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**Natal philopatry model – rank effects**

In the present version of the natal philopatry model, subordinates are no longer considered equal, but their reproductive success and decisions over group membership differ according to their rank.

1) Reproductive success

In each breeding season, breeders of rank R produce FR(n,R) offspring. Owing to density dependent resource competition, the number of offspring produced declines with group size (n), and with rank (R) according to the following function:

The parameter α gives the strength of density dependence, and the parameter δ gives the “steepness” of the rank hierarchy. If δ=0, the effect of density dependence is the same for the dominant and all subordinates; but as δ increases, the effect of density dependence becomes stronger for lower ranking individuals.

Default values in the simulation are: α= 0.1, δ=0.

2) Rank inheritance

Another important effect of rank is that individuals form a strict breeding queue, that is, if one individual dies, all lower ranking individuals move up one rank. This rule applies to the dominant position as well, i.e., the acquisition of the dominant position is no longer randomly determined among subordinates.

3) Decisions over group membership

Because reproductive success depends on both group size and rank, the decisions over group membership (join vs disperse and accept vs reject) should also depend on group size and rank. To implement the effect of rank, we need two more alleles: A2 relates a *resident’s decision* whether to accept an offspring to her own rank, B2 relates an *offspring’s decision* whether to stay to rank, but in this case, the definition of rank depends on how rank is attained. An offspring’s decision whether to stay on the natal patch should depend on *the rank it can acquire if it stays*. We consider two possible scenarios: (i) All new offspring enter at the bottom of the queue. In this case, the rank they can *potentially* obtain, R, is given by R= n+1 (but does not contain any information). Note, however, that if more than 1, say m, offspring enter at the bottom of the queue, the rank (between n+1 and n+m) each offspring will eventually obtain, is determined at random. (ii) New offspring enter at the rank position below their mother. This is actually quite common in matrilineal primates. In this case R= mother’s rank +1, and it would mean that existing lower-ranking subordinates would be shifted downwards by one rank. Here, if F0 > 1, say m, all m surviving offspring enter the ranks below their mother, and existing subordinates are shifted downwards by m ranks.

An offsprings propability of staying is given by the following function:

(1)

A resident’s probability of accepting is given by the following function:

(2)

In equation (2) R is the resident’s own rank. In equation (1), the definition of R depends on how rank is attained (see above, R=n+1 under scenario (i), and R= mother’s rank +1 under scenario (ii)). We assume that x(n,R) and y(n,R) are determined at the beginning of the dispersal stage (see below), i.e, all individuals make their decisions simultaneously based on their information at the beginning of the dispersal stage.

4) Scheduling

So far we have assumed the following sequence of events: Reproduction – Dispersal – Survival – Colonization. I suggest changing the sequence of events as follows: Reproduction – Survival –Dispersal – Colonization. This change, however, may have the consequence (which I think is fairly realistic in nature) that when the decisions over group membership are made, some breeders may no longer be alive. Under scenario (ii) considered above, this means that mothers who have died cannot support their daughters any more. To determine the staying probability (x, equation 1), we need thus assume that the best rank those offspring can acquire is rank n+2 (since rank n+1 is the rank “reserved” for the offspring of the lowest-ranking subordinate).

5) Group formation: Who is in control?

We consider various different scenarios of group formation:

i) offspring control: group formation is determined solely by x(n,r).

ii) breeder control: group formation is determined only by y(n,r), and can take the following forms:

ii.1) “despotic”: Group formation is determined only by the dominant’s y.

ii.2) “egalitarian”: Group formation is determined by the mean of all breeders’ y’s.

iii3) “hierarchical”: An offspring is allowed to stay if its mother and all higher ranking mothers opt to accept it. In other words, for an offspring born to a mother of rank R, the acceptance probability is determined by the product:

Here again, if an offspring’s mother has already died, the offspring finds itself at the bottom of the queue, and all females in the group can potentially evict it, i.e., all the y’s from 1 to R are considered.

iii) both offspring and breeder control group membership, i.e., group formation is determined by the product of x(n,r) and y(n,r). The y’s are determined “despotically”, “egalitarian”, or “hierarchically” as above.

6) Minor changes

6.1 Takeovers: The probability of a group takeover is represented by an exponential rather than a logistic function:

6.2 Mutation: As before, mutations occur with a small probability μ (0.01). In that case, the allele of the offspring is given by the allelic value of the mother ± a small random number drawn from a **Cauchy (Lorentz-) Distribution** with center (location) 0 and width (scale parameter) 0.1. Starting conditions are A0 = A1 = A3= B0 = B1 = B3= 3.