Breeding dispersal of hoopoes in relation to reproductive success, sex and age

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Abstract

1. Dispersal is a key factor for the populations dynamic, is important for gene flow and connects meta-populations. Breeding dispersal is often impacted by sex, age and previous reproductive success, yet little is known about factors affecting dispersal between consecutive broods in the same breeding season.

2. We studied the breeding dispersal behaviour of hoopoes (*Upupa epops*) in the lower Valais (Switzerland), using capture-recapture data of eight years from an intense nest box study. We analysed breeding dispersal probability and distance, both between as well as within years, in relation to age, sex and reproductive output. We used multi-state capture-recapture models and generalized linear models for the analyses.

3. Female hoopoes disperse more often and over longer distances than males (mean distance females: 1.98 km; males: 0.83 km), whereas age did not have a strong effect on breeding dispersal. Reproductive success affected dispersal relatively weakly. Dispersal within years was affected by the same factors as dispersal between years, yet the probability was lower and it occurred over shorter distances than dispersal between years (mean distance females: 1.45 km; males: 0.46 km). Apparent survival strongly increased with increasing reproductive output, suggesting that individuals with low reproductive output either experience increased mortality or conducted extensive dispersal outside the study area.

5. Breeding dispersal of hoopoes was generally high, they often changed the breeding location between successive broods within the same season and between years. Together with the fact that immigration is an important component of hoopoe population dynamics, it highlights that successful hoopoe conservation must consider vast areas with a large amount of suitable breeding territories.

264 words.

Key words: breeding dispersal, multi-state capture-recapture models, reproductive success, within/between years dispersal, *Upupa epops*.

Introduction

Gains and losses of individuals are the two main drivers of population dynamics. A demographic mechanism strongly impacting gain and losses is dispersal. In species exhibiting a high dispersal capacity such as birds (Paradis et al., 1998), there is increasing evidence that the exchange of individuals between populations has a strong impact on local population dynamics and persistence (Newton and Marquiss, 1986; Lampila et al., 2006; Schaub and von Hirschheydt, 2009), and it enhances meta-population systems (Hanski, 1999; Baillie et al., 2000; Macdonald and Johnson, 2001; Kenward et al., 2002). Factors affecting dispersal are therefore potentially important drivers for population changes, and their identification increases the knowledge about how population dynamics works. Dispersal is subdivided into natal dispersal and breeding dispersal (Greenwood and Harvey, 1982). Natal dispersal is the movement from the site of birth to the site of first reproduction whereas breeding dispersal is the movement between sites of subsequent reproduction.

Breeding dispersal of birds can be affected by various extrinsic and intrinsic factors and it is relatively well studied. The factors most often identified include own previous breeding success, habitat quality, nest- or mate predation, density of conspecifics, reproductive success of conspecifics, age and sex (Haas, 1998; Doligez et al., 1999; Oro et al., 1999; Travis et al., 1999; Pasinelli et al., 2007; Kim et al., 2009; Schaub and von Hirschheydt, 2009). Generally, the probability of breeding dispersal declines with increasing reproductive success, it is lower in older than in young individuals and is lower in males than in females. Breeding dispersal can not only occur between breeding sites in different years, but also within the breeding season, if the species conduct two or more broods

(Newton, 2000; Klemp, 2003; Betts et al., 2008; Gilroy et al., 2010). In contrast to influencing factors of breeding dispersal between years, factors affecting dispersal decisions within a breeding season are not well studied. Most of the studies mentioned above did not explicitly study dispersal within a breeding season. The few that did so (Newton, 2000; Klemp, 2003; Gilroy et al., 2010) documented that dispersal movements took place along a habitat gradient or followed food availability peaks. However, with one exception (Klemp 2003), factors affecting the decision to disperse within the season were not studied. Grey wagtails *Montacilla cinerea* had a higher probability to disperse within the breeding season when their first brood was not successful, it was higher for younger than for older males, but was independent on female age (Klemp 2003). Moreover, the movements took place along an altitudinal gradient.

Dispersal is difficult to study basically because of two methodological problems. First, dispersal movements can extend over long distances and are therefore easily overlooked. While it is relatively straightforward to document dispersal within a fixed study area, it is very difficult to follow long dispersal movements beyond the study area. This problem can be overcome by following individuals with transmitters (Steenhof et al., 2005; Lehnen and Rodewald, 2009). Partially the problem can also be solved, if the study area is large and if the encounter probability of marked individuals within the study area is high. Second, due to imperfect detection, it is even possible to miss dispersal events occurring within the study area (Koenig et al., 1996; Macdonald and Johnson, 2001; Kenward et al., 2002). This problem can be overcome by the use of probabilistic models that account for imperfect detection (Lebreton and Pradel, 2002; Schaub and von Hirschheydt, 2009). Thus, it appears that dispersal is best studied in a large study area, where the encounter probability of marked individuals is high.

Here we studied the probability and distance of breeding dispersal of hoopoes (*Upupa epops*) in relation to previous reproductive success, age and sex. Factors affecting breeding dispersal of hoopoes have not been studied yet. Since hoopoes often conduct two clutches in a year, we studied breeding dispersal between two subsequent clutches within the same year in addition to the dispersal between years (the classical breeding dispersal). We were particularly interested in knowing, whether dispersal between and within breeding seasons are affected by the same factors. We conducted the study in an area with a large extension such that dispersal movements up to 40 km could be detected. The studied hoopoes almost exclusively breed in specially designed nest boxes, which allowed a close surveillance of dispersal events within the study area. We applied multistate capture-recapture models to account for imperfect detection, but in addition also classical logistic and linear regression models.

We think that our study area is a unique opportunity to study breeding dispersal, because of a number of reasons: First, in our study area the individuals can hardly breed outside our nest boxes (since 2002 we know of 1 case). Together with the high recapture probability this means that we have observed the vast majority of dispersal/non-dispersal events within our study area. Second, the study area has a large extension, and therefore we can study not only dispersal over very short distances. Third, the studied bird population is isolated in the sense that it is not part of a continuous distribution. Thus, individuals that dispersed to another population must have performed movements that are significantly larger than the maximal distance we can observe in our study area.

Material and methods

Study site and study species

The hoopoe is a secondary cavity breeding, trans-Saharan migrant (Reichlin et al., 2009) mainly feeding on ground arthropods (Fournier and Arlettaz, 2001). Our study was conducted in the upper Rhône valley in south-western Switzerland between Sierre and Vernayaz (62km^2). The area is intensively farmed, consisting of fruit-tree plantations, vineyards, green houses, pastures and arable land. Natural breeding cavities are very scarce in the study area, and hoopoes in the study area breed in specifically designed nest boxes (entrance hole diameter 55 mm) that were installed since 1998. Most of these 700 nest boxes were fixed as pairs on the inside of small shacks lowering the risk of inter-specific competition among nest sites. Hoopoes often conduct a second brood in the same breeding season. Thus, breeding dispersal can not only occur from one year to the next, but also between successive broods within the same season.

Data collection

All nest boxes of the study area were checked every second week to detect new broods. Occupied nest boxes were surveyed every third day to gather information about brood phenology and success. Breeding adults were caught at breeding sites after chicks were at least four days old with different techniques (mist nets placed in front of the nest box; life trap, triggered by hoopoes; or taken directly from the nest box while brooding). The maximal duration of a capture event was two hours per day and about ten hours in total per brood. Captured adults were sexed (inspection of conspicuous uropygial gland; (Martín-Vivaldi et al., 2009), aged (2 classes based on moult: first year, older than first year) and marked with a ring. Nestlings were ringed at the age of 18 days. The number of ringed nestlings was taken as measure of reproductive success of this brood.

Data analysis

We performed several analyses on the impact of current breeding success, sex and age on breeding dispersal within the study area. Two key parameters, breeding dispersal probability and breeding dispersal distance were analysed. Because individuals may conduct one or two broods within a season, the definition of dispersal between years is difficult, since the reference brood could be the first or the second brood. We decided to take the last observed brood in a year as the reference location to study dispersal between years, but tried also the location of the first observed brood. Dispersal within a year was defined as the movement from the location of the first observed brood in year *t* to the location of the second observed brood in year *t*. Fig. 1 shows the different definitions graphically. The modelling of dispersal probability also requires the definition of a distance threshold – if an individual moved a longer distance than this threshold, we consider that it has dispersed. We set the threshold distance to 600 m, because after the movement over more than 600m it is likely that the home range of the individual has changed. The average home range radius of hoopoes in the study area was 355 m; assessed by telemetry,(Ioset, 2007), in France the home range radius was smaller; 223 m, (Barbaro et al., 2008). Dispersal probability between years was modelled with a multi-state capture-recapture model (Schaub and von Hirschheydt 2009) and with logistic regression models. The multi-state model has the advantage that it accounts for possibly imperfect detection and that it also estimates apparent survival. The latter allows getting some indications about possible dispersal outside the study area. The logistic regression model has the advantage that it allows more flexibility in modelling. If detection probability is high and does not depend on sex, age and breeding success, we expect similar results from both analyses regarding dispersal probability. We also used a logistic regression model to analyse dispersal probability within year. Dispersal distances, finally, were analysed using a linear regression model. In the following, we describe the different models and the corresponding data in more detail.

