A UNIFYING APPROACH TO DISCRETE SINGLE-SPECIES POPULATIONS MODELS

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Abstract. In this article, we write the recruitment function \( f \) for the discrete-time density-dependent population model
\[
p_{n+1} = f(p_n)
\]
as \( f(p) = p + r(p)p \) where \( r \) is the per capita growth rate. Making reasonable assumptions about the intraspecies relationships for the population, we develop four conditions that the function \( r \) should satisfy. We then analyze the implications of these conditions for the recruitment function \( f \). In particular, we compare our conditions to those of Cull [2007], finding that the Cull model, with two additional conditions, is equivalent to our model.

Studying the per capita growth rate when satisfying our four conditions gives insight into contest and scramble competition. In particular, depending on the properties of \( r \) and \( f \), we have two different types of contest and scramble competitions, depending on the size of the population. We finally extend our approach to develop new models for discontinuous recruitment functions and for populations exhibiting Allee effects.

1. General conditions. Historically, many discrete-time density-dependent population models
\[
p_{n+1} = f(p_n)
\]
have been developed, where \( p_n \) represents the biomass of the population after \( n \) time periods and \( f \) is the recruitment function. These models were developed by making reasonable assumptions about the intraspecies interactions and translating these into recruitment functions that model these interactions.

In this article, we develop our discrete models for population growth through a method inspired by the development of continuous population growth models. For the continuous case, letting \( p(t) \) represent the population size at time \( t \), a simple model might be to assume the change in population is jointly proportional to the population size and the time increment, that is,
\[
p(t + h) - p(t) = hr(t)p(t).
\]
Dividing both sides by \( h \) and taking the limit as \( h \) approaches zero gives the model \( p' = r(p)p \). Using the same approach for the discrete case, we use a population growth model of the form

\[
p_{n+1} = p_n + r(p_n)p_n
\]

(3)

where the per capita growth rate function \( r \) is based on the characteristics of the intraspecies interactions of the species. We then use model 3 to develop conditions that make this model reasonable. We note that this is somewhat analogous to developing conditions about the per capita recruitment, \( f(p)/p \), also known as the net reproductive rate. Since model 3 can be rewritten as

\[
\frac{p_{n+1}}{p_n} = \frac{f(p_n)}{p_n}
\]

(4)

then \( f(p)/p = 1 + r(p) \).

Our models will only consider the effect the density of the population has on the growth of the population, and ignore such things as age-structure and interrelationships with other species. We assume our population changes in discrete jumps, which might depend on say, mating seasons, but avoid cyclic growth rates.

Our first condition is that the per capita growth rate function \( r \) attains some maximum value, \( b \). This would occur when the combination of food and space available, and availability of a mate, is optimal for the species. We call \( b \) the \textbf{intrinsic per capita growth rate} for this species. For simplicity, we currently assume this occurs when the population size is \textit{near} zero, which we summarize as

\[ r(0) = b. \]

We acknowledge that assuming a growth rate for zero population makes no sense, but in reality we are assuming that the limit as \( p \) decreases to 0 equals \( b \).

For the second condition, we assume that as the population size increases, there is less food and space available, impinging on the per capita growth rate, that is, \( r \) is decreasing. Note that a sufficient condition for this to hold is \( r'(p) < 0 \) for \( p > 0 \), but it is not necessary in cases where \( r \) is not differentiable.

Later, we will modify these first two conditions to take into consideration species in which, if the size of the population is too small, it may be difficult to find a mate. In other words, if the population size is small, then as the population size increases, \( r \) may actually increase before decreasing, so the intrinsic per capita growth rate may occur at a population size other than 0. We note in this case that it is also possible that \( r(p) < 0 \) for \( p \in [0, c) \) for some \( c > 0 \). This will be dealt with in Section 5.

The third condition is that for a given species in a given location, there is an environmental carrying capacity \( L \) for that species, which is determined by, among other things, food and space available. This means that for some interval \( (a, L) \), if \( p \in (a, L) \) then \( r(p) > 0 \), and if \( p > L \), then \( r(p) < 0 \). For simplicity, we will let one unit of population equal \( L \). This means \( p_n \) gives the proportion that the population size is above or below the carrying capacity. Combined with the fact that \( r \) is decreasing, this condition can then be summarized as

\[ \lim_{p \to 1^-} r(p) \geq 0, \lim_{p \to 1^+} r(p) \leq 0. \]

If \( r \) is continuous, this condition implies that \( r(1) = 0 \).

If \( r \) is continuous, our three conditions imply that the per capita growth rate function \( r \) decreases from \((0, b)\) to \((1, 0)\). The simplest model would be to assume \( r \)
is linear, in which case it would be
\[ r = -bp + b \] (5)
Substitution of equation 5 into equation 3 and letting \( b = \beta - 1 \) and \( p_n = \frac{\beta}{\beta - 1} q_n \), the model becomes
\[ q_{n+1} = \beta q_n (1 - q_n) \] (6)
which is called the logistic equation for population growth and was studied by Robert May [1976]. This model is a discrete counterpoint to the Verhulst logistic equation.

