

2. Advanced statistical models

Within Pair allopreening

To examine the relationship between our proxies of long and short term fitness of each pair (the average breeding success of the pair and current breeding success, respectively) on the preen rate of each individual within a pair, we fitted a linear mixed model to our data (using the method of restricted maximum likelihood (REML) Patterson & Thompson 1971). The following independent variables were included as fixed effects (note the abbreviated version shown in brackets for use in Table 1 below): (1) arriving vs. incubating bird (Arriver); (2) sex of the preener (Sex); (3) average breeding success (Ave_BS); (4) current breeding success (BS); (5) male age (Age_M); (6) female age (Age_F); (7) number of previous breeding attempts i.e., length of the pair bond/experience (BA_P) and (8) number of chicks previously successfully produced i.e., positive breeding experience (CF_P). For variables 5-8, both linear and quadratic (quad) effects were examined. Terms were added in order of significance (determined from when fitted alone in the model) to produce the full fitted model before sequentially dropping non-significant terms from the model. No interactions were significant. See Table 1 (a) for the output from the full fitted model.

Neighbour allopreening

To investigate the relationship between long and short term fitness on the rate of preening carried out by an individual towards its neighbours, we fitted a similar model to our data in the same way as described above. The following independent variables were included as fixed effects (1) sex of the preener (Sex); (2) sex of the neighbour (Sex_neigh); (3) number of years they had been neighbours (no_yrs_neigh); (4)

average breeding success (Ave_BS) and (5) current breeding success (BS). The same model selection criteria were used as within pair analysis. See Table 1 (b) for output from the full fitted model.

Reciprocity

To examine whether the preen rate between neighbours was reciprocal, we fitted a linear mixed model to test whether the preen rate of a bird towards its neighbour was related to the rate of preening it received from its neighbour during each observation period. We could not carry out a similar analysis on mate reciprocity because of the nature in which the data within pairs was collected (see ESM_1); instead, we carried out correlations between mean preen rates among pairs.

Neighbour fighting

To assess whether there is a relationship between the frequency of fights between neighbours and breeding outcome we fitted a generalized linear mixed model (GLMM) with a Poisson distribution and logarithm function to the number of fights initiated by an individual from the observation nest. The following independent variables were included as fixed effects: (1) sex of the bird at the observation nest i.e., the fight initiator or non-initiator (Sex); (2) sex of the bird at the neighbouring nest (Sex_neigh) and (3) current breeding success (BS). The order in the model was determined by their significance when fitted alone in the model (as in pair and neighbour allopreening models). Non significant effects were sequentially dropped from the model. See Table 1 (c) for output from the full fitted model.

In all of the above models the individual identity of the preener/fighter was included as a multi-level random effect, with the exception of reciprocity among neighbours within which we used a new identity variable that combined the identity of the preener and the recipient (i.e., four combinations for two neighbouring pairs). Random factors account for cumulative effects of individual-specific properties, thereby allowing the main effects in the model to be estimated independently. It also accounts for any pseudo replication effects. All models were fitted using REML in Genstat 8th edition (VSN International Ltd 2005) version 8.2.0.158 and are presented by comparing the Wald statistics (W) to chi-squared distributions with appropriate degrees of freedom (Schall 1991). All explanatory variables added to the fixed model were centred on their respective mean values (Pinheiro & Bates 2000).

References

- Patterson, H. D. & Thompson, R. 1971 Recovery of inter-block information when block sizes are unequal. *Biometrika* **58**, 545-554.
- Pinheiro, J. C. & Bates, D. M. 2000 *Mixed-effects models in S and S-Plus*. New York: Springer-Verlag.
- Schall, R. 1991 Estimation in generalised linear models with random effects. *Biometrika* **78**, 719-727.

Table illustrating the output from the full fitted linear mixed models (REMLs) for (a) within pair allopreen rates, b) neighbour allopreen rates and c) the generalised linear mixed model (GLMM) on the number of fights between neighbours. The significance values given are generated after sequentially removing non-significant terms from the model (Type III tests).

a)						
Fixed effects:	SE	Wald	P value	Random effects:	Component	SE
Arriver	0.089	21.59	<0.001	Individual	0.113	0.044
Sex	0.123	7.14	0.008			
Ave_BS	0.228	6.44	0.011			
Sex_arr	0.089	1.17	0.278			
BA_P	0.014	0.32	0.572			
CF_P	0.083	0.57	0.450			
CF_P (quad)	0.002	0.48	0.491			
BA_P (quad)	0.008	0.17	0.682			
Age_M	0.011	0.11	0.712			
Age_M (quad)	0.002	0.14	0.741			
BS	0.184	0.03	0.864			
Age_F	0.002	0.02	0.878			
Age_F (quad)	1.523	0.25	0.614			

b)						
Fixed effects:	SE	Wald	P value	Random effects:	Component	SE
BS	0.016	4.04	0.044	Individual	0.00068	0.00039
Sex_neigh	0.010	0.23	0.631			
Sex	0.016	0.05	0.828			
Ave_BS	0.029	0.04	0.842			
no_yrs_neigh	0.004	0.03	0.890			

c)						
Fixed effects:	SE	Wald	P value	Random effects:	Component	SE
BS	1.035	8.15	0.004	Individual	5.64930	3.08296
Sex	1.553	1.68	0.195			
Sex_neigh	0.293	1.21	0.272			