Dispersal probability: multi-state capture-recapture models

We used the multi-state model introduced by Schaub and von Hirschheydt (2009) to analyse the capture-recapture data. The key idea of this model is to estimate state-transition probabilities where states refer to a combination of classes of reproductive success and whether or not the individual has dispersed. The first step is to create individual capture histories that contain information about observed dispersal events and reproductive success. For each individual that was captured in a year, we calculated the total number of fledglings that it had produced within the complete breeding season. We then created a categorical variable with three levels (no: no reproductive success; medium: 1-8 chicks fledged; high: > 8 chicks fledged). The grouping was performed in such a way to have a strong contrast, although it resulted in unequal sizes of groups. The threshold of eight chicks was chosen, because this was the upper limit of the size of single broods (only 19 from 906 observed broods were observed with > 8 fledglings). This means that most individuals that produced more than 8 fledglings needed two successful broods. For each brood and individual we then defined, whether or not it has dispersed (according to 600 m threshold) compared to the last observed brood. The reference broods were the location of the last observed brood in each year (see Fig. 1). The combination of the three classes of reproductive success and two classes of dispersal resulted in six possible states. For example, consider an individual that was observed first without reproductive success. In the second year it was recaptured at a site more than 600 m away from that in the first year and it had medium reproductive success, then it was not recaptured in the third year, in the fourth year it was recaptured again at the same site than in the second year and had high reproductive success. Finally, it was not recaptured in the fifth year. The resulting capture history is then coded as 14060.

Different probabilities can be derived from such capture histories. Conditional on first recording with a certain reproductive success, individuals may i) return to the study area (apparent survival probability, ϕ), they may ii) disperse within the study area (breeding dispersal probability, *d*), given that they returned, they may iii) change reproductive success (*b*), given that they returned and whether or not they dispersed within the study area, and iv) they may be recaptured (recapture probability, *p*), given their reproductive success of the current year. These probabilities can be estimated and modeled as a function of covariates using the multi-state model introduced by Schaub and von Hirschheydt (2009). Uncertainties regarding the state due to imperfect recapture (in the example above there is uncertainty in the third and fifths year) are overcome with the probabilistic nature of the model.

We used E-Surge (Version 1.4.6)(Choquet et al., 2009) to analyse the multi-state capture-recapture histories. To study the impact of the factors (age, sex, year, breeding success and dispersal) on the parameters we performed model selection in several steps. Starting from the most general model {ϕ(success * sex + age), *d*(success * sex + age), *b*(dispersal * sex), *p*(success + sex + year)}, we modelled sequentially the parameter types recapture, change of reproductive success, dispersal and survival using the Akaike's Information Criterion (AIC; (Burnham and Anderson, 2002). At each step we identified the structure of best models that were within 2 units of AIC and combined them with the candidate models for the next parameter type. The candidate models for the parameter types were usually constructed in such way that they contained a combination of factors sex, age and reproductive success. Yet, for the change of the reproductive success we additionally considered models where this change was either Markovian (i.e. change of success depend on success of preceding year) or random (i.e. change of success does not depend on success of preceding year). For the breeding dispersal probability we considered models where it was affected by the reproductive success either only in males or only in females. All candidate models are shown in Appendix (Table S1). To make inference we performed model averaging across all models within 3 AIC values of the last step.

To test whether model assumptions (identity of rates, independence among individuals) were met we performed a goodness of fit test with U-Care; Version 2.3; (Choquet et al., 2009).

Dispersal probability: logistic regression models

For these models we only considered cases where an individual was caught either in two consecutive years (for dispersal between years) or in two consecutive broods within a year. We then defined, whether or not an individual has dispersed (600 m threshold) between the two events, and analysed this boolean variable with a logistic regression model. Each individual was considered only once. If an individual would fulfil the criteria to be included several times, we selected randomly one event. This procedure avoided problems due to pseudoreplication. Theoretically, the need for this restriction could be relaxed by considering the individual identity as a random factor, but we failed to get convergence.

We defined 20 candidate models that could explain dispersal probability in relation to sex, age and reproductive success. In contrast to the multi-state analysis, we included the reproductive success as a continuous variable. For the analysis of dispersal between years, the reproductive success was the total number of fledglings produced in the first year, while for the analysis of dispersal within year, reproductive success was the number of fledglings of the first brood. We also included models with the two-ways interactions sex*reproductive success and age*reproductive success to test whether potential effects of reproductive success were consistent between sexes and age classes. We ranked the models according to the AIC and performed model averaging (over all twenty models). The candidate models for the analyses of dispersal probability between and within year were identical.

Dispersal distance: linear regression models

We analysed log-transformed dispersal distances using linear regression models. As before, we only considered cases where an individual was caught either in two consecutive years (for dispersal between years) or in two consecutive broods within a year (for dispersal within year). We considered only distances that were larger than 0 m, i.e. we modelled distance provided that individuals have changed the breeding location. If several dispersal distances for the same individual were available, we again selected one at random to avoid pseudoreplication.

Explanatory variables, candidate models and model selection procedure were the same as for the analyses of dispersal probabilities (see above).

All the analysis using logistic and linear regression models were performed with R (version 2.10.0, The R Foundation for Statistical Computing).

Results

In total 712 adult hoopoes (367 females, 345 males) were caught from 2002 until 2009 of which 187 were recaptured at least once again in another year (89 males, 98 females). Of 985 captures (507 females, 478 males), 44 (26 females, 18 males) had low (zero), 727 (353 females, 374 males) had middle and 214 (128 females, 86 males) had high reproductive success. Between year dispersal histories of 158 individuals (76 males, 82 females) and within year dispersal histories of 247 individuals (98 males, 149 females) could be observed.

Dispersal probability and apparent survival: multi-state capture-recapture models

The goodness-of-fit test of the multi-state model was not significant (X^2_{72} = 45.409, *P* = 0.99). The complete model selection results are summarized in Appendix (Table S1). The best models for recapture contained either a sex effect or no explanatory variable (constant recapture probability). The second step revealed that the change of the class of reproductive success depended only on whether or not the individuals dispersed and on the previous breeding success (Markovian transitions). Sex and age were not important. The best models for breeding dispersal included either a sex effect, no effect at all, or an effect of the reproductive success in males. Finally, apparent survival was clearly dependent on the reproductive success, and there was some uncertainty about sex and age effects (Table 1).

Model averaged breeding dispersal probability of females was constant for all classes of reproductive success, independent on age and generally relatively high (~0.7, Fig. 2). In males, breeding dispersal probability was dependent on reproductive success, but again not on the age. It was highest for medium reproductive success, and tended on averaged to be lower than that of females. Model averaged apparent survival was nearly identical for both sexes and age classes, but strongly increased with increasing reproductive success (Fig. 3). The recapture probability was constant across years, sex, age classes and classes of reproductive success (0.71, SE=0.05). Because recapture probability did not depend on any of the factors that were studied, dispersal modelling without considering imperfect capture should not have induced spurious patterns.

The probabilities to change classes of reproductive success differed for individuals that had initially no reproductive success between philopatric and dispersing individuals (Fig. 4). Individuals with low reproductive success that dispersed were more likely to achieve a higher reproductive success than philopatric individuals. For individuals that initially had medium or high reproductive success, the probability to change classes of reproductive success did not depend on the dispersal status.

Dispersal probability: logistic regression models

Dispersal between years

Model selection revealed that several models achieved similar support by the data (Table 2). The best model included an age effect only, while the next best models had in addition also a sex effect. The best model including an effect of the reproductive success was lower ranked, but still received some support. Model averaged estimates showed that females had higher probability to dispere than males, that young individuals were more likely to disperse than old individuals, and that dispersal probability slightly declined with increasing reproductive success (Fig. 5). However, all effects were small compared to the confidence intervals. Similar results were obtained for an analysis that considered the first broods in a year as reference (Appendix, Table S2 and Fig. S1), indicating that the choice of the reference brood had a negligible impact on our conclusions.

Dispersal within year

In contrast to the modelling of dispersal between years, modelling of dispersal between first and second brood produced three models that had clearly more support by the data than the other candidate models (Table 3). However, all considered factors were included in these three top models. Model averaged probabilities of dispersal between first and second brood were clearly higher in females than in males (Fig. 5). The probability declined quite strongly with increasing reproductive success of the first brood in old males, while in young males and in females the decline was marginal. The age effect was relatively strong in males while in females it was almost inexistent.

Dispersal distance: linear regression models

Dispersal distance between years

The frequency distribution of dispersal distances showed that female dispersal occurred more often over longer distances than male dispersal (Fig. 6). The mean dispersal distance for females was 1.98 km (SE: 0.413 km; median: 0.667 km; range: 0 - 32.7 km; n = 118) and for males 0.83 km (SE: 0.176 km; median: 0.509 km; range: 0 – 19.4 km; n = 115).

Modelling dispersal distance revealed that many candidate models were similarly well supported by the data (Table 4). The null model was the worst model, indicating that dispersal distance was affected by the variables considered. Model averaged dispersal distance declined slightly with increasing reproductive success and it was on average lower in older than in younger individuals (Fig. 7). The most striking difference was due to sex: females dispersed over larger distances than males. The same pattern was observed if first broods were considered only (Appendix Table S3 and Fig. S2).

Dispersal distance within year

The frequency distribution of dispersal distances between first and second broods showed that female dispersal occurred more often over larger distances than male dispersal (Fig. 6). The mean dispersal distance for females was 1.45 km (SE: 0.244 km; median: 0.447 km; range: 0 – 26.2 km; n =184) and for males 0.46 km (SE: 0.066 km; median: 0.289 km; range: 0 – 5.6 km; n = 114).

As for dispersal distance between years, modelling of dispersal distance between first and second brood revealed that many candidate models were similarly well supported by the data (Table 5). Yet, the null model received little support, indicating that dispersal distance was affected by the variables considered. Model averaged dispersal distances between first and second brood showed similar pattern as dispersal distance between years (Fig. 7). They were shorter in males than in females and declined with increasing reproductive success. The dependence of the distance between first and second brood on reproductive success appeared to be stronger than for dispersal distance between years. Overall, the dispersal distance between first and second brood was shorter than dispersal distance between years.