As May knew, there is nothing about population growth that implies that a linearly decreasing function \( r \) is realistic. In fact, quite the opposite, since in this linear case there exists \( c > 0 \) such that for \( p > c \), \( r(p) < -1 \), that is, the population size will decrease by more than 100 percent. We therefore argue that for a discrete model to be anywhere close to realistic, the per capita growth rate \( r \) should never be less than \(-1\), leading to our fourth condition; as \( p \) increases, \( r \) decreases toward \(-1\), that is,
\[ \lim_{p \to -1} r(p) = -1. \]

Definition 1.1. The difference equation, \( p_{n+1} = p_n + r(p_n)p_n \) is a strict population model if the function \( r \) satisfies the conditions:
1) \( r(0) = b > 0 \)
2) \( r \) is decreasing
3) \( \lim_{p \to -1} r(p) \geq 0, \lim_{p \to 1^+} r(p) \leq 0 \)
4) \( \lim_{p \to \infty} r(p) = -1 \)

Since the per capita recruitment function is \( g = f/p = 1 + r \) when \( p \neq 0 \), these four conditions can be translated into the natural conditions on per capita recruitment: 1) \( \lim_{p \to 0^+} g = 1 + b \), 2) \( g \) is decreasing, 3) \( \lim_{p \to 1^-} g(p) \geq 1 \), \( \lim_{p \to 1^+} g(p) \leq 1 \), and 4) \( \lim_{p \to \infty} g(p) = 0 \).

Applying conditions 1) to 4) to the rational function
\[ r(p) = \frac{a_1 p^k + a_4 p^j}{a_2 + a_3 p^j} \] (7)
results in
\[ r(p) = \frac{b(1 - p^j)}{1 + bp^j} \] (8)
which then simplifies to the population model
\[ p_{n+1} = \frac{(1 + b)p_n}{1 + bp_n^j}. \] (9)

One example of the graphs for the recruitment function, per capita recruitment function, and per capita growth rate function for this model can be seen in Figure 1. These shapes are typical when \( j \leq 1 \). For the graph of the recruitment function, we also drew the line \( y = p \) on the graph, which intersects the recruitment function at the carrying capacity, \((1,1)\). We can use the identity function to determine the behavior of the growth of the function near the carrying capacity. In particular, if \( f \) is below the identity function to the left of the carrying capacity and above it to the right, as in Figure 1 a), then \( p_n \) increases to the carrying capacity if \( p_0 < 1 \) and decreases to 1 if \( p_0 > 1 \).
Similarly, Figure 2 displays the recruitment, per capita recruitment, and per capita growth rate functions for model 9 with \( j = 2 \) and \( b = 2 \). These shapes are typical for \( j > 1 \). In this case, since \( f \) has negative slope at \( p = 1 \), as seen in Figure 2 a), then the line \( y = p \) can be used to help us see that if \( p_0 \) is close to the carrying capacity, then \( p_n \) oscillates above and below the carrying capacity as it converges to 1.

We also note that in Figure 1, \( f/p \) and \( r \) are convex while in Figure 2, \( f/p \) and \( r \) both change convexity, going from concave to convex. This will be important in Section 5.

Figure 3 is the recruitment function for model 9 when \( j = 2 \) and \( b = 0.5 \). It is similar to the recruitment function of Figure 2 in that \( f \) eventually decreases, but it has a positive slope at the carrying capacity. In this case, if \( p_0 \) is large enough, the population size will drop below the carrying capacity, but then will increase to 1 instead of oscillating. For population sizes starting close to the carrying capacity, the population will not oscillate but will either increase or decrease toward 1 depending on the starting value.

Population model 9 was developed first by Beverton and Holt [1957] with \( j = 1 \) and later by J. Maynard-Smith and M. Slatkin [1973] for \( j \neq 1 \). It is often given in the form

\[
p_{n+1} = \frac{ap_n}{1 + cp_n^j}.
\]  

The third parameter in model 10 is a result of not normalizing the population size with respect to the carrying capacity.
If we use the rational function
\[ r(p) = \frac{a_1}{(a_2 + a_3p)^j} - 1 \] (11)
conditions 1) to 4) result in a normalized version of the Hassell model [1975]
\[ p_{n+1} = \frac{ap_n}{(1 + cp_n)^j} \] (12)
where \( a = 1 + b \) and \( c = (1 + b)^{1/j} - 1 \). For the Hassell model, the graph of the per capita growth rate function is similar to that in Figure 1 in that it is convex for all \( j \). For \( j \leq 1 \), the recruitment function \( f \) for model 12 is increasing, similar to that in Figure 1, but for \( j > 1 \), \( f \) has a maximum similar to that in Figure 2.

