Biodiversity and ecosystem function in ephemeral patches: some theory ideas

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Brief introduction to the model and parameters

Define the relationship between total investment budget M, parental investment (PI) m_i (i.e., the investment that each offspring receives), and total offspring produced n_i, as follows,

$$n_i = \frac{M_i}{m_i}.$$

Define the effect of competition of the offspring of j on the offspring of i as follows,

$$\alpha_{ij}(m_j, n_j) = \frac{m_j n_j}{R}.$$

In the above, R defines the total available resources on a patch. The fitness of an individual i (W_i), defined by number of *viable* offspring produced, will be the product of offspring produced n_j and the viability of each offspring, as affected by parental investment m_i and effects of competition $\alpha_{ij}(m_j, n_j)$ summed over all competitors $j$note_1,

$$W_i = \left(1 - e^{-c\left(m_i - m_{min} - \sum_{j=1}^{N} \alpha_{ij}(m_j, n_j)\right)}\right).$$

In the above, m_{min} is a minimum amount of investment required to produce a viable offspring. The parameter c defines the shape of the curve relating parental investment to viability (i.e., how 'diminishing' are the returns in fitness W_i as m_i increases). From the above equation, it is possible to figure out how much parental investment is optimal (m_i^*) for an individual i.

- **note_1:** I originally had this as just $m_j R^{-1}$, but this confuses what N really is, as I think it should be the competitors arriving at a patch, not the offspring that they produce; hence, more competitors, more offspring, and this needs to be reflected in the equation. Also note, of course, $m_j n_j = M_j$. Also, I've used this trick before in the context of inbreeding (Duthie et al. 2016), so I'm mostly building off of the hope that a lot of the same logic can apply to decreases in fitness from competitive effects #overlyhonestmethods.

Tedious maths to get optimal parental investment

This section can be skipped for anyone who is not interested in how to derive m_i^* from the equation for W_i, but I need the equations and code for the concrete example.

```
alpha_ij <- function(mi, R) sum(mi/R); # Note: using 'cc' to avoid confusing 'c()'.
W_i      <- function(mi, cc, mmin, mj, R) (1 - exp(-cc*(mi - mmin - alpha_ij(mj,R))));
fWi      <- expression((1-exp(-cc*(mi-mmin-Alpha))),'mi');
dfWi     <- D(fWi, 'mi');
```

For simplicity, we can define $m_{min} = 1$, so unity is the minimum amount of parental investment required to produce a viable offspring in the absence of competition. For simplicity, we can also set $c = 1$. In the absence of competition (as $R \to \infty$), we have the following slope.

```
m_vals <- seq(from = 0, to = 6, length = 1000);
viable <- W_i(c = 1, mi = m_vals, mmin = 1, mj = 1, R = Inf);
par(mar = c(5, 5, 2, 1));
plot(x = m_vals, y = viable, type = "l", lwd = 3,
     xlab = expression(paste("Parental Investment (",italic(m),")")),
     ylab = expression(paste("Individual fitness (",italic(W[i]),")")),
     cex.lab = 1.5, cex.axis = 1.5, xaxs="i", yaxs="i", ylim = c(0,1));
```
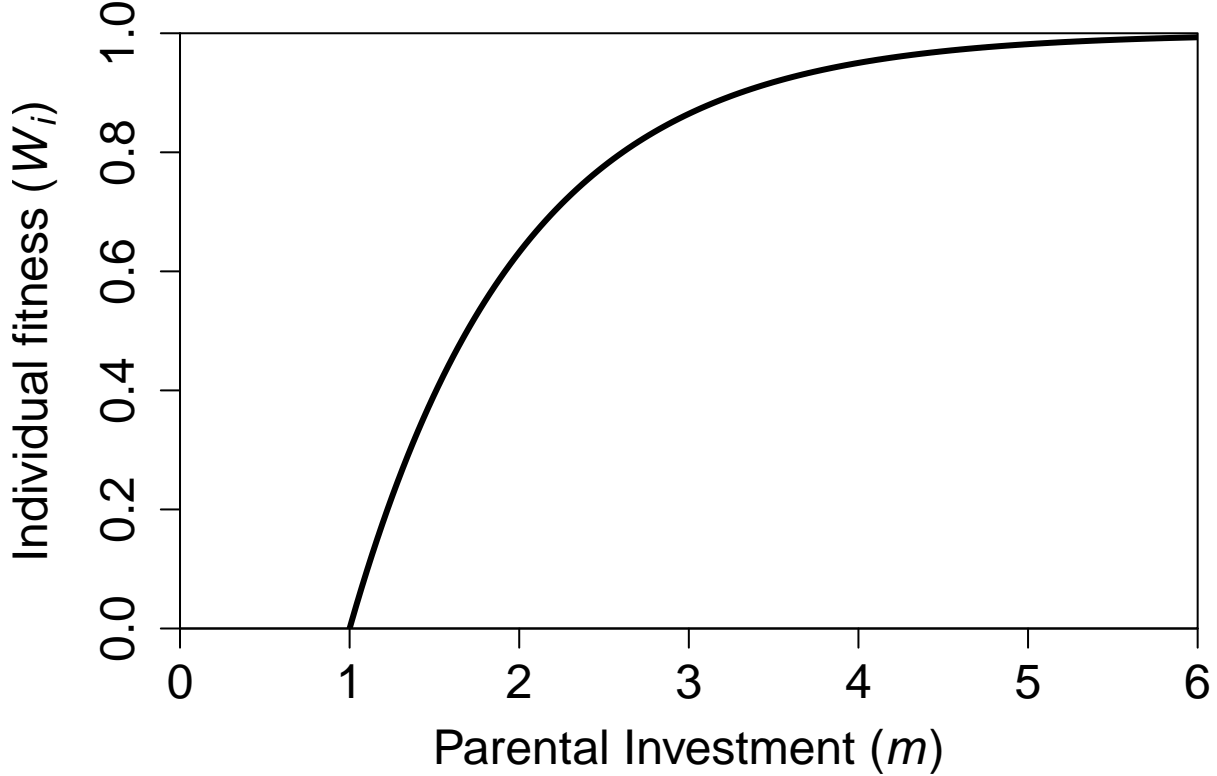