Discussion

Our results show that breeding dispersal probability distance between years as well as between first and second brood of the same year of hoopoes were affected by the same factors: they differed strongly between sexes, but little between age classes and they declined slightly with increasing previous reproductive success. Generally, dispersal probability between years was higher and occurred over longer distances than dispersal within years.

Dispersal probability between years analysed with the multi-state model and with the logistic regression model revealed similar results. In females the consistency was very good: dispersal probability in both analyses was hardly affected by previous reproductive success and age. In males, some differences between the two analyses emerged: the multi-state analysis showed that males with low reproductive success were quite philopatric, while the logistic regression model showed that dispersal probability did not depend on previous reproductive success. Because philopatry of individuals with no reproductive success is not expected (Haas, 1998; Doligez et al., 1999; Blakesley et al., 2006; Schaub and von Hirschheydt, 2009) we think that this is spurious result due to the low sample size. Consequently, we think that reproductive success had a weak impact on dispersal decisions only. Overall, the probabilities of dispersal between years obtained with the multi-state model were slightly higher than that obtained with the logistic regression models. This is to be expected because the former considered also the possibility that dispersed individuals were not recorded. The multi-state model also showed that the recapture probabilities were generally high and not impacted by any of the studied factors. Therefore, imperfect detection is unlikely to have produced spurious results on the analyses that did not include imperfect detection.

The sex had a strong impact on dispersal between years – generally females were more likely to disperse than males and over longer distances. In this respect, dispersal of hoopoes was similar to dispersal of many other species (Greenwood and Harvey, 1982; Korpimäki, 1993; Wiklund, 1996; Forero et al., 1999; Serrano et al., 2001; Hoover, 2003; Winkler et al., 2004; Blakesley et al., 2006; Calabuig et al., 2008; Eeva et al., 2008; Schaub and von Hirschheydt, 2009; Zuberogoitia et al., 2009). The same patterns were observed also for dispersal within year: females dispersed more often and over longer distances.

The age did not have a strong impact on dispersal probability and distance in hoopoes, both within and between years. Still, the effect size was in the expected direction, that younger individuals exhibit stronger dispersal than older individuals. In long-lived species such as black kites *Milvus milvus* (Forero et al., 1999), the Audouin's gull *Larus audouinii* (Oro et al., 2004) or the lesser kestrel *Falco naumanni* (Calabuig et al., 2008), age had a stronger effect on dispersal, than in short-lived species such as barn swallows *Hirundo rustica* (Schaub and von Hirschheydt, 2009), pied flycatchers *Ficedula hypoleuca* (Eeva et al., 2008) or hoopoes (this study). Perhaps short-lived birds do not change their dispersal behaviour with increasing age, or it is also possible that a potential change is difficult to detect, because the sample size of old individuals is much lower in short-lived than in long-lived species.

Many studies have reported a strong impact of the own previous reproductive output on dispersal (Wiklund, 1996; Haas, 1998; Doligez et al., 1999; Winkler et al., 2004; Pasinelli et al., 2007; Calabuig et al., 2008; Schaub and von Hirschheydt, 2009). This is consistent with the dispersal of hoopoes, although the impact of the reproductive output was relatively weak. Its impact was stronger in males than in females, especially as regards dispersal within year (Fig. 5). The weak relationship of reproductive output on dispersal in females may be explained by the fact, that females leave their brood before the chicks fledge. In the last nestling phase and during the post-fledging period the males feed the young alone and therefore have better knowledge about the reproductive output than females. The consequences of dispersal in terms of reproductive success were only apparent for individuals that had no reproductive success: these individuals had a higher change to increase reproductive success when they dispersed compared to when they remained philopatric. For individuals, however, that had medium or high reproductive success, which represent the vast majority of individuals, probabilities to change class of reproductive success was independent on the dispersal decision. This may explain, why the relationship between current reproduction and the dispersal decision in hoopoes was relatively weak.

Apparent survival of both sexes and age classes was the same, and it strongly increased with previous reproductive success. Since permanent emigration and mortality are confounded, it is not possible to decide whether individuals with low reproductive success have higher mortality or more often dispersed to another population than individuals with high reproductive success. However, there is some evidence favouring the hypothesis that the reason is more likely differential mortality than dispersal. First, if dispersal to another population would be the reason, we would have expected a stronger dependence of dispersal within the study area on reproductive success. For example, in barn swallow females, apparent survival also increased with reproductive success (albeit not that strongly as in the hoopoe), but at the same time there was a strong decline of dispersal probability within the study area with increasing reproductive success (Schaub and von Hirschheydt, 2009). Second, the change of the class of reproductive success was Markovian, i.e. it depended on the previous reproductive success (Fig. 4), pointing towards individual differences in reproductive performance. If there are strong individual differences in reproductive performance, it is not surprising to find also strong individual differences in survival. If this argumentation is true, then it appears that individual heterogeneity in terms of reproduction and survival in hoopoes is large and it would be interesting to study how they are maintained.

Few studies have focused on dispersal between the first and the second brood within the same year so far. Our study shows that dispersal was affected by the same factors as dispersal between years, suggesting that similar functional relationships existed. Overall, dispersal within year was a bit less pronounced that dispersal between years. It is possible that dispersal between first and second brood is more difficult and therefore less strong, because many territories are already occupied. Overall, breeding dispersal in hoopoes was very strong compared to many other bird species, where breeding dispersal is usually not very strong and most individuals are philopatric (Greenwood and Harvey 1982). In many species that exhibit low breeding dispersal, a main driver for dispersal is the current reproductive success (e.g. Pasinelli et al. 2007; Schaub and von Hirschheydt 2009). Thus, individuals having low reproductive success aim at dispersing to a territory of higher quality in the next year to increase reproduction. This seems to be different in hoopoes, as breeding dispersal is generally high and as the decision to disperse is only weakly impacted by the current reproduction. Thus, the reason to disperse is unlikely to be to achieve a territory of higher quality. Perhaps the reason of dispersal has to do with the nest site: frequent dispersal may help to avoid nest predation and negative effects due to nest parasites (Fitze et al., 2004), and thus to maintain, rather than to increase, reproductive success. Since hoopoes nest in cavities (thus at well defined places), predators may acquire knowledge about the location, if the same cavity is used many times. Also, nest parasites often more easily cumulate in cavities that are frequently used compared to those that are less frequently used (Stanback and Dervan, 2001; Mazgajski, 2007; Tomás et al., 2007). Avoidance of parasites can affect nest site choice, as shown experimentally in Eastern blue birds which preferred to conduct their second brood in previously unoccupied cavities containing less parasites (Stanback and Dervan, 2001).To confirm or reject these hypotheses, further studies will be necessary.

Our study shows that breeding dispersal in hoopoes is strong. Compared with the barn swallow which has a similar survival probability and reproductive output, dispersal probability in hoopoes was much higher, both within and between years (Schaub and von Hirschheydt, 2009). This is consistent with a population study which demonstrated that immigration and emigration are important factors determining hoopoe population dynamics (Reichlin et al. in review). Hoopoes often changed the breeding location between first and second brood, highlighting the need for a high offer of suitable breeding cavities throughout the season.

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Tables

Table 1: Model selection results of apparent survival (ϕ), breeding dispersal (*d*), change of reproductive success (*b*) and recapture (*p*) using the multi-state capture-recapture analysis. Shown are the best 10 models from the last modelling step; the other fitted models are presented in Appendix (Table 1). Given are ΔAIC: AIC-value (Akaike Information Criterion) of a model minus the AIC value of the best model, AICw: AIC weight of the given model, K: number of estimated parameters of the model, Dev: deviance. Model notations: disp: dispersal, .: constant, success: reproductive success (3 classes).

Model	ΔAIC	AICw	K	Dev
ϕ(success), *d*(male: success; female: .), *b*(disp), *p*(.)	0.000	0.173	20	1878.166
ϕ(success), *d*(.), *b*(disp), *p*(.)	1.076	0.101	17	1885.242
ϕ(success+sex+age), *d*(male: success; female: .), *b*(disp), *p*(.)	1.090	0.100	22	1875.256
ϕ(success), *d*(sex), *b*(disp), *p*(.)	1.691	0.074	18	1883.857
ϕ(success), *d*(male: success; female: .), *b*(disp), *p*(sex)	1.807	0.070	21	1877.973
ϕ(success+sex+age), *d*(.), *b*(disp), *p*(.)	2.146	0.059	19	1882.312
ϕ(success*sex+age), *d*(male: success; female: .), *b*(disp), *p*(.)	2.704	0.045	25	1870.870
ϕ(success+sex+age), *d*(sex), *b*(disp), *p*(.)	2.759	0.044	20	1880.925
ϕ(success), *d*(.), *b*(disp), *p*(sex)	2.879	0.041	18	1885.045
ϕ(success+sex+age), *d*(male: success; female: .), *b*(disp), *p*(sex)	2.963	0.039	23	1875.129

Table 2: Model selection results of hoopoe breeding dispersal probability between years obtained from logistic regression models. The models are ordered by their support of the data, with the best model at the top. Given are the ΔAIC (difference between the current and the best AIC value), AICw: Akaike weight, K: Number of estimated parameters, Dev: Deviance. The 90% best models are bold printed (n = 158).