If we use an exponential function
\[ r(p) = ac^{-p^j} - 1 \] (13)
the conditions 1) to 4) result in a normalized version of the \( \theta \)-Ricker/Bellows equation
\[ p_{n+1} = p_n(1 + b)^{1-p^j\theta} \] (14)
which was developed by W. E. Ricker [1954] with \( j = 1 \), with the general version being studied by T. S. Bellows [1981]. For model 14, the recruitment function \( f \) has a maximum similar to that in Figure 2 for all \( j \). On the other hand, for \( j \leq 1 \) the per capita growth rate function \( r \) is convex, similarly to that in Figure 1, but if \( j > 1 \), then it switches concavity, similarly to that in Figure 2.

We note there are two standard shapes for the recruitment function, increasing and having a maximum, and two shapes for the per capita growth rate and per capita recruitment functions, convex and with a change on concavity. Depending on the choice of \( j \) in the models 9, 12, and 14, we get three of the four possible combinations, missing the case where the recruitment function is increasing but the per capita growth rate switches concavity. We can create such a case artificially as in Figure 4, which is model 9 with \( b = 1.2 \), but with \( j = 1.5 \) for \( p \leq 1 \) and \( j = 0.5 \) for \( p > 1 \). We find it interesting that conditions 1) through 4) applied to rational and exponential per capita growth rate functions result in precisely the models that were historically developed. We also find it interesting that one combination of recruitment and per capita growth rate functions did not result from these models. The different pairing of shapes of \( f \), \( f/p \) and \( r \) will be important when we consider contest and scramble competition in Section 5.
2. Comparison of population models. Cull [2007] proposed that a difference equation of the form 1 is a population model if the recruitment function $f$ satisfies:

5) $f \in C[(0, \infty), [0, \infty)]$

6) $f(0) = 0$

7) There exists $L$ such that $f(p) > p$ for $p < L$, $f(L) = L$ and $f(p) < p$ for $p > L$

8) If there exists $0 < p_0 < L$ such that $f'(p_0) = 0$, then $f'(p) > 0$ for $p < p_0$ and $f'(p) < 0$ for $p > p_0$.

We will call such a difference equation a **Cull population model**. We note that models 9, 12 and 14 satisfy conditions 5) through 8), so are Cull population models.

Consider the model,

$$p_{n+1} = \frac{p_n^2 + p_n^{2/3}}{p_n + 1}$$

(15)

As can be seen in Figure 5, the recruitment function satisfies conditions 5) to 8), but the per capita growth rate function does not satisfy condition 1) as

$$\lim_{p \to 0^+} r(p) = \infty$$

and does not satisfy condition 4) as $r$ actually increases back to 0 instead of going to $-1$ as $p$ goes to infinity. The fact that this model does not satisfy condition 1) implies an unreasonably rapid growth for small populations sizes. This problem can be avoided with the additional assumption that $f'(0)$ exists and

9) $f'(0) > 1$

We note that $f'(0) = 1 + r(0) = 1 + b$.

The fact that $r$ increases to 0 as $p$ goes to infinity means that for initial population sizes that are extremely large, the population size would decrease at an unreasonably slow rate, given how far the population size exceeds the carrying capacity. In fact, the larger the population size, the slower the rate of decrease. This problem can be solved by adding the condition

10) $\lim_{x \to \infty} \frac{f(x)}{x} = 0$

which is equivalent to condition 4) given that $f/p = 1 + r$. We note that

$$\lim_{x \to \infty} \frac{f(x)}{x} = 1$$

for model 15.
Figure 5. Recruitment function (on left) and per capita growth rate function (on right) for model 15

The previous discussion can be summarized as: Assuming the recruitment function is continuous and differentiable at 0, our strict population model is equivalent to the Cull model with the addition of conditions 9) and 10). The point is that for a particular population model, if conditions 9) or 10) are not satisfied (or equivalently, conditions 1) or 4)), then care should be taken when applying this model to populations when the population size can be small (for condition 9)) or large (for condition 10). We note that Cull [2007] was interested in showing that local stability for a class of population models implies global stability. Instead of considering population models from a biological point of view, the goal was to apply these results to as large a class of recruitment functions as possible, which were those satisfying conditions 5) through 8). This class of functions includes strict populations models as a subclass.

3. Contest versus scramble competition. Suppose we have a strict population model. We now show that conditions 1) to 4) can give additional insight into species exhibiting scramble versus contest competition, discussed quite extensively in the literature. Loosely speaking, scramble competition is where all of the individuals in the species are equally adept at finding food and space, while in contest competition the species has a hierarchy in the ability of individuals to find and use resources. Many species exhibit a combination of contest and scramble competition, which we will refer to later.

