Natal philopatry model 12.11.2015

\*\*\* The numbers in brackets are numerical values of the model parameters \*\*\*

Population structure

We consider a population structured into m (1000) patches. Patches are further divided into a (potentially infinite) number of breeding sites, n of which are occupied by a single female breeder. We assume that females form a linear rank hierarchy. The first female to arrive on a patch becomes the dominant breeder, and is assigned rank R=1. Females remaining on their natal patch (offspring born on that patch, see dispersal below) become subordinate breeders, and obtain a rank position below the dominant. We consider two different scenarios how rank is attained: (i) All new group members (females) enter the queue at the bottom, being placed randomly at positions n+1, n+2, etc. (ii) New philopatric females enter at the rank positions below their mother, being placed randomly at positions R+1, R+2, etc. In the second scenario, offspring of the highest-ranking female are placed in the hierarchy first (shifting all other females downwards), followed by the offspring of the second-highest female, etc. Females move up one rank if a female above them in the hierarchy dies. This rule applies to the dominant position as well.

Females that decide to disperse (rather than to stay on the natal patch) join a pool of non-resident, non-breeding floaters (outside the patches). Floaters can colonize patches on which all resident females have died (and which have thus turned into empty patches), or they can try to forcefully take over patches by evicting all former residents.

Mating system

We assume that all males disperse from their natal patch to join a pool of non-resident male floaters. We consider two possible mating systems:

1) Random mating

Under this scenario, males are not associated with females. In each breeding bout (see reproduction, below) each female breeder mates with a randomly chosen male. This male is drawn at random from the pool of male floaters. At the start of the simulations there are nMF= 900 floater males in the population.

2) Male residency

Under this scenario males are permanently associated with females. In addition to the females, there is one breeding male on each patch. Males do not occupy female breeding sites. Whenever a male breeder dies, a new male is drawn at random from the pool of male floaters to occupy the vacant breeding position. All females at a patch mate exclusively with the male breeder on their patch! At the start of the simulations 90% of patches are occupied with both a breeding female and a breeding male (i.e., a breeding pair), whereas the number of male floaters nMF= 0.

Life cycle

1) Reproduction

We model population dynamics in discrete time. In each breeding season, each breeder produces F0 (1) offspring, not all of which, however, survive to sexual maturity. Owing to density dependent resource competition, we assume that fecundity declines with increasing group size (n). We further assume that lower ranking females suffer more strongly from resource competition than higher ranking females, such that fecundity declines with increasing female rank (R, with R=1 being the highest ranking female). Lastly, we allow for a positive effect of group size on fecundity, e.g. through helping behaviours. The fecundity (F) of a breeder of rank R in a group of size n is thus given by 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 all individuals; but as δ increases, the effect of density dependence becomes stronger for lower ranking individuals. Lastly, the parameter k determines the effect of helping on fecundity, with smaller values of k representing a stronger dependence on helping for successful reproduction. Default values in the simulation are: α= 0.1, δ=0, k=10.

We determine the sex of each offspring. With probability ½ it is a son (that is assumed to disperse to the floater pool), with probability ½ it is a daughter that is given the decision whether to disperse or whether stay at her natal patch (see next step).

2) Dispersal

Female offspring are given the decision whether to stay on the natal patch, or whether to disperse to the floater pool. At the same time, resident females are given the decision whether to accept offspring willing to stay, or whether to evict them. Because reproductive success depends on both group size and rank, the decisions over group membership (stay vs disperse and accept vs evict) should also depend on group size and rank. To implement these decisions, we model the probability of an offspring to stay on the natal patch (x), and the probability of a breeder at rank R to accept an offspring (yR), using the following functions:

B0 and A0 are the intercept of a logistic function relating, respectively, an offspring’s probability to stay in the group, and a breeder’s probability to accept an offspring to group size (n) and rank (R). B1 and A1 describe, respectively, how an offspring’s decision to stay in the group, and a resident’s decision to accept an offspring depend on group size (n). Lastly, B2 describes how an offspring’s decision whether to stay in the group depends on the *rank of her mother*, and A2 describes how a resident’s decision whether to accept an offspring depends on the resident’s rank.