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29 The optimal parental investment m_i^* is obtained by finding the line tangent to the curve that passes through
30 the origin; the point where the curve and this line meet defines m_i^* because it maximises the rate at which
31 viable offspring are produced. To get the tangent line, we first need to get the derivative of W_i with respect
32 to m_i,

$$\frac{\partial W_i}{\partial m_i} = ce^{-c\left(m_i - m_{min} - \sum_{j=1}^{N} \alpha_{ij}(m_j, n_j)\right)}.$$

33 A function for the above is below,

```
dW_i <- function(mi, cc, mmin, mj, R) cc * exp(-cc * (mi - mmin - alpha_ij(mj, R)));
```

34 In general, the equation for any line that is tangent to a function f (with derivative f') at the point a is,

$$y = f'(a)(x - a) + f(a).$$

35 Because we want to pass through the origin where $x = 0$ and $y = 0$, we use the following to describe the
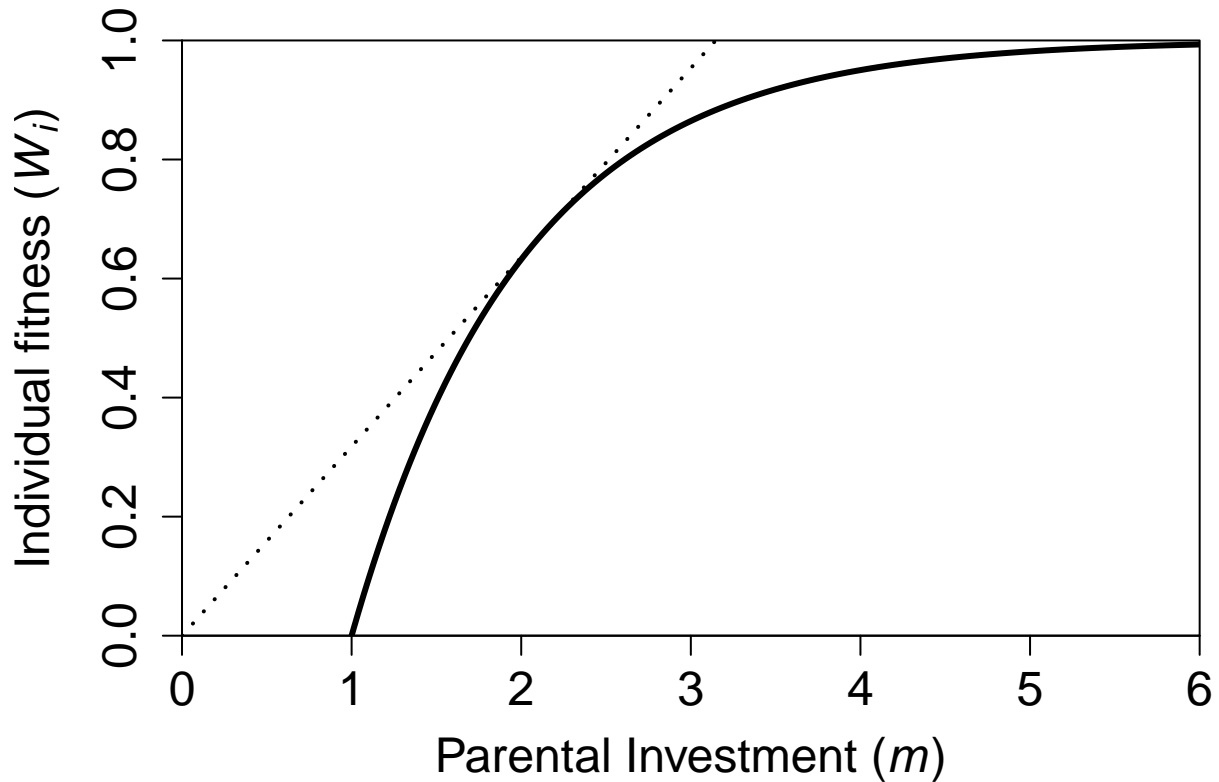36 tangent line above,