One approach to determining contest versus scramble competition, given in Bellows [1981], is to compare $s_n/p_n$ to $p_n$ where $s_n$ represents survivors of time period $n$. Since our model only considers population size, we assume $s_n$ is proportional to $p_{n+1}$ and consider a variation on Bellows, comparing the per capita recruitment $p_{n+1}/p_n$ to $p_n$. The idea is that for scramble competition at low population density, there is plenty of food available so the values $p_{n+1}/p_n$ should remain somewhat constant so the points $(p_n, p_{n+1}/p_n)$ should be approximately horizontal for small population sizes. This corresponds to the same proportion surviving when there is plenty of food to share. When the population size is large, the proportion surviving should be smaller since there is not enough food to go around and many may starve, so the points $(p_n, p_{n+1}/p_n)$ should be relatively near the horizontal axis. Taken together, these points should have a somewhat sigmoidal shape. Graphically, this means these points should form a curve that switches from concave to convex. On the other hand, for contest competition, as the density increases, those at the low
end of hierarchy in finding and using resources will have a higher mortality and lower fecundity, so the points \((p_n, p_{n+1}/p_n)\) should be decreasing.

It is clear that if the points \((p_n, p_{n+1}/p_n)\) are on a convex curve, they will be decreasing. Hassell [1975, p 286] stated that: “Normally, some element of contest is always likely since some individuals will be more successful than others.” We agree and therefore only state that if the per capita recruitment function is convex, the graphs do give some indication of some scramble competition. “We interpret his comment as meaning purely contest or no simple interpretation of these plots which distinguishes between contest and scramble competition.” We interpret his comment as meaning purely contest or scramble, since as we have discussed, the graphs do give some indication of some amount of scramble or contest competition.

Considering the population model, \(p_{n+1} = p_n + r(p_n)p_n\), the idea is to consider the graph of the per capita recruitment function

\[
g(p) = \frac{p + r(p)p}{p} = 1 + r(p)
\]

The function \(r\) has a point of inflection if and only if \(g\) has a point of inflection, that is, \(g\) has sigmoidal shape if and only if \(r\) switches from concave to convex. Similarly, \(r\) is convex if and only if \(g\) is convex. We therefore state the following two conditions.

- **\(C_1\) (Contest Competition)** The per capita growth rate function \(r\) is convex (equivalently the per capita recruitment function is convex), a sufficient condition being that \(r''(p) > 0\) for \(p > 0\).

- **\(S_1\) (Scramble Competition)** The per capita growth rate function \(r\) switches concavity at some value \(p_0 > 0\), a sufficient condition being that \(r''(p) < 0\) for \(0 < p < p_0\) and \(r''(p) > 0\) for \(p > p_0\).

As seen in Figures 1 and 2, the Maynard-Smith/Slatkin model 9 appears to satisfy \(C_1\) if \(j < 1\) and satisfy condition \(S_1\) if \(j > 1\). Since \(r\) is given by equation 8,

\[
r''(p) = -bj(1+b)p^{j-1} \left( \frac{j-1-bp^j(j+1)}{(1+b)^j} \right)
\]

(17)

We can now verify our observations are correct. Since the intrinsic growth rate \(b > 0\), we have that \(r''(p) > 0\) for \(p > 0\) if \(j < 1\), and \(r''(p) < 0\) for \(p \) in some interval \((0, p(j))\) if \(j > 1\). The length of the interval on which \(r\) is concave approaches 0 as \(j\) decreases to 1.

For the Hassell model 12, we find that

\[
r''(p) = (j^2 + j)(1+b) \left( (1+b)^{1/j} - 1 \right)^2 \left( 1 + ((1+b)^{1/j} - 1)p \right)^{-j-2} > 0 \quad (18)
\]

for \(p \geq 0\) meaning that \(r\) is always convex. This means model 12 satisfies \(C_1\) for all \(j > 0\).

Checking the concavity for the \(\theta\)-Ricker/Bellows model 14 by computing

\[
r''(p) = -j \ln(1+b)(1+b)^{-1-p^j} \left( j - 1 - j \ln(1+b)p^j \right)
\]

(19)

we see that \(-j \ln(1+b)(1+b)^{-1-p^j} < 0\) and \(-j \ln(1+b)p^j\) goes to zero as \(p\) goes to zero. The important term is \(j - 1\). If \(j \leq 1\), then \(r''(p) > 0\) for \(p > 0\) so \(r\) is
convex. If \( j > 1 \), then \( r''(p) < 0 \) on some interval \((0, p(j))\), and therefore switches from concave to convex, which agrees with our observations in Section 1. Thus, the \( \theta \)-Ricker/Bellows equation satisfies condition \( C_1 \) if \( j \leq 1 \) and condition \( S_1 \) if \( j > 0 \), so can exhibit contest or scramble competition.

We note that our analysis implies elements of one type of competition but does not deny elements of the other type of competition.

