}{c[a - hD]}$$

(17)

We can now consider the effect of varying the strength of the effect of inbreeding depression ($B$) on the system steady states. First, we observe that if $B$ is too high, specifically if

$$B > r - A$$

(18)

then the prey population is unable to grow and both populations go extinct. If a non-trivial equilibrium exists then Equations (10) and (12) describe the effect of increasing $B$ on the steady states of the two populations. The prey equilibrium population is unaffected by increasing $B$, but the predator population is reduced.

4. Population dynamics

When inbreeding depression has no effect on the prey (i.e. $B = 0$) the local stability of the model can be obtained analytically with relative ease using the Ruth-Hurwitz
Figure 1. Diagram showing the effect of varying the prey carrying capacity \((K)\) and inbreeding parameter \((B)\) on the existence and stability of the internal equilibrium. In the stable region, the two populations both settle to constant values; in the unstable region, both perform oscillations about the equilibrium values. The boundary between the two represents points in parameter space where the real parts of the eigenvalues of the Jacobian evaluated at the equilibrium point are all zero. This was found numerically. The constant \(K\) value of this line was in agreement with the analytic value given in Equation (19).

Criteria (e.g. see Nisbet and Gurney, 1982). This is done in the Appendix. The internal steady state is stable provided that the real parts of both eigenvalues of the Jacobian evaluated at the equilibrium are negative. This is ensured, providing that

\[
K \leq \frac{1}{c} + \frac{2D}{c(a-hD)}
\]  

(19)

is met. When \(B\) has a non-zero value, the Jacobian has three eigenvalues. The effect of the strength of inbreeding depression \((B)\) on stability of the non-trivial steady state was investigated by numerical solution of the eigenvalues of the Jacobian. The results are shown in Figure 1 where other parameter values are chosen to be the same as those used in Hartt and Haefner (1995).

As can be seen, the size of the coefficient of inbreeding depression \((B)\) has no effect on the stability properties of the system for these parameter values. Further numerical investigations suggest that this result holds generally for any choice of parameter values. Indeed, this result could be obtained using the Ruth-Hurwitz criteria for three interacting species but the algebra required is very involved. Fortunately, it is easy to understand this result by examination of the equation above. Notice that the stability condition in the absence of inbreeding depression is independent of the size of the intrinsic death rate of the prey \((A)\). Since inbreeding depression serves only to increase the size of the prey's intrinsic death rate, it comes as no surprise that inbreeding depression has no effect on the stability of the system.
5. Discussion

The main conclusion of the analysis of the statics of the system is that increasing the strength of inbreeding depression in the prey species (increasing $B$) has no effect on the size of the prey equilibrium population but decreases that of the predator. This effect was demonstrated for a limited set of parameter values by the numerical simulations of Hartt and Haefner (1995), but here I show that the result holds quite generally. The practical implication of this result is that, in natural systems, inbreeding depression in one species may apparently have no harmful effect on that species but may be having a considerable detrimental effect on another species. Hence, when wildlife managers monitor the effect of inbreeding depression it may be advisable to look beyond the population dynamics of single species and study the whole ecosystem in which they interact, since other species may suffer great change at population level which does not occur in the principle species of interest. Notice also that this result should not be taken to suggest that the species suffering the inbreeding depression is itself not in danger. Notice in the model that if $B$ becomes higher than a threshold value then both populations crash to extinction.

Models can not only predict the size of equilibrium populations, they can also predict the effect of perturbing the system from this equilibrium. If the equilibrium is stable, then perturbations die out and the system returns to equilibrium; if the system is unstable, then perturbations grow and the system can cycle around the equilibrium. Changes to a system which have little effect on equilibrium values can still have a considerable effect on the change stability properties. The oscillations set up can cause populations in the trough of the cycles to fall to dangerously low levels. My analysis is able to demonstrate that all the effects observed by Hartt and Haefner (1995) occur through a reduction in the predator equilibrium density population and not through destabilisation. However, changes in stability through inbreeding depression should be of concern to environmental managers, as outlined below.

There is no reason why inbreeding depression should act only in the prey species and not in the predators. Indeed, in general, predators tend to be bigger than their prey and to live in smaller populations and so may be more prone to inbreeding depression. One of the strengths of the analytical techniques used here is that we can use the results we already have to predict the effects of adding inbreeding depression in the predator species. If we consider that inbreeding depression serves to decrease the predators' prey conversion efficiency ($\alpha$), then from Equation (10) we see that this will always increase the size of the prey population, from Equation (12) that its effect on the predator population depends on the size of other parameters, and from Equation (19) that unstable dynamics will become less likely. This suggests that inbreeding depression might, in some cases, produce a beneficial effect of reducing the propensity of populations to fluctuate. However, there will be some cost in terms of reduced population means. The model should allow managers to quantify these two effects.

Whilst I suggest that the analysis presented here can be more powerful than the numerical simulations used by Hartt and Haefner (1995), I do not mean to suggest that such simulations are redundant. They can provide information which cannot be obtained analytically, such as investigation of the amplitude of any oscillations in population values. Both approaches should be used together. The genetic issues involved in the conservation of small populations is an area of intense current interest and there is growing awareness that genetic and population dynamic considerations must be considered together. Mathematical modelling is quick, inexpensive and non-invasive...
and should be a useful tool in helping to understand the interaction between these two considerations, both at population and ecosystem levels.

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References


Appendix

The Ruth-Hurwitz criteria for local stability of a system of two interacting populations is that both the determinant of the Jacobean evaluated at equilibrium should be positive and the trace should be negative (see, for example, Nisbet and Gurney, 1982). When B is set to zero, the Jacobean for the simplified predator-prey model is given by

\[
\begin{pmatrix}
(b-A)\left(1-\frac{2N}{P}\right) & \frac{cP}{(1+\text{chN})^2} & -\frac{CN}{1+\text{chN}} \\
acP & 0
\end{pmatrix}
\]

where

\[N = \frac{D}{c(a-hD)}\]  \hspace{1cm} (20)

and

\[P = \left(\frac{b-A}{c}\right)\left(1-\frac{N}{K}\right)(1-\text{chN})\]  \hspace{1cm} (21)

By inspection, the determinant is always positive when the internal steady state exists. The other condition can be recast as

\[
\frac{cP}{(1+\text{chN})^2} - (b-A)\left(1-\frac{2N}{K}\right) > 0
\]

We now use a rearrangement of relation (21).
\[
\frac{cP}{1+chN} = (b - A) \left(1 - \frac{N}{K}\right) \tag{23}
\]

Substituting this into the stability condition above and rearranging gives
\[
\left( b - A \right) \left( \frac{N}{K} \right) (1 + 2chN - chK) > 0 \tag{24}
\]

If the non-trivial steady state exists then both the terms in the first two parentheses are positive; hence, we have that this equilibrium is locally stable when
\[
K < \frac{1 + 2chN}{ch} \tag{25}
\]