$$0 = ce^{-c(m_i - m_{min} - \sum_{j=1}^{N} \alpha_{ij}(m_i))}(0 - m_i) + \left(1 - e^{-c\left(m_i - m_{min} - \sum_{j=1}^{N} \alpha_{ij}(m_j, n_j)\right)}\right).$$

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We can just solve this numerically for the parameters set in finding `viable` above. Below is a quick function
to get m_i^*.

```
get_mi <- function(low_guess, high_guess, cc = 1, mmin = 1, mj = 1, R = Inf){
    fm <- function(mi, cc = cc, mmin = mmin, mj = mj, R = R){
        W_val <- W_i(mi = mi, cc = cc, mmin = mmin, mj = mj, R = R);
        W_der <- dW_i(mi = mi, cc = cc, mmin = mmin, mj = mj, R = R);
        return( W_der*(0-mi) + W_val );
    }
    lg  <- fm(mi = low_guess, cc = cc, mmin = mmin, mj = mj, R = R);
    hg  <- fm(mi = high_guess, cc = cc, mmin = mmin, mj = mj, R = R);
    if(lg > 0){
      u <- low_guess;
      l <- high_guess;
    }else{
      u <- high_guess;
      l <- low_guess;
    }
    fml <- fm(mi = l, cc = cc, mmin = mmin, mj = mj, R = R);
    fmu <- fm(mi = u, cc = cc, mmin = mmin, mj = mj, R = R);
    if((fml > 0 & fmu > 0) | (fml < 0 & fmu < 0)){
      return("Value of m is outside the range");
    }else{
      check  <- 1;
      mguess <- 0.5 * (l+u);
      i        <- 0;
      while(abs(check) > 0.000001 & i < 1000000){
          check <- fm(mi = mguess, cc = cc, mmin = mmin, mj = mj, R = R);
          if(check > 0){
            u      <- mguess;
            mguess <- 0.5*(l + mguess);
          }else{
            l      <- mguess;
            mguess <- 0.5*(u + mguess);
          }
          i <- i+1;
      }
    return(mguess);
  }
} # Running the below returns the estimate
m_star <- get_mi(low_guess = 0, high_guess = 6, cc = 1, mmin = 1, mj = 1, R = Inf);
```

Running the above code gets an m_i^* value of 2.1461921. We can plot the tangent line on the function using
the code below.

```
m_vals <- seq(from = 0, to = 6, length = 1000);
viable <- W_i(c = 1, mi = m_vals, mmin = 1, mj = 1, R = Inf);
par(mar = c(5, 5, 2, 1));
plot(x = m_vals, y = viable, type = "l", lwd = 3,
     xlab = expression(paste("Parental Investment (",italic(m),")")),
     ylab = expression(paste("Individual fitness (",italic(W[i]),")")),
     cex.lab = 1.5, cex.axis = 1.5, xaxs="i", yaxs="i", ylim = c(0,1));
slope_mstar <- W_i(mi = m_star, cc = 1, mmin = 1, mj = 1, R = Inf) / m_star;
abline(a = 0, b = slope_mstar, lty = "dotted", lwd = 2);
```

Where am I going with all of this?