A second method for studying contest versus scramble competition suggested by Bellows [1981] was to consider the recruitment function, that is the points \((p_n, p_{n+1})\) (really \((p_n, s_n))\). If these points are on an increasing curve, the species exhibits elements of contest competition in that larger populations result in larger recruitments, while if the points are on a humped curve, the species has scramble competition in that a larger population could result in smaller recruitment because with equal competition, all individuals have less resources resulting in higher mortality and lower fecundity. To use these ideas we need to determine if, for the difference equation, \( p_{n+1} = f(p_n) \), the function \( f \) has an absolute maximum or is always increasing. Assuming recruitment to be differentiable, we can identify such a case by showing \( f'(p_0) = 0 \) for some \( p_0 > 0 \) (and that the curve decreases after that point). We summarize as:

- \( C_2 \) (Contest Competition) \( f'(p) > 0 \) for \( p > 0 \).
- \( S_2 \) (Scramble Competition) \( f \) has an absolute maximum.

For the Hassell model 12, the recruitment function is

\[
f(p) = \frac{(1+b)p}{(1 + ((1+b)^{1/j} - 1)p)^j}.
\]

This function starts at \((0, 0)\) and either increases to infinity or to a horizontal asymptote if \( 0 < j \leq 1 \) so would satisfy \( C_2 \) and therefore exhibit contest competition as before. For \( j > 1 \), the function starts at \((0, 0)\) and decreases to zero as \( p \) goes to infinity, so must have a finite maximum, satisfying \( S_2 \) and exhibiting scramble competition. Thus, the two definitions for contest and scramble competition are not equivalent. These two approaches indicate two different forms of scramble competition.

We note that this means for the Hassell model, when \( 0 < j \leq 1 \), the graphs of the recruitment, per capita recruitment, and per capita growth rate are similar to those for Maynard-Smith/Slatkin \( 0 < j \leq 1 \), seen in Figure 1. On the other hand, we see that when \( j > 0 \), these functions have the shapes in Figure 6.
For the Maynard-Smith/Slatkin equation 9, \( f(p) = (1 + b)p/(1 + bp') \) satisfies \( C_2 \) for \( 0 < j \leq 1 \) and \( S_2 \) for \( j > 1 \). Thus, Figures 1 and 2 give a complete picture of the behavior for this model. For the \( \theta \)-Ricker/Bellows equation 14, we have that \( f(p) = p(1 + b)^{1-r'} \). For \( j > 0 \) and \( b > 0 \), this function starts at \((0, 0)\) and approaches 0 as \( p \) goes to infinity, so it satisfies \( C_2 \). Combined with previous results, if \( j \leq 1 \), the functions for model 14 are similar in shape to Figure 6 while if \( j > 1 \), their shapes are similar to shapes in Figure 2.

We believe that conditions \( C_1 \) and \( S_1 \) relate to small populations sizes since the analysis was relevant to \( p \) close to zero, while \( C_2 \) and \( S_2 \) relate to large population sizes since the analysis concerns whether the function \( f \) eventually starts decreasing or continues to increase. This means species that satisfy \( C_1 \) and \( C_2 \) exhibit contest competition at all population sizes and have what we call strong contest competition (Maynard-Smith/Slatkin and Hassell, both for \( j \leq 1 \)). Species that satisfy both \( S_1 \) and \( S_2 \) exhibit scramble competition at all populations sizes and have strong scramble competition (\( \theta \)-Ricker/Bellows and Maynard-Smith/Slatkin, both with \( j > 1 \)). Species that satisfy \( C_1 \) and \( S_2 \) exhibit contest competition at small population sizes but scramble competition at larger populations sizes (Hassell for \( j > 1 \) and \( \theta \)-Ricker/Bellow for \( j \leq 1 \)). Species that satisfy conditions \( S_1 \) and \( C_2 \) exhibit scramble competition at small population sizes and contest competition at larger population sizes. It is of note that none of these standard models satisfy these conditions, although Figure 4 displays a hybrid model that does. For these last two cases, we say the species displays mixed competition. Thus, we expand on Bellows in that, while it is difficult to determine the type of competition solely from the recruitment function or per capita recruitment function, we can get a good deal of information from considering the pair of graphs.

4. **Discontinuous rates.** Up to now, we have been considering population models in which the recruitment function is continuous. There have been several papers which model population growth using a discontinuous recruitment function. For example, Williamson [1974] proposed the model

\[
p_{n+1} = \begin{cases} 
  a^+ p_n & p_n < c \\
  a^- p_n & p_n \geq c 
\end{cases}
\]  

(21)

using \( c \) for the ‘carrying capacity’ and assuming \( a^+ > 1 \), \( 0 < a^- < 1 \). Letting the carrying capacity be \( c = 1 \), the model can be written as \( p_{n+1} = p_n + r(p_n)p_n \) where the per capita growth rate is

\[
r(p) = \begin{cases} 
  b^+ & p < 1 \\
  b^- & p > 1 
\end{cases}
\]  

(22)

where \( b^+ > 0 \) and \( -1 \leq b^- < 0 \). This model leads to cyclic behavior when \( -1 < b^- \) and does not have a stable carrying capacity. Note that it does not satisfy our assumption 4) unless \( b^- = -1 \), but this would always lead to extinction.