Model	ΔAIC	AICw	K	Dev
age	**0.000**	**0.134**	**2**	**215.751**
sex + age	**0.047**	**0.130**	**3**	**213.798**
sex * age	**0.777**	**0.091**	**4**	**212.529**
sex	**1.182**	**0.074**	**2**	**216.933**
Null model	**1.258**	**0.071**	**1**	**219.009**
M: age; F: success + age	**1.509**	**0.063**	**4**	**213.260**
success + age	**1.802**	**0.054**	**3**	**215.554**
M: success + age; F: age	**2.047**	**0.048**	**4**	**213.798**
sex + success	**2.430**	**0.040**	**3**	**216.182**
M: .; F: success	**2.536**	**0.038**	**3**	**216.287**
sex * age + success	**2.608**	**0.036**	**5**	**212.359**
success	**2.670**	**0.035**	**2**	**218.422**
M: success * age; F: age	**2.870**	**0.032**	**5**	**212.621**
M: success; F: .	**3.017**	**0.030**	**3**	**216.768**
M: age; F: success * age	**3.225**	**0.027**	**5**	**212.977**
success * age	3.275	0.026	4	215.026
success * age + sex	3.439	0.024	5	213.191
success * sex + age	3.508	0.023	5	213.260
success * sex	4.371	0.015	4	216.122
success * age + sex * success	5.133	0.010	6	212.884

Table 3: Model selection results of hoopoe breeding dispersal probability within years (between first and second brood) obtained from logistic regression models. The models are ordered by their support of the data, with the best model at the top. Given are the ΔAIC (difference between the current and the best AIC value), AICw: Akaike weight, K: Number of estimated parameters, Dev: Deviance. The 90% best models are bold printed (n = 247).

Model	ΔAIC	AICw	K	Dev
M: age ; F: success * age	**0.000**	**0.330**	**5**	**291.508**
sex * age	**0.437**	**0.265**	**4**	**293.945**
sex * age + success	**0.453**	**0.263**	**5**	**291.961**
M: success * age; F: age	**3.973**	**0.045**	**5**	**295.481**
M: .; F: success	4.690	0.032	3	300.198
sex * success	6.250	0.014	4	299.758
sex + success	6.397	0.013	3	301.905
M: age; F: success + age	6.644	0.012	4	300.152
sex	7.415	0.008	2	304.923
success * sex + age	8.216	0.005	5	299.724
M: success; F: .	8.975	0.004	3	304.483
sex + age	9.415	0.003	3	304.923
age * success + sex * success	10.089	0.002	6	299.597
success * age + sex	10.377	0.002	5	301.885
M: success + age; F:age	10.974	0.001	4	304.482
success	21.333	0.000	2	318.841
success + age	23.328	0.000	3	318.836
success * age	25.192	0.000	4	318.700
age	25.344	0.000	2	322.852
Null model	40.964	0.000	2	56.931

Table 4: Model selection results of hoopoe breeding dispersal distance between years obtained from linear regression models. The models are ordered by their support of the data, with the best model at the top. Given are the ΔAIC (difference between the current and the best AIC value), AICw: Akaike weight, K: Number of estimated parameters, Dev: Deviance. The 90% best models are bold printed (n = 132).

Model	ΔAIC	AICw	K	Dev
success * age +sex	**0.000**	**0.135**	**6**	**142.062**
sex + age	**0.025**	**0.133**	**4**	**146.461**
M: age; F: success + age	**0.546**	**0.103**	**5**	**144.828**
sex + success	**1.138**	**0.076**	**4**	**147.700**
M: success + age; F: age	**1.672**	**0.058**	**5**	**146.069**
age * success + sex * success	**1.769**	**0.056**	**7**	**141.814**
sex	**1.874**	**0.053**	**3**	**150.794**
M: age ; F: success * age	**1.932**	**0.051**	**6**	**144.157**
sex * age	**2.024**	**0.049**	**5**	**146.459**
success * sex + age	**2.170**	**0.046**	**6**	**144.416**
M: .; F: success	**2.194**	**0.045**	**4**	**148.886**
sex * age + success	**2.298**	**0.043**	**6**	**144.557**
M: success; F: .	**2.811**	**0.033**	**4**	**149.584**
sex * success	**3.116**	**0.028**	**5**	**147.676**
success * age	3.525	0.023	5	148.135
M: success * age; F: age	3.584	0.022	6	145.972
age	4.394	0.015	3	153.701
success + age	4.919	0.012	4	151.992
success	5.239	0.010	3	154.687
Null model	5.600	0.008	2	157.479

Table 5: Model selection results of hoopoe breeding dispersal distance between first and second brood obtained from linear regression models. The models are ordered by their support of the data, with the best model at the top. Given are the ΔAIC (difference between the current and the best AIC value), AICw: Akaike weight, K: Number of estimated parameters, Dev: Deviance. The 90% best models are bold printed (n = 208).

Model	ΔAIC	AICw	K	Dev
M: success; F: .	**0.000**	**0.189**	**4**	**273.051**
M: success + age; F: age	**0.881**	**0.122**	**5**	**271.586**
sex * age + success	**0.893**	**0.121**	**6**	**269.003**
sex + success	**1.187**	**0.105**	**4**	**274.614**
sex * success	**1.358**	**0.096**	**5**	**272.210**
M: success * age; F: age	**1.772**	**0.078**	**6**	**270.142**
success * sex + age	**2.165**	**0.064**	**6**	**270.653**
sex * age	**2.242**	**0.062**	**5**	**273.368**
sex	**3.448**	**0.034**	**3**	**280.298**
Success * age + sex	**3.632**	**0.031**	**6**	**272.569**
sex + age	3.741	0.029	4	278.006
age * success + sex * success	4.164	0.024	7	270.652
sex + success	4.823	0.017	4	279.457
M: age; F: success + age	5.025	0.015	5	277.051
M: age; F: success * age	5.447	0.012	6	274.957
success	13.404	0.000	3	294.041
success + age	14.046	0.000	4	292.127
success * age	15.661	0.000	5	291.586
Null model	16.775	0.000	2	301.732
age	17.231	0.000	3	299.501

Figures

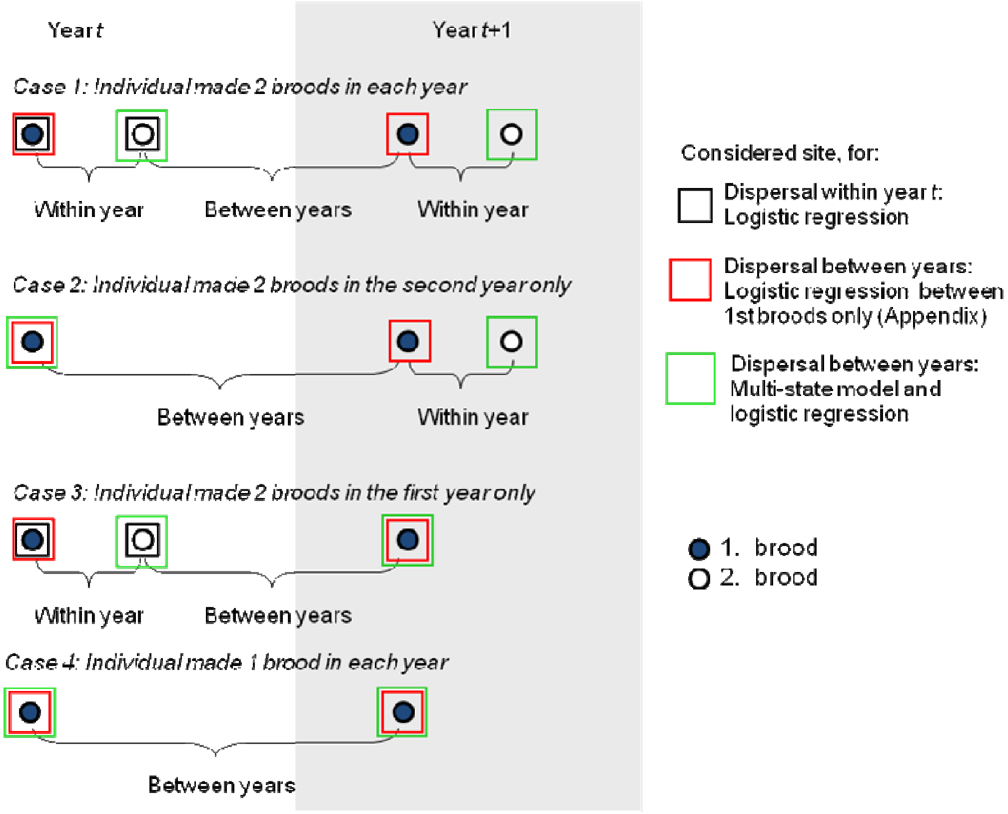


Fig. 1: Graphical presentation of the definitions of dispersal between years as used in this study. Several definitions are possible, because hoopoes often conduct two broods within a season.