I've removed all competition in the tedious maths bits above by setting $R = \infty$ so that resources are limitless and the offspring of parents feed without restriction. Note that there is still an optimum parental investment *above the minimum* because the viability of the offspring is affected by parental investment *independent of competition* – this could be something like the probability of being able to fight off pathogens or persevere through abiotic stress (i.e., some component of fitness that is independent of density). Now, I want to **see what happens when competition decreases viability**. Given finite resources, assume that parental investment m_i influences both competitive ability and viability independent of competition (e.g., something like body size or feeding rate). **It seems intuitive that if competition is high, then it might increase fitness to increase investment to produce fewer competitive offspring**. Note that this also assumes a situation in which an individual moving to a different patch to oviposit is either not possible, or is costly (i.e., at least more costly than it would be to stay and invest optimally on the current patch).

The corrected version of $\alpha_{ij}(m_j, n_j)$ to include n_j should make things easier by recognising that *total* competition should depend on the total investment budgets of the individuals arriving to a patch to oviposit. In other words, total competition does not depend on the parental investment decisions of other individuals – at least not yet. This type of recursion (in which, e.g., competition changed with *realised* viability given different parental investment) is just going to be too complicated of a starting point, so it is better to first consider **how optimal parental investment, and therefore offspring number, is modified by existing competitors on a patch**, without thinking about feedbacks that follow. In a more formal analysis, it might be interesting to consider the PI decisions for an initial coloniser of a patch, followed by the decision of the second arriver, and a third, and so forth. This would link with the established literature optimal foraging and oviposition per patch somehow, which has been studied in ovipositing wasps, though not (to my knowledge), in the context of parental investment where individuals might adjust allocation of resources to eggs or modify behaviour (e.g., guarding).

A simple, concrete example to get started

I will begin with an example of a single ovipositing female on a patch of resources where $R = 100$. The female has a total investment budget of $M_i = 10$. Conveniently, the way $\alpha_{ij}(m_j, n_j) = m_j n_j R^{-1}$ is defined allows to just substitute $M_j = m_j n_j = 10$, so $\alpha_{ij}(m_j, n_j) = M_j R^{-1} = 10R^{-1} = 0.1$. We can start working from the general equation,

$$W_i = \left(1 - e^{-c\left(m_i - m_{min} - \sum_{j=1}^{N} \alpha_{ij}(m_j, n_j)\right)}\right).$$

And we can substitute in the relevant values for competition; assume $c = 1$ and $m_{min} = 1$ for simplicity,

$$W_i = \left(1 - e^{-(m_i - 1 - 0.1)}\right).$$

If a focal female's fitness W_i is **not** decreased by competition among her offspring, then we had a optimal PI m_i^* of 2.1461921, as above. Now that we have added some competition among her offspring, optimal PI per offsrping is calculated with the code below.

```
m_star_1 <- get_mi(low_guess = 0, high_guess = 6, cc = 1, mmin = 1, mj = 10, R = 100);
```

The value of `m_star_1`, and optimal PI m_i^* given competition amongst offspring is therefore 2.2912745, a value that is **higher than optimal PI in the absence of competition**.

Okay, now let's consider what happens when the next competitor arrives *immediately after the first* to oviposit (i.e., ignore any priority effects for now). Assume that she notices that the first competitor is there and can adjust her PI accordingly. If her own total investment budget is also 10, then $\sum_{j=1}^{N} \alpha_{ij}(m_j, n_j) = (10 + 10)/100 = 0.2$. We can do the same exercise as before to figure out *her* optimal parental investment.

```
m_star_2 <- get_mi(low_guess = 0, high_guess = 6, cc = 1, mmin = 1, mj = c(10, 10), R = 100);
```