Kocic and Kostrov [2013] studied a discontinuous Beverton-Holt model. After normalizing the units, their model can be rewritten as \( p_{n+1} = p_n + r(p_n)p_n \) with

\[
r(p) = \frac{k(p) - p}{k(p) + p}
\]  

(23)

where
\[ k(p) = \begin{cases} a_1 & p < M_1 \\ a_1 - c_1 & p > M_1 \end{cases} \quad \text{and} \quad j(p) = \begin{cases} a_2 & p < M_2 \\ a_2 - c_2 & p > M_2 \end{cases} \]

with \( a_2 > \max\{0, c_2\} \) and \( a_1 > c_1 > 0 \). In this case, \( r \) has jump discontinuities at \( M_1 \) and \( M_2 \). To insure \( r \) is nonincreasing, one of the following two conditions must hold:

- \( c_2 > 0 \) and either \( M_2 < \min\{M_1, a_1\} \) or \( a_1 - c_1 > M_2 > M_1 \)
- \( c_2 < 0 \) and either \( M_1 > M_2 > a_1 \) or \( M_2 > \max\{M_1, a_1 - c_1\} \)

Figure 7 b gives the graph for \( r \) for one of these cases, with Figure 7 a) giving the corresponding recruitment function.

![Figure 7](image)

**Figure 7.** Discontinuous Beverton Holt model with \( a_1 = 1, a_2 = 0.5, c_1 = 0.5, c_2 = 0.3, M_1 = 1.5, M_2 = 0.5.**

If neither of the two conditions hold, instead of the per capita growth rate function, \( r \), dropping lower at \( M_2 \), as in Figure 7, it will jump higher. This conflicts slightly with condition 3). This does not seem to be a serious conflict. We note that outside of the two discontinuities, this model behaves similarly to the continuous Maynard-Smith/Slatkin model with \( j \leq 1 \), that is, \( f \) is increasing and \( r \) is convex, so this model appears to satisfy conditions \( C_1 \) and \( C_2 \), so the species exhibits strong contest competition.

We note that for this model, the intrinsic growth rate is \( r(0) = a_2 \). There are three cases:

- If \( M_1 > a_1 \), then \( r(a_1) = 0 \) so \( a_1 \) is the carrying capacity
- If \( M_1 < a_1 - c_1 \), then \( r(a_1 - c_1) = 0 \) and \( a_1 - c_1 \) is the carrying capacity
- If \( a_1 > M_1 > a_1 - c_1 \), then \( M_1 \) is considered the carrying capacity in the sense that \( r(p) > 0 \) for \( p < M_1 \) and \( r(p) < 0 \) for \( p > M_1 \): \( M_1 \) is not stable in this case since \( p_n \) will oscillate above and below \( M_1 \).

We might ask, under what circumstances might a recruitment function be discontinuous. One possible situation is for scramble competition in which the per capita growth rate decreases at an increasing rate, then decreases at a decreasing rate. In previous models, this arose when \( r \) had a point of inflection. Thus, there might be a discontinuity at the point of inflection, as there is a sudden decrease in \( r \). Thus, a modified \( \theta \)-Ricker model or Maynard-Smith Slatkin model might be appropriate, such as

\[ r(p) = \frac{b(p)\left(1 - p^j\right)}{1 + b(p)p^j} \quad \text{or} \quad r(p) = (1 + b(p))^{1-p^j} - 1 \]
with \( j > 1 \) and

\[
b(p) = \begin{cases} b_1 & p < c \\ b_2 & p > c \end{cases}
\]

where \( 0 < c < 1 \) and \( b_1 > b_2 \). A graph of such a situation can be seen in Figure 8. Recruitment function \( f \) satisfies condition \( S_2 \) and the per capita growth rate satisfies condition \( S_1 \). Such a species exhibits strong scramble competition.

**Figure 8.** The Maynard-Smith/Slatkin discontinuous model 25.

5. **The Allee effect.** We have been modeling species with what are called compensatory models. We now model a species with what are called depensatory models. For a good discussion, see Liermann and Hilborn [2001]. Specifically, we consider a species in which, as the population density decreases to zero, the growth rate \( r \) decreases, possibly becoming negative, in which case it is called critical depensation and in which the population is said to exhibit the strong Allee effect. This might be for a species in which, for small densities, there is difficulty finding a mate, for species which forage in packs so for small densities, they are less efficient in finding food, or for species in which when in large groups, they are better able to defend themselves from predators. For such species, instead of conditions 1) and 2), there is a positive population density for which the species has its maximum per capita growth rate \( r \).