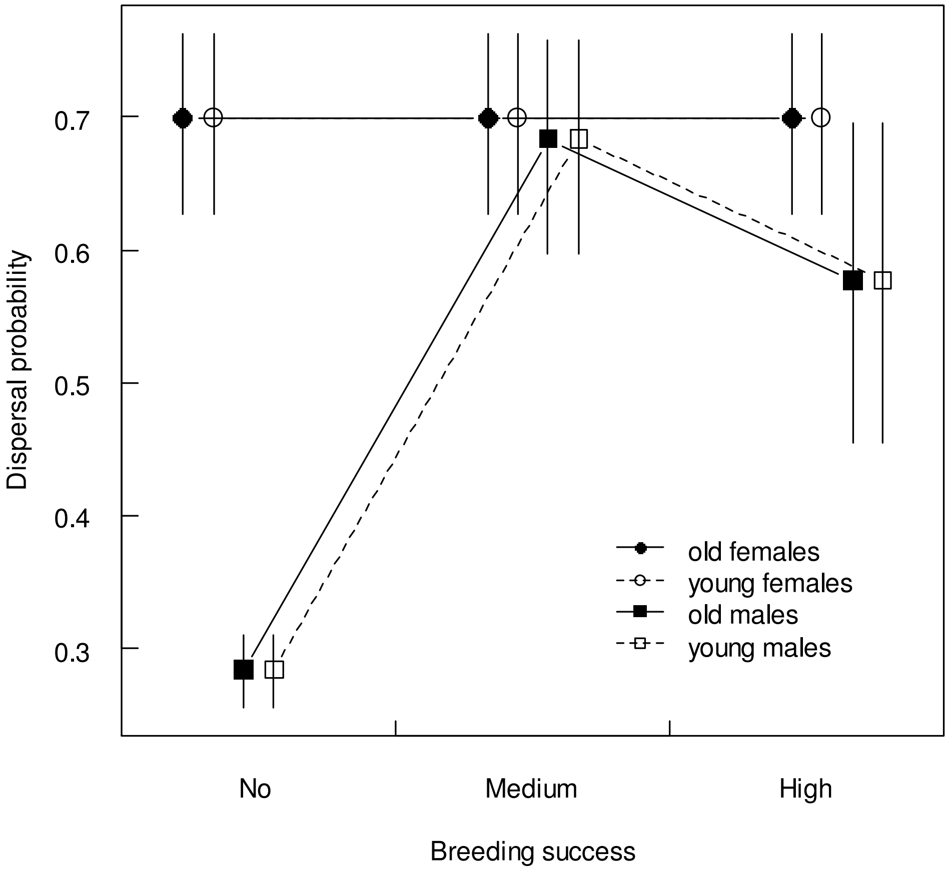


Fig. 2: Model averaged dispersal probabilities estimated with the multi-state capture-recapture model. Error bars are 95% confidence intervals.

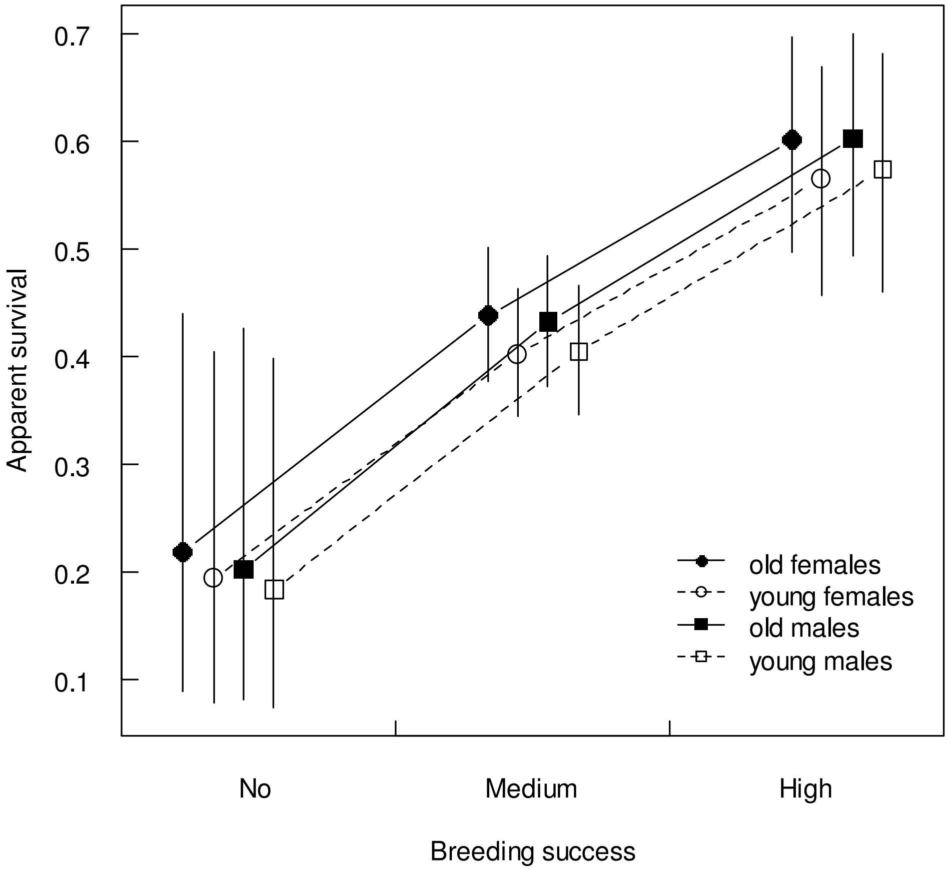


Fig. 3: Model averaged apparent survival of both sexes and age classes (last year old, older than one year) of hoopoes estimated with multi-state capture-recapture models. Error bars are 95% confidence intervals.

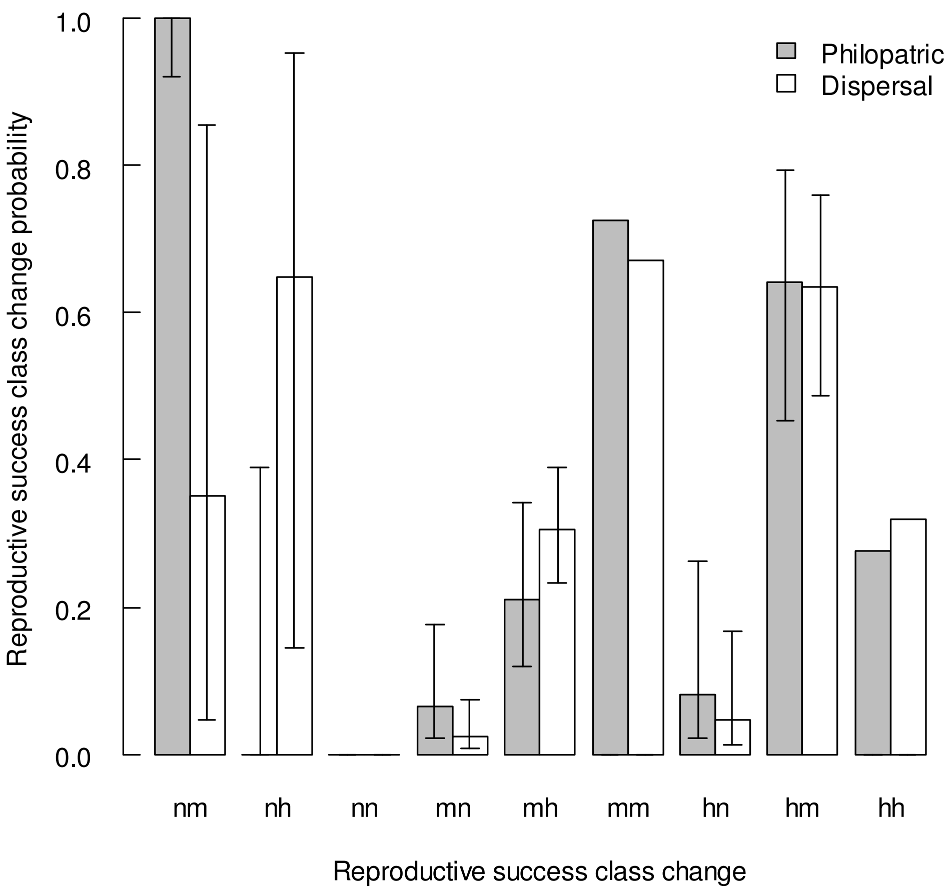


Fig. 4: Model averaged probabilities to change classes of reproductive success in relation to dispersal status (philopatric, dispersed) of hoopoes. n: no reproductive success, m: middle reproductive success, h: high reproductive success. Code explanation: nm: change from no to middle reproductive success. Errors bars are 95% confidence intervals.