The value of `m_star_2` given this increased competition is now 2.4336133. Continuing with this logic, we can see how optimal parental investment changes with up to 100 arriving competitors.

```
m_stars  <- NULL;
tot_comp <- 1:100;
for(competitors in tot_comp){
    mjs     <- rep(x = 10, times = competitors)
    m_star  <- get_mi(low_guess = 0, high_guess = 20, cc = 1,
                      mmin = 1, mj = m_stars, R = 100);
    m_stars <- c(m_stars, m_star);
}
par(mar = c(5, 5, 2, 1));
plot(x = tot_comp, y = m_stars, type = "l", pch = 20, lwd = 3,
     xlab = "Number of competitors on a patch",
     ylab = expression(paste("Optimal parental investment (","m*"[i],")")),
     cex.lab = 1.5, cex.axis = 1.5);
```
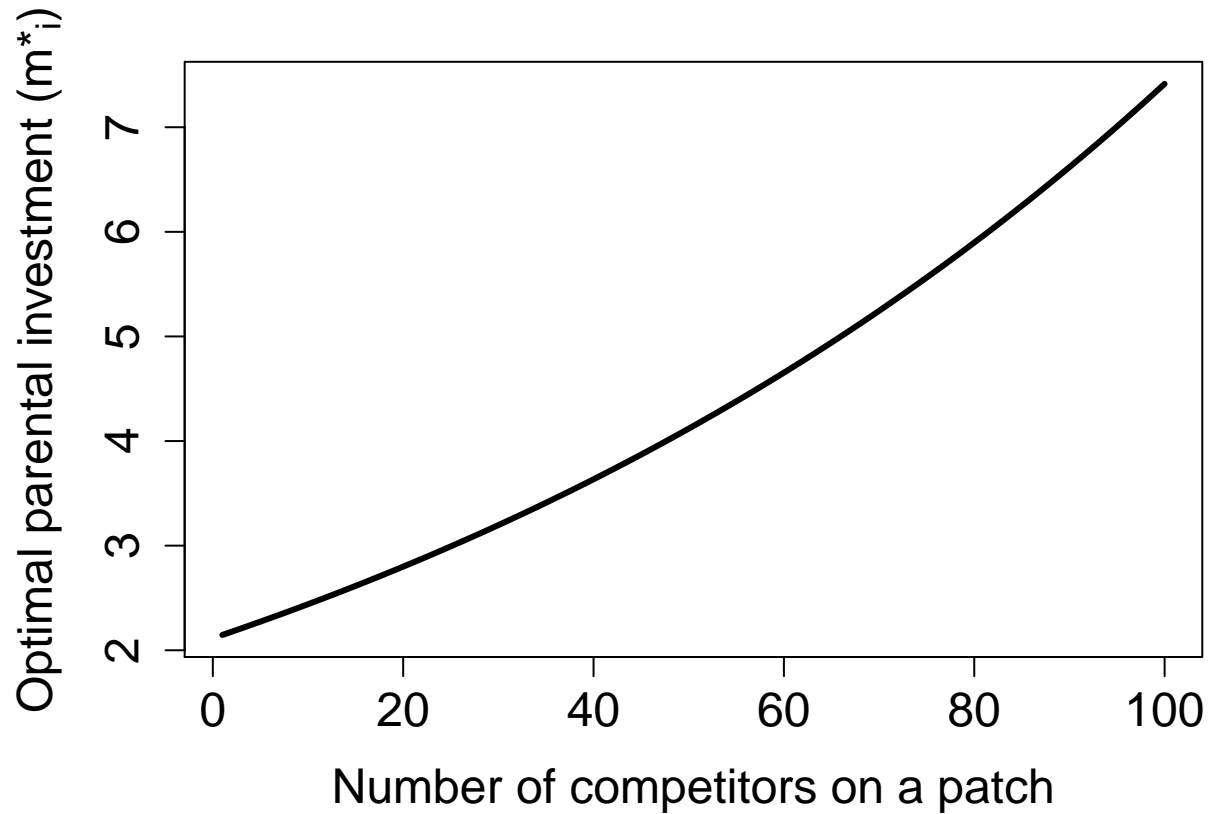
This seems like a substantial change in optimal parental investment when competition affects offspring survival, but can be mitigated with increasing PI. Note that total offspring produced per competitor also changes in accordance with $n_i = M_i m_i^{-1}$.

```
n_prod <- 10 / m_stars;
par(mar = c(5, 5, 2, 1));
plot(x = tot_comp, y = n_prod, type = "l", pch = 20, lwd = 3,
     xlab = "Number of competitors on a patch",
     ylab = expression(paste("Offspring per competitor (","n"[i],")")),
     cex.lab = 1.5, cex.axis = 1.5);
```
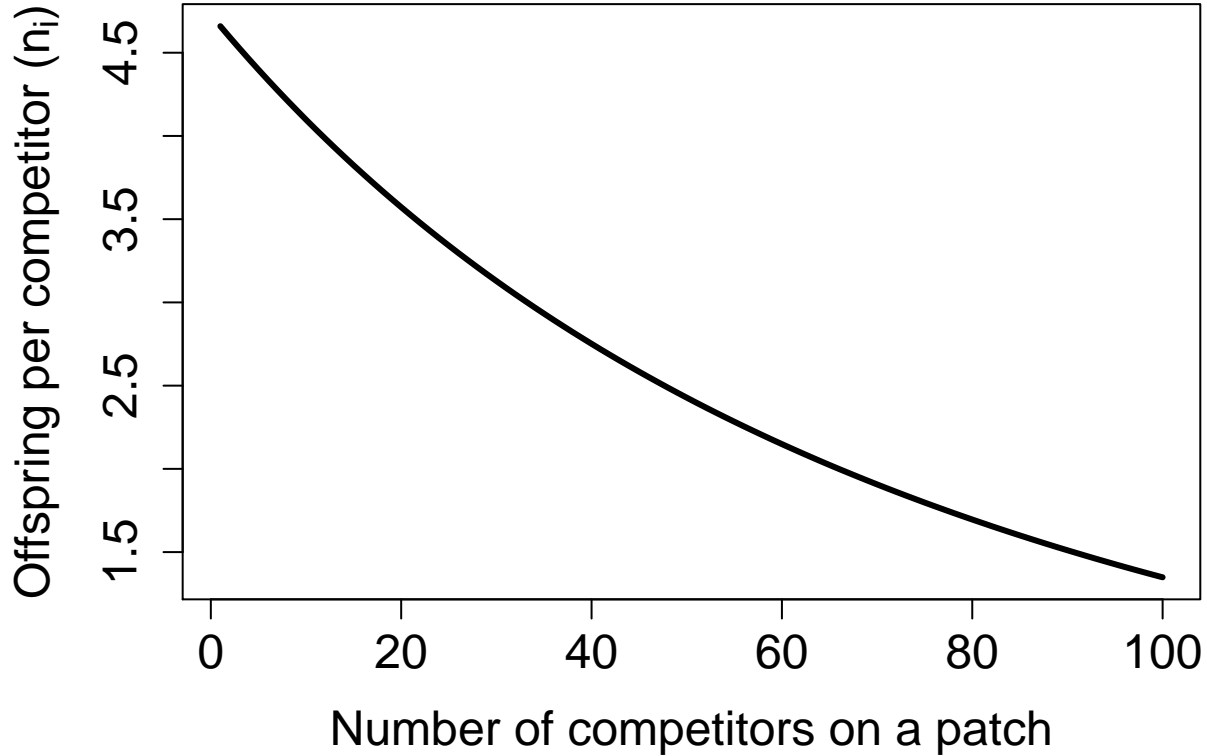
Given the assumptions underlying this model, it does not seem unreasonable to expect fairly substantial decreases in how an individual arriving to a patch chooses to allocate from their total investment budget M_i.