**Definition 5.1.** The difference equation, \( p_{n+1} = p_n + r(p_n)p_n \) is a population model exhibiting the **Allee effect** if the function \( r \) satisfies the conditions:

1) The function \( r \) increases to a maximum \((m, b), 0 < m < 1\), then decreases
2) \( \lim_{p \to 1^-} r(p) \geq 0 \), \( \lim_{p \to 1^+} r(p) \leq 0 \)
3) \( \lim_{p \to \infty} r(p) = -1 \)

We note there have been some models that use a downward parabola for this function. This would work for continuous models, but not for discrete models since they do not satisfy condition 4). Instead, we develop a rational and an exponential model by translating the Maynard-Smith/Slatkin model 9 and the \( \theta \)-Ricker model 14. For the modified Maynard-Smith/Slatkin equation, we get that

\[
r(p) = b\frac{1 - |p - m|^j}{1 + b|p - m|^j}
\]

while for the modified \( \theta \)-Ricker model

\[
r(p) = (1 + b)^{1 - |p - m|^j} - 1
\]
We note in both cases that for $0 < j \leq 1$, there will be a cusp at $p = m$, the peak of the function $r$ resulting in $r'(m)$ not existing. Figure 9 is a graph of the recruitment and per capita growth rate functions for equation 27 with $j = 2$, $b = 0.8$, and $m = 0.6$. Figure 10 is a graph of the recruitment and per capita growth rate functions for equation 27 with $j = 0.7$, $b = 0.8$, and $m = 0.6$.

**Figure 9.** The recruitment function (graph a)) for the per capita growth rate function 27 (graph b)) with $j = 2$, $b = 0.8$, and $m = 0.6$. Minimum viable population size is 0.2.

**Figure 10.** The recruitment function (graph a)) for the per capita growth rate function 28 (graph b)) with $j = 0.7$, $b = 0.8$, and $m = 0.6$. Minimum viable population size is 0.2.

For both the rational and exponential models, if $0 < m \leq 0.5$, the per capita growth rate is not negative for $p < 1$, and is said to exhibit the weak Allee effect. If $0.5 < m < 1$, then, in both cases, $r(2m - 1) = 0$ ($r(0.2) = 0$ for Figure 9) and $r(p) < 0$ for $p < 2m - 1$. In this case there is an unstable fixed point at $p = 2m - 1$, which is called the minimum viable population size. In such a case, if for some $n$, $0 < p_n < 2m - 1$, then the population will tend to 0, and so exhibits the strong Allee effect. We also note for these models, that as $m$ increases to one, $r(0)$ decreases to $-1$, which makes physical sense, the important point being that $r(p) > -1$ for all $p > 0$, $j > 0$ and $0 \leq m < 1$. This analysis leads us to propose one additional condition,

12) There exists $a_0$ such that $r(p) < 0$ for $p \in (0, a_0)$

If in addition to conditions 3), 4) and 11), the model satisfies condition 12), then the model exhibits the strong Allee effect.
We note some differences for the cases for model 27 where \( j \leq 1 \) (Figure 10) and \( j > 1 \) (Figure 9). When \( j \leq 1 \), the recruitment function increases, and past the cusp \((m, b)\), the per capita growth rate is convex. Thus, the population seems, to some extent, to have strong contest competition in that \( C_1 \) holds past \( m \) and \( C_2 \) holds since \( f \) is increasing. On the other hand, if \( j > 1 \), the recruitment function has a maximum and satisfies \( S_2 \). In addition, the per capita growth rate function changes convexity past \( m \) so satisfies \( S_1 \) and this species exhibits strong scramble competition. Also, in this case, if \( 0.5 < m < 1 \), as in Figure 9, then since the recruitment function decreases to 0, if the initial population size is too large, the next population size will be below the minimum population size and will go extinct.

For model 28 with \( j > 1 \), we get the same behavior as Figure 9 except \( r \) approaches -1 faster. If \( j \leq 1 \), the per capita growth rate behaves similarly to Figure 10 b) but the recruitment function approaches 0 after reaching a cusp. Thus, model 28 with \( j \leq 1 \) has mixed competition, satisfying \( C_1 \) and \( S_2 \). For \( 0.5 < m < 1 \), it also results in large initial populations resulting in the next population size dropping below the positive minimum viable population with eventual extinction.