A0, A1, A2, B0, B1, and B2 are assumed to be gene-loci determining the aforementioned probabilities. We assume that individuals are diploid, each carrying two alleles at the gene-locus of interest, i.e. each individual has two A0 alleles, two A1 alleles, etc.. An individual’s genotype at the relevant gene locus (A0, A1, A2, B0, B1, B2) is determined by the mean of the two alleles (additive gene action), i.e.,

A0= mean(A01, A02), A1= mean (A11, A12), etc.

2.1) Group formation: Who is in control?

We consider various scenarios concerning the decision whether a given offspring remains in the group:

i) offspring control: the probability that an offspring remains in the group is solely determined by x(n,R).

ii) breeder control: the probability that an offspring remains in the group is solely determined by y(n,R) of the breeders; this probability can take the following forms:

ii.1) “despotic”: the probability that an offspring remains in the group is determined by the dominant’s y(n,R).

ii.2) “kin”: the probability that an offspring remains in the group is determined by her mother’s y(n,R).

ii3) egalitarian”: the probability that an offspring remains in the group corresponds to the average value of the y(n,R) values of the breeders.

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(n,R)’s are determined “despotically”, “egalitarian”, or by “kin” as above.

3) Survival

Owing to enhanced vigilance and possible dilution effects, residents may survive better in larger groups than in smaller groups. The survival probability of residents (breeding females, the male) thus increases with group size according to the following function:

Where Sx represents the survival parameter in question (SB for breeding females, SM for the male), Smax is the species-specific maximum annual survival probability, n is female group size, and the parameters Θ (0.8) and γ (0) specify the shape of the function relating survival to group size.

Female floaters survive with survival probability SF (0.6), and male floaters survive with probability SMF (0.8).

4) Colonization and takeovers

Empty patches can be colonized by floaters, and occupied patches can be taken over by floaters. In each time-step of the model, therefore, each territory is tested whether it is encountered by one or more floaters. The probability that the territory is discovered by k floaters is given by a Poisson distribution with mean λ= ε \* nF, where ε (0.005) is the floaters’ ‘speed’ of discovering territories, and nF the number of floaters.

If an empty patch is discovered by at least one floater, one floater is drawn at random from the floater pool to occupy the patch (and to become the new breeder on that patch). If the patch is already occupied, the patch will be subject to k takeover attempts. The probability of a takeover attempt to be successful (t) depends on the number of individuals defending the territory (only females are assumed to defend the territory):

where d (0) is the degree of synergy arising through jointly defending the territory against outsiders, and t0 (0.05) the baseline takeover probability. If at least one of the k takeover attempts is successful, one floater is drawn at random from the floater pool, and this floater becomes the new breeder. All females formerly inhabiting the territory are evicted (and assumed to die).

After all colorizations and takeovers occurred, the life cycle starts again.

Inheritance/ Evolution, and starting conditions

We assume that individuals reproduce sexually. At each gene-locus, offspring inherit one allele from their mother and one allele from their father. Alleles are drawn at random from the two alleles each parent has at each locus, i.e.,

Offspring A01= prob= ½ mother A01, else mother A02,

Offspring A02= prob= ½ father A01, else father A02,

Offspring A11= prob= ½ mother A11, else mother A12,

Offspring A12= prob= ½ father A11, else father A12,

etc.

Once an offspring has been assigned all its 12 alleles, with a small probability μ (0.01), a mutation occurs. In that case, the allele of the offspring is given by the allelic value of the parent ± a small random number drawn from a **Cauchy (Lorentz-) Distribution** with center (location) 0 and width (scale parameter) 0.1. Starting conditions are A0 = B0 = 5, A1 = A2= B1 = B2= 0. These values give an initial probability of group formation close to zero.

Calculation of relatedness

We calculate **mean relatedness among group members** as the degree of “genetic similarity” using a regression approach:

where *a* is the allelic value of a focal individual, and *a’* the allelic value of another group member. We calculate the covariance across all possible pairs of individuals within groups. Likewise, we calculate var(a) as the variance of the relevant allelic values within groups. This measure of r is equivalent to the least-squares regression coefficient of a linear regression of a’ against a (again over all pairs of individuals within groups). In this way, we have calculated the degree of genetic similarity at one allelic position. Repeating this process for all 12 allelic positions, and taking averages, should give us the mean relatedness (genetic similarity) among group members with respect to the six gene loci in our study.