Key thoughts before a more general derivation

It is important to recognise that decreased offspring production as a consequence of shifting parental investment *is* competition in a community ecology sense. If, for example, a focal individual ultimately *increases* their fitness by producing fewer viable offspring, competition has still occurred. Further, if a focal individual decreases the number of offspring that they produce due to increasd density of other individuals, then competition has occurred **even if those other competitors fail to produce offspring** (e.g., due to sterility). This is because competition is simply defined as an interaction in which the density of a species i decreases the growth rate of a species j (including where $i = j$). Using absolute competition coefficients α_{ij} describing the total effect of species j on species i, this is described by the following equation (Chesson 2000),

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \sum \alpha_{ij} N_j\right).$$

In the above, N defines species densities and r is the intrinsic rate of growth in the absence of competition. Competition is merely defined by the presence of a species j (N_j) on the growth rate of species i (and vice versa); no particular mechanism is assumed. If more j causes focal individuals to shift towards producing fewer i, then competition has occurred, though this is counterintuitive. The term **"intimidation competition"** seems appropriate, and apparently has not been coined in the literature. I'll need to dig a bit more to see if the general concept has been pointed out already.

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General derivation of PI affected by competition

This section can be skipped for anyone who does not need convincing that optimal parental investment m_i^* will increase with an increase in competition more generally. To demonstrate this is the case, we need to show that $\partial m_i^* / \partial \alpha_{ij}(m_j, n_j)$ for a wide range of conditions. Assume that $\alpha_{ij}(m_j, n_j)$ is positive. We can then start with the general equation for which $m_i = m_i^*$,

$$0 = ce^{-c(m_i - m_{min} - \sum_{j=1}^{N} \alpha_{ij}(m_i))}(0 - m_i) + \left(1 - e^{-c\left(m_i - m_{min} - \sum_{j=1}^{N} \alpha_{ij}(m_j, n_j)\right)}\right).$$

Substituting m_i^* for m_i, we have the following,

$$0 = -m_i^* ce^{-c(m_i^* - m_{min} - \sum_{j=1}^{N} \alpha_{ij}(m_i^*))} + 1 - e^{-c\left(m_i^* - m_{min} - \sum_{j=1}^{N} \alpha_{ij}(m_j, n_j)\right)}.$$

Just to keep the notation simpler for a moment, allow,

$$\alpha_{ij}(m_j, n_j) \equiv \sum_{j=1}^{N} \alpha_{ij}(m_j, n_j).$$

We can isolate $\alpha_{ij}(m_j, n_j)$ algebraically from the above (the package Ryacas is useful here).