We make some additional observations about the modified \( \theta \)-Ricker and Maynard-Smith/Slatkin models. In both cases, using methods in Sandefur [1990], it is relatively easy to show that \( p = 0 \) is an unstable equilibrium for \( 0 < m \leq 0.5 \), and for \( 0.5 < m < 1 \), \( p = 0 \) is a stable equilibrium and \( p = 2m - 1 \) is an unstable equilibrium. We note that for the modified Maynard-Smith/Slatkin model, relatively simple analysis also shows that the carrying capacity \( p = 1 \) is stable for all \( b \) if \( j \leq 2 - 2m \), but if \( j > 2 - 2m \), then \( p = 1 \) is stable only for

\[
 b \leq \frac{1}{2(1-m)} - 1
\]

As \( b \) increases past this value, there is period doubling to chaos. It is also relatively easy to show that for the modified \( \theta \)-Ricker model, \( p = 1 \) is stable when

\[
 b \leq e^{2(1-m)} - 1
\]

Again, as \( b \) increases past this value, period doubling to chaos begins.

We now have that the two continuous models 27 and 28 exhibit the Allee effect. Higgins et al (2015) proposed the following model as a discontinuous difference equation which models the strong Allee effect:

\[
p_{n+1} = F(p_n) \text{ where } F(p) = \begin{cases} f(p) & 0 < p < a \\ g(p) & a < p < b \\ h(p) & b < p \end{cases}
\]

with the conditions that \( f \), \( g \), and \( h \) are increasing functions on their domains, \( f(p) < p \), \( g(p) > p \), and \( h(p) < p \). In addition \( f(0) = 0 \) and \( \lim_{p \to \infty} h(p) = H > 0 \). For example, Figure 11) shows a graph of the recruitment function \( F \) along with the line \( y = p \) on the left and the per capita growth rate \( r \) on the right where

\[
f(p) = p - 0.3p^2 \quad 0 < p < 1
\]

\[
g(p) = \begin{cases} 0.1p^2 + 2 & 1 < p < 2 \\ p^2 + 1 & 2 \leq p < 3 \end{cases}
\]

\[
h(p) = \sqrt{p} \quad p > 3.
\]
The line \( y = p \) makes it easy to see when \( F(p) > p \) and \( F(p) < p \). Looking at the graph, we can see that \( a = 1 \) is the minimum viable population size. We also note that \( b = 3 \) is the carrying capacity in the sense of condition 3) in that

\[
\lim_{p \to 3^-} r(p) \geq 0 \text{ and } \lim_{p \to 3^+} r(p) \leq 0
\]

From Figure 11, we observe some unusual behavior. The recruitment function \( F \) is increasing and less than \( p \) on the interval \((0, 1)\), and \( r = -0.1p \) is negative so there is a strong Allee effect. On the other hand, \( r \) is decreasing on \((0, 1)\). In most situations of the Allee effect, as the population size increases toward the minimal viable population size, the negative growth rate is increasing, not decreasing. On the interval \((1, 3)\), \( g \) also satisfies conditions for 31. In this case, the per capita growth rate \( r \) is positive in the interval \((1, 3)\), but instead of increasing, then decreasing, it decreases, then increases. Thus, the conditions given for \( f \) and \( g \) for model 31 seem insufficient in describing appropriate behavior for population growth. As with the Cull model, the Higgins model includes appropriate population models but is more general. On the other hand, the condition

\[
\lim_{p \to \infty} h(p) = H > 0
\]

is too restrictive. This condition is sufficient to imply that

\[
\lim_{p \to \infty} r(p) = -1
\]

but is not necessary, as the example \( h(p) = \sqrt{p}, \ p > 3 \) in our example indicates. This does not satisfy their limit condition, but it does convert to \( r(p) = 1/\sqrt{p} - 1 \) which is negative for \( p > 3 \) and decreases to \(-1\), so satisfying condition 4).

6. Conclusion. Many discrete population growth models have been developed using a dynamical system of the form \( 1, p_{n+1} = f(p_n) \), where conditions were applied to the recruitment function \( f \) to parallel assumptions made about the species being modeled. In this paper we, in addition, considered conditions on the per capita growth rate function, \( r \), when modeling a species. From this perspective we were able to give a collection of conditions, either on \( f \) or on \( r \), that model population growth for a large range of density-dependent species. We then considered how these conditions fit with a number of existing population models, such as the Maynard-Smith/Slatkin, Hassell, and \( \theta \)-Ricker/Bellows models. We noted that these conditions were more restrictive, but more natural than some other population models,
such as those of Cull, although noting that depending on how the model was being used, models not satisfying our conditions might still be useful.

One of the more important aspects of our approach is that it may help give clearer geometric insight into differences between species exhibiting scramble and contest competition. In particular, two different considerations of these concepts were merged leading to a differentiation between these concepts according to the behavior of both the recruitment function and the per capita recruitment function.

Finally, we showed how this approach could be extended to species with discontinuous growth rates or those exhibiting the Allee effect, by first developing modified conditions which then led to what we believe are new models that may be useful in modeling such species. We hope that these models, extensions of classic models, will be found useful for researchers in this area of population studies.

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