

This is an interesting paper about the value in using a sink with a variable environment in a two-habitat system for a species that has two stages (juvenile and adult). The baseline case is juvenile movement and juvenile predation in the sink, but cases in which adult move or experience predation (or both) are also examined. They find advantages to using the sink (in terms of increasing growth rate) in some cases for all four scenarios except adult movement with adult predation, with the greatest benefit with juvenile dispersal and adult predation when adult survival is low and juvenile recruitment is high (there is a trade-off between these). The manuscript does not include density dependence, or temporal autocorrelation in juvenile recruitment (which is the quantity that varies), both of which could increase the value of the sink.

I found the text, and especially the explanation of the results, hard to follow in some places (as detailed below).

Specific comments (_ indicate that what follows is a subscript, and I will spell out Greek letters).

Abstract, second to the last sentence, add “sometimes” after “maximum growth rates” and change “juveniles” to “individuals”.

Line 9, change “From” to “In”.

Line 29, replace “that” with “in which a population”.

Line 45, add “the” after “at” (I also don’t think “maladaptive” needs a hyphen, or “individual scale” as used here).

Line 54, add “is” after “but”.

Line 62, change “they” to “these patches”.

Line 75. The frogs spend 2-3 years as juveniles, and yet your matrix model has a zero juvenile survival term (so any juvenile that doesn’t move to the adult class the year after birth is assumed to die).

Lines 78-86. The fish feed on frog larvae, which I assume means tadpoles, but in your model, mortality is in the term for juvenile recruitment (growth into adults). This is confusing. Why not multiply the f_1 term (for habitat 1) by $(1-d)$? Then the number of juveniles born in habitat 1 is reduced by predation, and then it is clear that movement is after predation (and I think this gives the same results as your matrix). But in several places you imply that movement is before predation, such as in the abstract where you write “some juveniles disperse to the trap” or on line 228 where you mention “juveniles mis-reading cues”, which suggests that juveniles are moving to a habitat where they will experience predation. This paragraph discusses adults choosing oviposition sites. So it is adults that are misreading cues and dispersing to the trap in the real system. That is what is in matrix A. The equation for the number of adults in the trap is $n_{S1}(t+1) = J_1(1-p)d n_{J1}(t) + S_1 n_{S1}(t) + J_2 d n_{J2}(t)$. The middle term is survival of adults from the previous year, and the other terms are recruitment of juveniles. The last term is recruitment of juveniles from habitat 2, which has probability J_2 , which means they recruit in habitat 2 and then a fraction d move to habitat 1. Therefore, the model is actually for movement of individuals right after recruitment (which are adults), after which they don’t move. Your “adult migration” is different in that new recruits do not move by adults can move each year after that. Line 82, change “oviposition” to “oviposition”.

Lines 88-89, change first “at rate” to “from one year to the next with probability”, delete the second “at rate” and add “offspring per year” after “f”, delete the second “and”, add “(move into the adult class)” after “recruit”, change “at” to “with” and change “rates” to “probabilities”. You should point out that juveniles that do not recruit the year after birth are assumed to die, and that those that do recruit one year

reproduce the next year regardless of adult survival. I wouldn't define the standard deviation of J_i here, because you actually specify below the entire distribution of J_i . Of course, that has a standard deviation, but you are not using the standard deviation directly, except in the analysis of the Doak model, so you can define σ_{J_i} there.

Line 91, change “reduce” to “kill a fraction p of juveniles, reducing”.



The matrix M_J is incorrect. If a fraction d settles in the patch with predation (this is patch 1, and you need to state this), then the first row of the matrix should be “ d ” and the second row “ $1-d$ ”.

Line 103. I think you should define each of the population sizes. Also, why are you using an “ S ” subscript for “adult” – why not use “ A ”? (Also, why not have recruitment be “ R ” so that “ J ” doesn't represent two different things?)

Line 104, change “evolution is” to “demographics are” (or state that the equation projects the population in each class from one year to the next).

Table 1, change “average” state to “fair” or something else, since the average state could mean the average of the four states.



Line 112. Density dependence could change the results. There is normally density dependence in a source to keep the population bounded. A sink would generally have a lower population and less (negative) density dependence. The reduced density dependence could cause use of the sink to be more favored than would be indicated by ignoring density dependence (but it might depend on the stage that experiences the density dependence).

Line 114, add “logarithm of the” before “metapopulation”. Mention that λ is the dominant eigenvalue of matrix A .

Line 117, change “survival” to “recruitment” (or add “juvenile” before “survival”). I would also delete the “ $\sigma_{J_i} = 0$ ”, since “no inter-annual variation” is clear.

Lines 119-121. Check this – I get the predator patch with a growth rate just barely above 1 at 20% predation (with the parameters in the table) and less than 1 above this (also, the growth rate cannot be negative for a discrete-time model).

Line 130, change “a random draw” to “independent random draws”. (The next section mentions that the value between patches are independent, at least until you introduce spatial correlation, but it is also important that within each patch, states from year to year are independent, so there is no temporal autocorrelation.)