$$\alpha_{ij}(m_j, n_j) = m_i^* - m_{min} + \frac{1}{c} \log\left(\frac{1}{m_i^* c + 1}\right).$$

From here, we can differentiate $\alpha_{ij}(m_i)$ with respect to m_i^*.

```
fWi_opt      <- expression((mi - mmin + (1/cc)*log(1/(mi * cc + 1))), 'mi');
dfWi_opt     <- D(fWi_opt, 'mi');
```

The result is as follows,

$$\frac{\partial \alpha_{ij}(m_j, n_j)}{\partial m_i^*} = 1 - \frac{c(m_i^* c + 1)}{c(m_i^* c + 1)^2}.$$

This actualy simplifies nicely to the following (double-checked with R and mathomatic),

$$\frac{\partial \alpha_{ij}(m_j, n_j)}{\partial m_i^*} = \frac{m_i^* c}{m_i^* c + 1}.$$

And via the chain rule of calculus, we can do the following,

$$\frac{\partial m_i^*}{\partial \alpha_{ij}(m_j, n_j)} = \frac{m_i^* c + 1}{m_i^* c}.$$

Overall, for any $m_i^* > 0$ and $c > 0$ (parental investment increases offspring viability), optimal parental investment will increase with increasing competition. We can therefore conclude that this relationship is general in that the specific form of the competition function does not matter as long as competition decreases offspring viability, nor does the value of $m_m in$. **It is potentially interesting to note** that if $\alpha_{ij}(m_j, n_j) < 0$ (mutualism or facilitation), then optimal parental investment should actually decrease with increasing density of other individuals, ultimately producing more offspring.

Different competition functions

I have only looked at a simple competition function,

$$\alpha_{ij}(m_j, n_j) = \frac{m_j n_j}{R}.$$

But this might be an unrealistic assumption. For example, allocating twice the parental investment to half the number of offspring will result in an identical $\alpha_{ij}(m_j, n_j)$, but it might be that competition is not linearly related to the product of m_j and n_j. Rather, twice as much PI in half as many offspring might increase (or decrease) the total value of $\alpha_{ij}(m_j, n_j)$. We can modify the effect of each m_j and n_j on competition using the exponents a and b,

$$\alpha_{ij}(m_j, n_j) = \frac{m_j^a n_j^b}{R}.$$

If $a = 1$ and $b = 1$, then $\alpha_{ij}(m_j, n_j)$ remains constant as m_j^a varies (because $M_j = m_j n_j$; see solid line below). If, e.g., $a = 2$ and $b = 1/2$, then $\alpha_{ij}(m_j, n_j)$ increases with increasing parental investment m_j of competitors (see dashed line below). If, e.g., $a = 1/2$ and $b = 2$, then $\alpha_{ij}(m_j, n_j)$ decreases with increasing parental investment m_j of competitors (see dotted line below).

```
M_j      <- 10;
aij_exp <- function(mj, nj, a, b, R = 100) ((mj^a) * (nj^b)) / R;
mj_vals <- seq(from = 0, to = 6, length = 1000);
comp_1  <- aij_exp(mj = mj_vals, nj = M_j/mj_vals, a = 1,   b = 1,   R = 100);
comp_2  <- aij_exp(mj = mj_vals, nj = M_j/mj_vals, a = 2,   b = 0.5, R = 100);
comp_3  <- aij_exp(mj = mj_vals, nj = M_j/mj_vals, a = 0.5, b = 2,   R = 100);
par(mar = c(5, 5, 2, 1));
plot(x = mj_vals, y = comp_1, type = "l", lwd = 2, ylim = c(0, 1),
     xlab = "Parental investment of competitors", ylab = "Total competition on offspring",
     cex.axis = 1.5, cex.lab = 1.5);
points(x = mj_vals, y = comp_2, type = "l", lty = "dashed", lwd = 2);
points(x = mj_vals, y = comp_3, type = "l", lty = "dotted", lwd = 2);
```