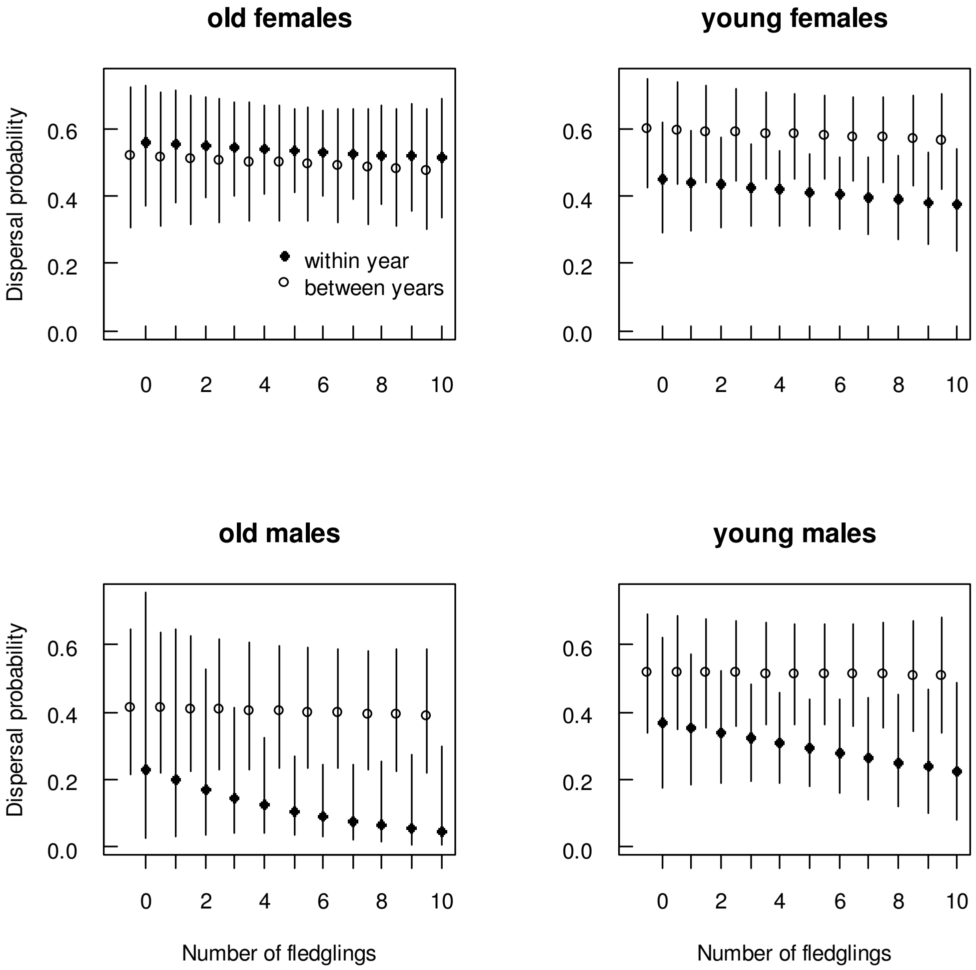
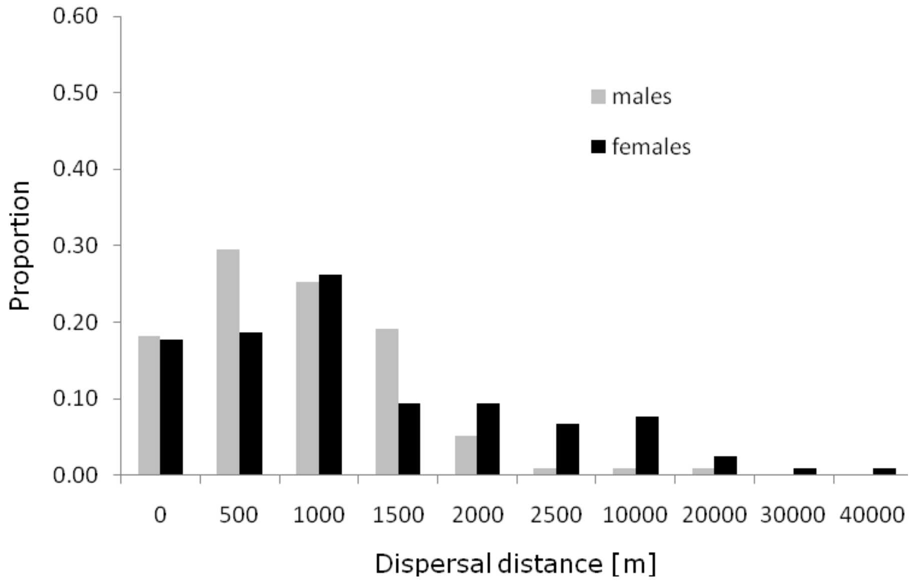


Fig. 5: Model averaged dispersal probabilities of hoopoes between and within years in relation to the number of fledglings (sum of fledglings of the whole breeding season for dispersal between years; number of fledglings of first brood for dispersal within year), separated for both sexes and age classes. Error bars are 95% confidence intervals.

A



B

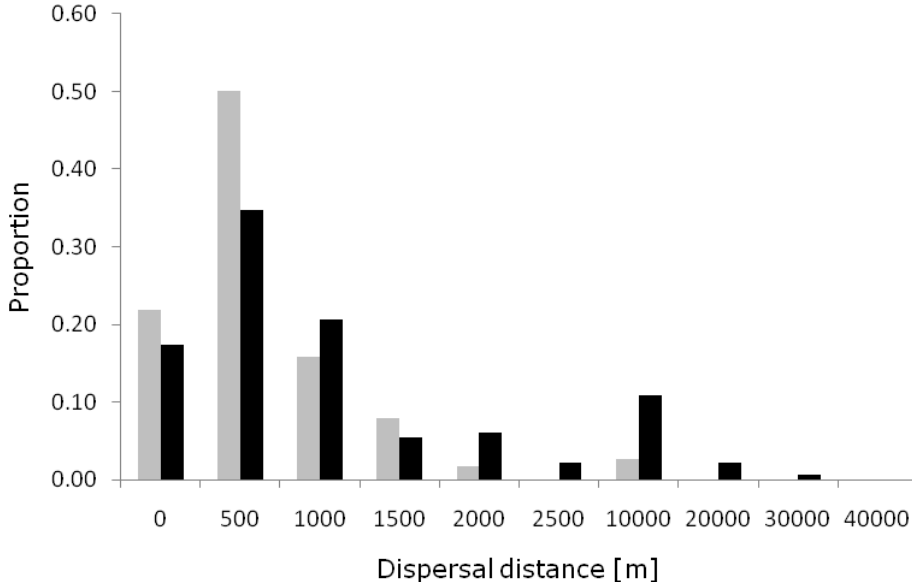


Fig. 6: Distribution of the proportion of observed dispersal distances of male and female hoopoes between years (A) and within years (B). Due to presentation style, the last four dispersal distance classes are on another scale (10’000m steps) than before (500m steps). Sample sizes: dispersal between years: 115 males and 118 females; dispersal within year: 114 males and 184 females.

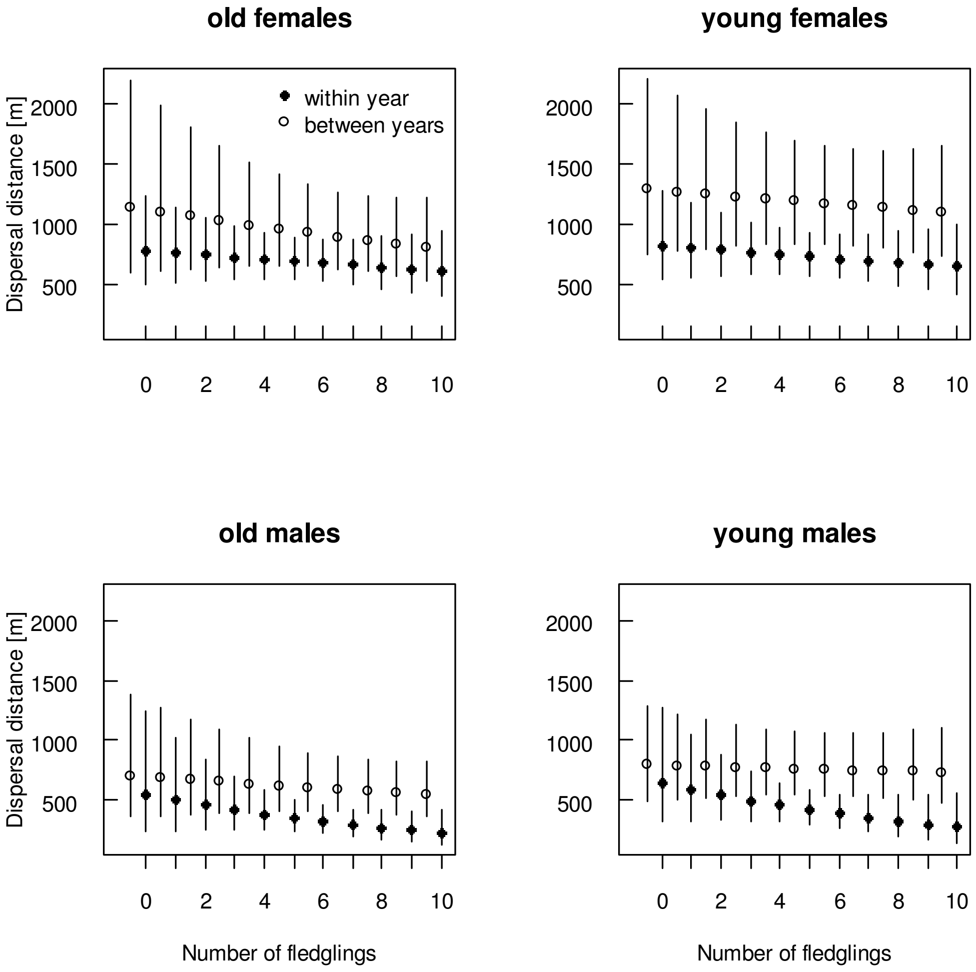


Fig. 7: Model averaged dispersal distances of hoopoes between and within years in relation to the number of fledglings (sum of fledglings of the whole breeding season for dispersal between years; number of fledglings of first brood for dispersal within year), separated for both sexes and age classes. Error bars are 95% confidence intervals.

Appendix

Table S1: Summary results of all tested multi-state capture-recapture models. The step wise manner of the model selection is shown: **A**: Modeling recapture probability (p), **B**: Modeling probability to change class of reproductive success (b), **C**: Modelling dispersal probability between years (d), **D**: Modelling apparent survival probability (ϕ). Model notation is the following:

Success: dependent on classes (3 levels) of reproductive success, sex: sex dependent, age: age dependent, const: constant, disp: dependent on dispersal (yes or now). Specification for b: indicates whether the probability to change class of reproductive success was modelled randomly or Markovian. ΔAIC: the current AIC value of the model minus the AIC value of the best model. AICw: AIC weight, K: Number of estimated parameters, Dev.: Deviance.