Line 132, delete “with variation σ_{J_i} ” - again, you have specified the four possible values are how they are chosen (equal probability, independent). This sentence might suggest that you are drawing a random variable from a distribution with standard deviation σ_{J_i} .

Line 134. As long as the habitats are uncorrelated, there are only 16 different, equally likely types of year (4 year types for 2 habitats), so you could have just averaged the logarithms of the λ s for these 16 types, rather than running 1,000,000-year simulations. (With spatial correlation, they are not all equally likely.)

Lines 138-139, change the sentence to “For predation rates up to 60%, the growth rate was a unimodal function of dispersal to the predator patch (Fig. 2).” Also, “unimodal” is spelled incorrectly in numerous places and is sometimes hyphenated, sometimes not (I would not hyphenate).

Line 140, change “low” to “0”.

Line 147. The Doak reference is not in the reference list.

Line 148. The meaning of “i” and “j” is not clear. They are indices that run through the stochastic vital rates, which are J_1 and J_2 . So maybe it would be more clear if you wrote i and $j = 1$ to 2 , and then use subscripts “ J_i ” and “ J_j ” (or better “ R_i ” and “ R_j ”, if you change the recruitment parameters to R_i). Also, you need to state what “sensitivity” means, and that $\rho_{i,j}$ is the correlation coefficient between J_i and J_j (including when $i=j$, so I think “cross-parameter correlation” is misleading).

Figure 2 legend, add “juvenile” before “survivorship” (or use “recruitment”).

Line 152, I think you are assuming the mean of J_1 = the mean of J_2 . If $J_1 = J_2$, they are perfectly correlated, which you are not assuming. Also, you are assuming $S_1 = S_2 = S$, $f_1 = f_2 = f$.

Equation after line 154. I do not get the same result. I think you took the partial derivative of the mean growth rate with respect to J and used it for the partial derivatives with respect to J_1 and J_2 . As I point out above, you are assuming the mean values of J_1 and J_2 are the same, but J_1 and J_2 are not. Therefore, for the sensitivity to J_1 , you should write the mean growth rate in terms of the mean of J_1 and J_2 , take the partial derivative with respect to J_1 , and then set $J_1 = J_2 = J$. I think this gives you $df(1-p)/v$ instead of your $f(1-dp)/v$. I also think you need a 2 in front of the ρ term, since there are two cross-product terms.

Lines 169-172. What’s the point in coming up with this equation if you don’t use it? You could always numerically solve it for “ d^* ”, for example, fixing all parameters except one, which you could vary over several values, calculating d^* for each. Another thing you could do is find the sign of the derivative at $d = 0$ (since the slope at 0 differentiates the unimodal from the monotonic case in your numerical results). Setting $d = 0$ makes the last term 0 and all other terms are negative, so the derivative is negative, so λ_s decreases with d for very small d . For my expression mentioned in the preceding paragraph, the derivative is always negative, so λ_s always decreases with increasing d . So it appears that the analytical expression won’t give you the unimodal pattern. Maybe this is because of the small variation assumption used to derive the formula. Your varying parameters vary by a factor of 200. It is the most extreme value (failure year) that is probably most important for your numerical results (since the geometric mean is most affected by low values) and it occurs 25% of the time. Also, I don’t understand the sentence after the equation.

Line 173ff. I would change “autocorrelation” to “correlation” (although I suppose this is a matter of taste).

Line 175, add “of” after “value”.

Lines 194 and 195, add “sometimes” after “is”.

Lines 195-197. What is the abscissa in Figure 4? It is labeled “proportional investment in juveniles.” All the text says is that recruitment rate was multiplied by 0.1-2 and S adjusted to make the mean $J/(1-S)$ the same, and then this sentence refers to investment in juvenile recruitment and adult survival. With the baseline numbers, $J/(1-S) = 0.01555$, so keeping this ratio constant means that $J/0.01555 + S = 1$. So I guess you could mean that $J/0.01555$ is the proportional investment in juveniles, and S that for adults.

(since they add to 1). But the reader should not have to figure that out (and probably will not). You need to state what you are doing. Also, for Figure 4, the curves are identified incorrectly (except for the solid one), and “predation” is spelled incorrectly in the last entry of the graph key.

Lines 208 and 210. It is a little confusing that the text refers to “adult survival” here when the graph label is “proportional investment in juveniles”. If you want to emphasize the effect of adult survival, why don’t you make that the abscissa? Anyway, make sure that in defining whatever abscissa you choose, you are clear that juvenile recruitment and adult survival investments are negatively related.

Lines 211-212. In some cases, the dotted line is higher than the solid line, so this sentence needs to be qualified.

Line 217, change “decrease” to “decreases”.

Line 219, add “sometimes” after “is”.

Lines 235-237. Holt (1997) does not assume organisms have perfect information – a fixed fraction each generation goes to the source and the rest to the sink, as in your model.

Lines 243-248. It seems obvious that a patch with 100% predation could provide no benefit. However, your results also show no advantage at 80%, or at 50% if there is high spatial correlation. So just state that there is no benefit if predation is sufficiently high (and it does not have to be so high that the predator-free patch always has higher recruitment).