Figure axes: Total competition on offspring (y-axis, 0.0 to 1.0) vs. Parental investment of competitors (x-axis, 0 to 6)
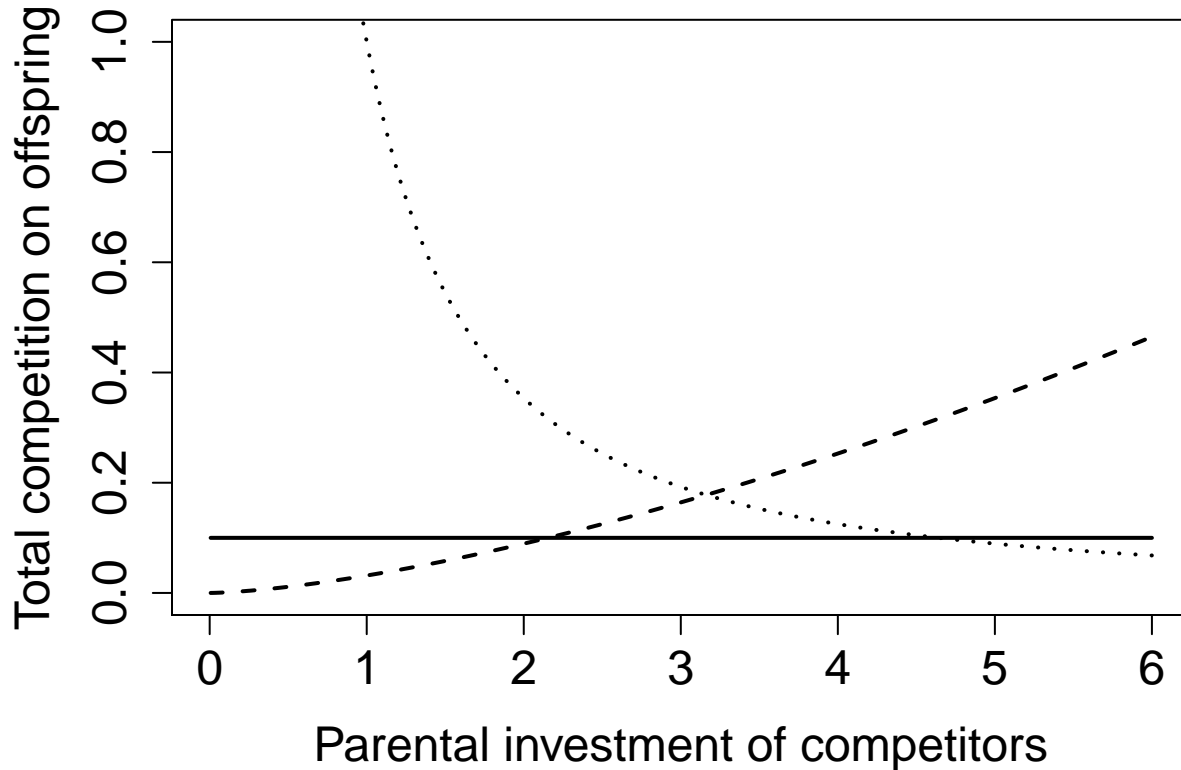
While the general result that optimal parental investment increases with increasing competition should not change, just how much competition is predicted to change as a result of changes in parental investment might therefore depend on how competition is affected differently by changes to m_j versus n_j. **This might have interesting consequences for community ecology** and ecological and evolutionary feedbacks more generally, in that changes in PI could increase or decrease population growth, which could in turn affect changes in PI through changing species densities.

Empirical predictions

One potentially interesting way to test this could be by looking for the *intimidation competition* that I mentioned earlier. As an example, we can imagine a focal female arriving at a patch to oviposit (though any individual that reproduces in an ephemeral patch should work – potentially including plants in temporary ponds). She has the ability to somehow modulate how many offspring she produces and how much investment goes into each offspring (note again for emphasis – 'parental investment' is not synonymous with 'parental care', and investment might take the form of, e.g., increased egg provisioning or egg guarding). If she observes the density of competitors to be low, then she should make relatively low PI and produce more offspring. If she observes the density of competiters to instead by high, her PI should be elevated and conseqent offspring reduction reduced. It might be possible to test for this by comparing a focal female's offspring production across a density gradient of competitors who are fertile versus sterile. Consider, e.g., the simple case:

1. A focal female ovipositing on a patch at low density of competitors.
2. A focal female ovipositing on a patch at high density of competitors.
3. A focal female ovipositing on a patch at high density of **sterile** competitors.

If females cannot or do not modulate PI with competition, then we would predict no significant difference between a focal female's offspring production in 1 and 3. But if females can modulate PI with competition, then we would predict offspring produced in 3 to be *lower* than offspring produced in 1 due to the effect of intimidation from competitors, but perhaps for these offspring to have traits more associated with higher viability (e.g., larger body size, higher feeding rate). We should also predict offspring production to be much

161 lower in 2 than either 1 or 3 due to effects of competition among larvae.

References

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166 offspring. Proceedings of The Royal Society B 20161845.