A

Model	**Specification for b**	**ΔAIC**	**AICw**	**K**	**Dev.**
ϕ(success*sex+age),d(success*sex+age),b(disp*sex), p(const)	Markovian	0.000	0.517	41	1852.691
ϕ(success*sex+age),d(success*sex+age),b(disp*sex), p(sex)	Markovian	1.852	0.205	42	1852.543
ϕ(success*sex+age),d(success*sex+age),b(disp*sex), p(year)	Markovian	3.252	0.102	47	1843.943
ϕ(success*sex+age),d(success*sex+age),b(disp*sex), p(success)	Markovian	3.398	0.094	43	1852.089
ϕ(success*sex+age),d(success*sex+age),b(disp*sex), p(success+sex)	Markovian	5.145	0.039	44	1851.836
ϕ(success*sex+age),d(success*sex+age),b(disp*sex), p(sex+year)	Markovian	5.340	0.036	54	1832.031
ϕ(success*sex+age),d(success*sex+age),b(disp*sex), p(success+sex+year)	Markovian	8.437	0.008	50	1843.128
ϕ(success*sex+age),d(success*sex+age),b(disp*sex), p(success+year)	Markovian	22.477	0.000	61	1835.168

B

Model	**Specification for b**	**ΔAIC**	**AICw**	**K**	**Dev.**
ϕ(success*sex+age),d(success*sex+age),b(disp), p(const)	Markovian	0.000	0.709	29	1868.332
ϕ(success*sex+age),d(success*sex+age),b(disp), p(sex)	Markovian	1.892	0.275	30	1868.224
ϕ(success*sex+age),d(success*sex+age),b(disp*sex), p(const)	Markovian	8.359	0.011	41	1852.691
ϕ(success*sex+age),d(success*sex+age),b(disp*sex), p(sex)	Markovian	10.211	0.004	42	1852.543
ϕ(success*sex+age),d(success*sex+age),b(const), p(const)	Random	28.390	0.000	18	1918.722
ϕ(success*sex+age),d(success*sex+age),b(sex), p(const)	Random	28.476	0.000	19	1916.808
ϕ(success*sex+age),d(success*sex+age),b(const), p(sex)	Random	30.355	0.000	19	1918.687
ϕ(success*sex+age),d(success*sex+age),b(sex), p(sex)	Random	30.456	0.000	20	1916.788
ϕ(success*sex+age),d(success*sex+age),b(const), p(const)	Markovian	105.877	0.000	18	1996.209
ϕ(success*sex+age),d(success*sex+age),b(sex), p(const)	Markovian	106.497	0.000	19	1994.829
ϕ(success*sex+age),d(success*sex+age),b(const), p(sex)	Markovian	107.705	0.000	19	1996.037
ϕ(success*sex+age),d(success*sex+age),b(sex), p(sex)	Markovian	108.362	0.000	20	1994.694
ϕ(success*sex+age),d(success*sex+age),b(disp), p(const)	Random	131.733	0.000	25	2008.065
ϕ(success*sex+age),d(success*sex+age),b(disp), p(sex)	Random	133.283	0.000	26	2007.615
ϕ(success*sex+age),d(success*sex+age),b(disp*sex), p(const)	Random	141.112	0.000	33	2001.444
ϕ(success*sex+age),d(success*sex+age),b(disp*sex), p(sex)	Random	142.537	0.000	34	2000.869

C

Model	**Specification for b**	**ΔAIC**	**AICw**	**K**	**Dev.**
ϕ(success*sex+age),d(male: success; female: .),b(disp), p(const)	Markovian	0.000	0.235	25	1870.870
ϕ(success*sex+age),d(const),b(disp), p(const)	Markovian	1.107	0.135	22	1877.977
ϕ(success*sex+age),d(sex),b(disp), p(const)	Markovian	1.697	0.101	23	1876.567
ϕ(success*sex+age),d(male: success; female: .),b(disp), p(sex)	Markovian	1.891	0.091	26	1870.761
ϕ(success*sex+age),d(success+sex+age),b(disp), p(const)	Markovian	2.062	0.084	26	1870.933
ϕ(success*sex+age),d(success),b(disp), p(const)	Markovian	2.136	0.081	24	1875.006
ϕ(success*sex+age),d(const),b(disp), p(sex)	Markovian	3.005	0.052	23	1877.875
ϕ(success*sex+age),d(sex),b(disp), p(sex)	Markovian	3.590	0.039	24	1876.460
ϕ(success*sex+age),d(success*sex),b(disp), p(const)	Markovian	3.679	0.037	27	1870.549
ϕ(success*sex+age),d(success+sex+age),b(disp), p(sex)	Markovian	3.957	0.033	27	1870.827
ϕ(success*sex+age),d(success),b(disp), p(sex)	Markovian	4.035	0.031	25	1874.905
ϕ(success*sex+age),d(success+sex),b(disp), p(const)	Markovian	5.383	0.016	25	1876.253
ϕ(success*sex+age),d(male: .; female: success),b(disp), p(const)	Markovian	5.383	0.016	25	1876.253
ϕ(success*sex+age),d(success*sex+age),b(disp), p(const)	Markovian	5.461	0.015	29	1868.332
ϕ(success*sex+age),d(success*sex),b(disp), p(sex)	Markovian	5.569	0.015	28	1870.440
ϕ(success*sex+age),d(success+sex),b(disp), p(sex)	Markovian	7.276	0.006	26	1876.146
ϕ(success*sex+age),d(male: .; female: success),b(disp), p(sex)	Markovian	7.276	0.006	26	1876.146
ϕ(success*sex+age),d(success*sex+age),b(disp), p(sex)	Markovian	7.353	0.006	30	1868.224

D

Model	Specification for b	ΔAIC	AICw	K	Dev.
ϕ(success),d(male: success; female: .),b(disp), p(const)	Markovian	0.000	0.173	20	1878.166
ϕ(success),d(const),b(disp), p(const)	Markovian	1.076	0.101	17	1885.242
ϕ(success+sex+age),d(male: success; female: .),b(disp), p(const)	Markovian	1.090	0.100	22	1875.256
ϕ(success),d(sex),b(disp), p(const)	Markovian	1.691	0.074	18	1883.857
ϕ(success),d(male: success; female: .),b(disp), p(sex)	Markovian	1.807	0.070	21	1877.973
ϕ(success+sex+age),d(const),b(disp), p(const)	Markovian	2.146	0.059	19	1882.312
ϕ(success*sex+age),d(male: success; female: .),b(disp), p(const)	Markovian	2.704	0.045	25	1870.870
ϕ(success+sex+age),d(sex),b(disp), p(const)	Markovian	2.759	0.044	20	1880.925
ϕ(success),d(const),b(disp), p(sex)	Markovian	2.879	0.041	18	1885.045
ϕ(success+sex+age),d(male: success; female: .),b(disp), p(sex)	Markovian	2.963	0.039	23	1875.129
ϕ(success*sex),d(male: success; female: .),b(disp), p(const)	Markovian	3.457	0.031	23	1875.623
ϕ(success),d(sex),b(disp), p(sex)	Markovian	3.498	0.030	19	1883.663
ϕ(success*sex+age),d(const),b(disp), p(const)	Markovian	3.811	0.026	22	1877.977
ϕ(success+sex+age),d(const),b(disp), p(sex)	Markovian	4.014	0.023	20	1882.180
ϕ(success*sex+age),d(sex),b(disp), p(const)	Markovian	4.401	0.019	23	1876.567
ϕ(success*sex),d(const),b(disp), p(const)	Markovian	4.572	0.018	20	1882.738
ϕ(success*sex+age),d(male: success; female: .),b(disp), p(sex)	Markovian	4.595	0.017	26	1870.761
ϕ(success+sex+age),d(sex),b(disp), p(sex)	Markovian	4.632	0.017	21	1880.798
ϕ(success*sex),d(sex),b(disp), p(const)	Markovian	5.156	0.013	21	1881.322
ϕ(success*sex),d(male: success; female: .),b(disp), p(sex)	Markovian	5.297	0.012	24	1875.463
ϕ(success*sex+age),d(const),b(disp), p(sex)	Markovian	5.709	0.010	23	1877.875
ϕ(success*sex+age),d(sex),b(disp), p(sex)	Markovian	6.294	0.007	24	1876.460
ϕ(success*sex),d(const),b(disp), p(sex)	Markovian	6.406	0.007	21	1882.572
ϕ(success*sex),d(sex),b(disp), p(sex)	Markovian	6.997	0.005	22	1881.163

φ(age),d(male: success; female: .),b(disp), p(const)	Markovian	8.350	0.003	19	1888.516
φ(success+age),d(male: success; female: .),b(disp), p(const)	Markovian	8.533	0.002	21	1884.699
φ(age),d(const),b(disp), p(const)	Markovian	9.284	0.002	16	1895.450
φ(success+age),d(const),b(disp), p(const)	Markovian	9.467	0.002	18	1891.633
φ(age),d(sex),b(disp), p(const)	Markovian	9.897	0.001	17	1894.063
φ(success+age),d(sex),b(disp), p(const)	Markovian	10.080	0.001	19	1890.246
φ(age),d(male: success; female: .),b(disp), p(sex)	Markovian	10.303	0.001	20	1888.469
φ(success+age),d(male: success; female: .),b(disp), p(sex)	Markovian	10.476	0.001	22	1884.642
φ(const),d(male: success; female: .),b(disp), p(const)	Markovian	11.213	0.001	18	1893.379
φ(age),d(const),b(disp), p(sex)	Markovian	11.237	0.001	17	1895.403
φ(success+age),d(const),b(disp), p(sex)	Markovian	11.410	0.001	19	1891.575
φ(age),d(sex),b(disp), p(sex)	Markovian	11.850	0.000	18	1894.016
φ(success+age),d(sex),b(disp), p(sex)	Markovian	12.023	0.000	20	1890.189
φ(const),d(const),b(disp), p(const)	Markovian	12.147	0.000	15	1900.313
φ(const),d(sex),b(disp), p(const)	Markovian	12.760	0.000	16	1898.926
φ(const),d(male: success; female: .),b(disp), p(sex)	Markovian	13.187	0.000	19	1893.353
φ(sex),d(male: success; female: .),b(disp), p(const)	Markovian	13.196	0.000	19	1893.362
φ(const),d(const),b(disp), p(sex)	Markovian	14.121	0.000	16	1900.287
φ(sex),d(const),b(disp), p(const)	Markovian	14.130	0.000	16	1900.296
φ(const),d(sex),b(disp), p(sex)	Markovian	14.734	0.000	17	1898.900
φ(sex),d(sex),b(disp), p(const)	Markovian	14.743	0.000	17	1898.909
φ(sex),d(male: success; female: .),b(disp), p(sex)	Markovian	15.138	0.000	20	1893.304
φ(sex),d(const),b(disp), p(sex)	Markovian	16.072	0.000	17	1900.238
φ(sex),d(sex),b(disp), p(sex)	Markovian	16.685	0.000	18	1898.851

Table S2: Model selection results of hoopoe breeding dispersal probability between years obtained from logistic regression models. We considered in each year the first brood as the reference brood, and the number of fledglings of the first brood only. The models are ordered by their support of the data, with the best model at the top. Given are the ΔAIC (difference between the current and the best AIC value), AICw: Akaike weight, K: Number of estimated parameters, Dev: Deviance. The 90% best models are bold printed (*n* = 158 individuals).