Lines 250-251, delete “of the unimodal relationship between attractiveness of the trap and”.

Lines 252-253. The predator patch does not always have lower fitness with positive spatial correlation (unless the correlation coefficient is 1). I also don’t think the environment is more predictable – each patch individually still has an unpredictable sequence of year types (although with correlation, if you knew what state one patch was in, that would make the state of the other more predictable – but in your scenario, then it would be too late for that to be useful). What the spatial correlation does is to reduce the value of bet hedging, which is helpful when the source has a bad year and the sink a good year. This is less likely with spatial correlation, because then the source and sink are more likely to have good and bad years at the same time. What would make the environment more predictable is temporal autocorrelation. But this could make the sink more helpful (if there is no spatial correlation), because then there could be cases in which the source has a run of bad years and the sink a run of good years.

Lines 264-265. The basis for the first clause of this sentence is not clear (from the paper). The metapopulation survives if its geometric mean growth rate is above 1. The geometric mean is heavily influenced by low values, which occur during recruitment failure years. As adult survival goes down, the growth rate in failure years goes down, pulling the geometric mean down. In fact, I think the “source” geometric mean fitness for $S = 0.05$ (and J increased to have the same average life span) is less than 1, so it is not a source at the left end of figure 4. If so, this should be mentioned, since in those cases the source couldn’t survive unless some dispersal to the trap increased the metapopulation growth rate sufficiently.

Lines 271-272. I assume this paragraph is about the juvenile-predation case (you should be clear about that). The reason adults in a predator patch have lower fitness is that their offspring face predation each year (since as I state above, in your matrix A , predation is before movement). The next sentence is sometimes true and sometimes not. As far as the last sentence in the paragraph, which is presumably about why increased adult investment leads to a lower $\log \lambda_{s,MAX}$ (so I would say the trap is less helpful), I think there are other reasons also. With increased S , the relation between growth rate and

juvenile recruitment is weaker. At the highest $S = 0.95$, the growth rate is always at least 0.95, and in good years it is only 1.2 in the source (and lower in the sink). So the source is not too bad in even failure years and the sink isn't particularly good when it has a good year. There is much more variability in growth rates with a lower S (and as I state above, the lowest value is the most important).

Lines 276-279. This is not clear. It is true that "increasing adult survival decreases the value of dispersal toward a trap to an even greater degree" if this means that the slope of the dashed line in Figure 4 is higher than the slope of the solid line (the plot is the maximum benefit from using the trap, and increasing survival means going to the left). However, this is an odd way to describe these curves. For most values of juvenile investment, the value of the trap is higher with adult predation than with juvenile predation, so maybe the dashed curve drops faster because it is higher and both are going to 0. So I think what needs to be explained is why the trap can be more helpful with adult predation, even though the adults don't move and so face the risk of predation (50%) every year. It might be because all adults reproduce at least once. So even if predation were 100%, a juvenile going to the sink in a good year could recruit to an adult and reproduce 150 offspring, some of which will end up back at the source, before the adult is eaten. If there were 100% juvenile predation in the sink, then obviously the sink is a dead end.

Lines 283ff. I guess this paragraph is meant to explain the dotted curve in Figure 4, but that is not at all clear. If that is true, at least state that you are back to considering juvenile predation. I think the first question about the dotted line is why it is generally lower than the solid curve. I think a reason is that new adults reproduce before they move. So a juvenile born in the predator lake faced predation and recruits to an adult, which reproduces there before it moves. So its first-year offspring are also born in the sink and face predation. So there is an extra penalty from using the sink with adult movement. The magnitude of this penalty depends on how important an adult's first year's reproduction is. If adult survival is low (right end of fig. 4), then it is very important, and the penalty is high. If adult survival is high, each adult reproduces many times, so the fate of the first batch is not that important.

As far what you wrote, I don't think more individuals benefit from good years in the sink. With juvenile migration, a fraction d of all juveniles recruit in the sink. With adult migration, a fraction d of all adults move to the sink, lay their eggs, and those juveniles recruit in the sink. So the fraction recruiting in the sink are the same. It is true that adults are not stuck in the trap, so with high adult survival adult movement can be better than juvenile movement (but this sentence is not clear). At very low investment in juveniles, adults have very high survival, so it is not surprising that use of the sink eventually becomes less beneficial, for reasons you mention in lines 266-269.

Lines 295ff. I again am having trouble understanding your argument. Each adult does not spend the same proportion of time in the trap (some live only one year as an adult, so they either spend 0 or 100% of their time there), and even if it did, that would not say anything about whether there is any benefit in using the sink. Actually, with adult dispersal and adult mortality, I would think that using the sink would often be beneficial. If $S = 0.05$, the fitness in the "source" (I don't think the no-predation habitat is a source in this case) and sink are not that different, because

predation just lowers adult survival, which is already low. So it would seem that you would get the bet-hedging benefit and not pay too much of a penalty.

Lines 306-307, change “an” to “any” and add “average” after “decreases”. Clearly, if the source is in a failure year and the sink is not, individual fitness is higher for individuals that move to the sink.

Line 333. I assume “decrease does” is supposed to be “decreases”.