Model	ΔAIC	AICw	K	Dev
sex	**0.000**	**0.170**	**2**	**212.486**
M: .; F: success	**0.786**	**0.114**	**3**	**211.272**
success + age	**1.118**	**0.097**	**4**	**209.604**
sex * age	**1.304**	**0.088**	**3**	**211.790**
M: age; F: success + age	**1.465**	**0.082**	**3**	**211.951**
M: success; F: .	**1.644**	**0.075**	**5**	**208.130**
Null model	**1.999**	**0.062**	**3**	**212.485**
age	**2.360**	**0.052**	**4**	**210.846**
M: age; F: success * age	**2.785**	**0.042**	**4**	**211.271**
sex * success	**2.928**	**0.039**	**5**	**209.414**
M: success + age; F: age	**3.304**	**0.033**	**4**	**211.790**
sex + age	**3.509**	**0.029**	**5**	**209.996**
success	**3.519**	**0.029**	**5**	**210.005**
success * sex + age	3.915	0.024	1	218.401
M: success * age; F: age	4.360	0.019	5	210.846
success * age + sex	4.773	0.016	6	209.259
sex * age + success	5.477	0.011	2	217.964
sex + success	5.503	0.011	2	217.989
age * success + sex * success	7.157	0.005	3	217.644
success * age	8.567	0.002	4	217.053

Table S3: Model selection results of hoopoe breeding dispersal distance between years obtained from linear regression models. We considered in each year the first brood as the reference brood, and the number of fledglings of the first brood only. The models are ordered by their support of the data, with the best model at the top. Given are the ΔAIC (difference between the current and the best AIC value), AICw: Akaike weight, K: Number of estimated parameters, Dev: Deviance. The 90% best models are bold printed (*n* = 131 individuals).

Model	ΔAIC	AICw	K	Dev
sex	**0.000**	**0.169**	**3**	**167.023**
M: .; F: success	**0.564**	**0.128**	**4**	**165.203**
success + age	**0.983**	**0.104**	**4**	**165.731**
sex * age	**1.238**	**0.091**	**4**	**166.055**
M: age; F: success + age	**1.800**	**0.069**	**5**	**164.242**
M: success; F: .	**1.942**	**0.064**	**4**	**166.950**
Null model	**2.370**	**0.052**	**2**	**172.689**
age	**2.506**	**0.048**	**5**	**165.129**
M: age; F: success * age	**2.901**	**0.040**	**6**	**163.118**
sex * success	**3.144**	**0.035**	**5**	**165.935**
M: success + age; F: age	**3.237**	**0.034**	**5**	**166.053**
sex + age	**3.284**	**0.033**	**3**	**171.264**
success	**3.761**	**0.026**	**3**	**171.888**
success * sex + age	**3.799**	**0.025**	**6**	**164.240**
M: success * age; F: age	4.482	0.018	6	165.099
success * age + sex	4.500	0.018	6	165.122
sex * age + success	4.536	0.018	6	165.167
sex + success	4.971	0.014	4	170.855
age * success + sex * success	5.783	0.009	7	164.221
success * age	6.855	0.005	5	170.704

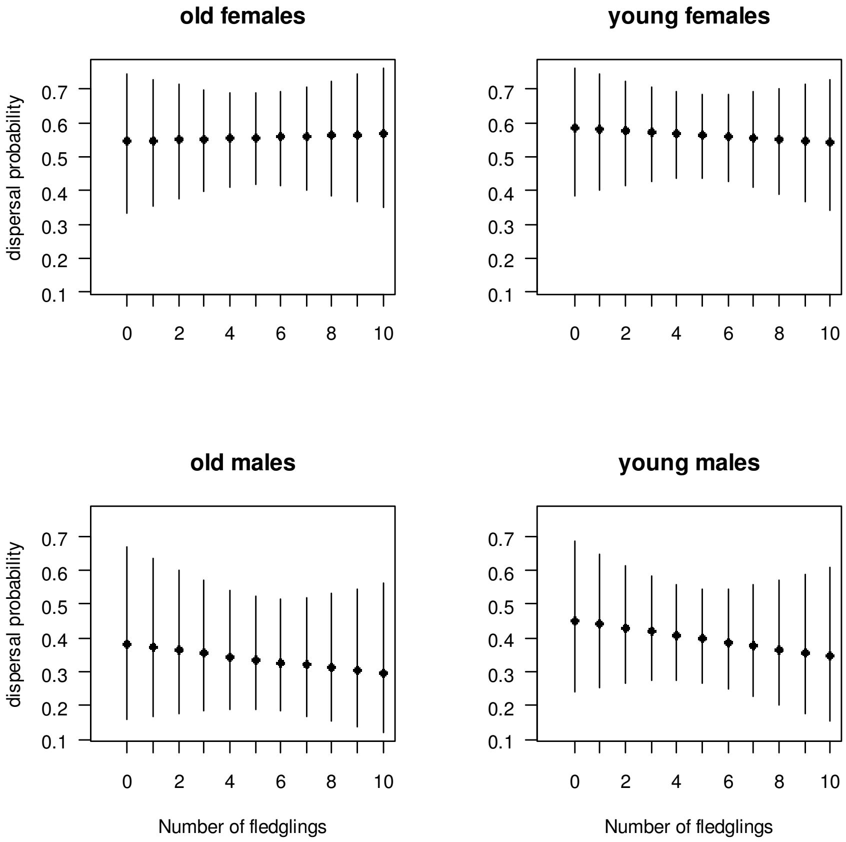


Fig. S1: Model averaged dispersal probabilities between years in relation to the number of fledglings of the first brood in the first year separated for both sexes and age classes. We considered in each year the first brood as the reference brood. Error bars are 95% confidence intervals.

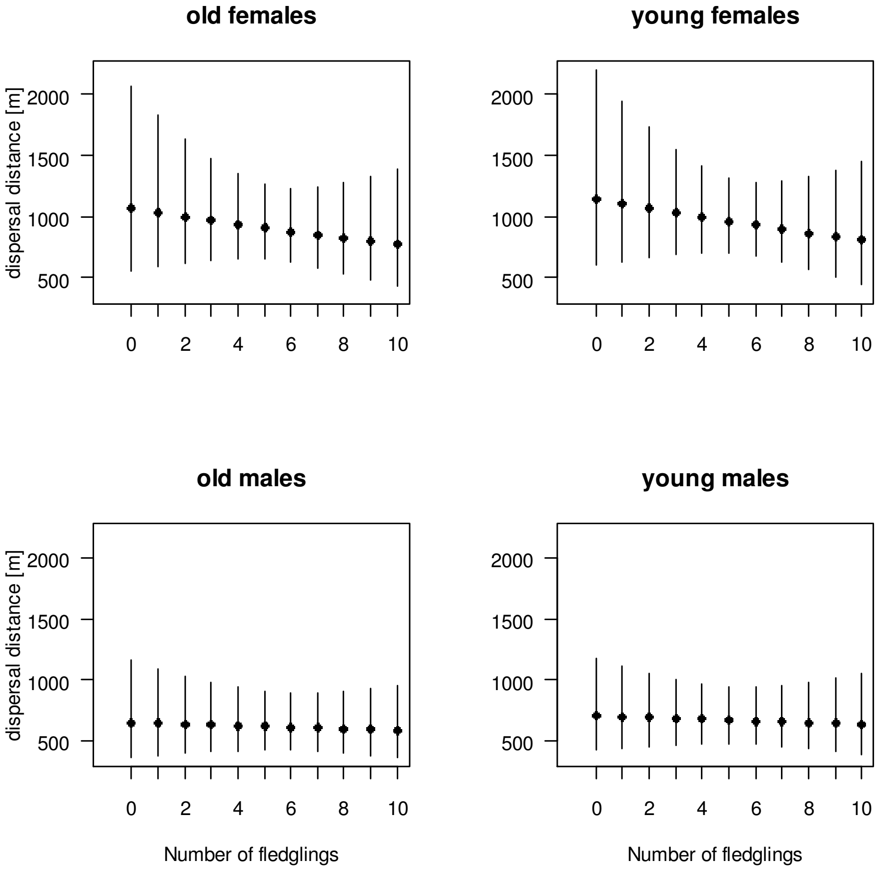


Fig. S2: Model averaged dispersal distances between years in relation to the number of fledglings of the first brood in the first year separated for both sexes and age classes. We considered in each year the first brood as the reference brood. Error bars are 95% confidence intervals.