



## BREEDING DISPERSAL OF EURASIAN HOOPES (*UPUPA EPOPS*) WITHIN AND BETWEEN YEARS IN RELATION TO REPRODUCTIVE SUCCESS, SEX, AND AGE

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**ABSTRACT.**—Breeding dispersal is often affected by previous reproductive success, age, and sex. Birds with multiple broods within a season can disperse not only between, but also within, years. Little is known about factors that govern dispersal within a season or how strong it is compared with dispersal between years. We studied breeding dispersal of Eurasian Hoopoes (*Upupa epops*) in Valais, Switzerland, using capture–recapture data collected over 8 years ( $n = 712$  individuals). We analyzed breeding dispersal probability and distance, both between and within years, in relation to age, sex, and reproductive output, using multistate capture–recapture models and generalized linear models. Between years, females dispersed more often and over longer distances than males (mean distance, females = 1.98 km; males = 0.83 km), but dispersal was only weakly affected by age and previous reproductive success. Dispersal within a year also differed between sexes (mean distance, females = 1.45 km; males = 0.46 km) and varied little with age or previous reproductive success. Dispersal probability within years was lower and occurred over shorter distances than dispersal between years. Thus, dispersal decisions did not seem to depend on different cues, although dispersal within the breeding season might be constrained by habitat saturation. Breeding dispersal was common in Hoopoes, compared with other bird species. Together with the fact that immigration is an important component of this species' population dynamics, such dispersal patterns suggest that successful conservation of Eurasian Hoopoes requires extended breeding grounds to maintain sustainable populations. *Received 7 April 2011, accepted 28 December 2011.*

**Key words:** breeding dispersal, Eurasian Hoopoe, multistate capture–recapture models, reproductive success, *Upupa epops*.

### Dispersión Reproductiva de *Upupa epops* en un Año y Entre Años en Relación con el Éxito Reproductivo, el Sexo y la Edad

**RESUMEN.**—La dispersión reproductiva por lo general se ve afectada por el éxito reproductivo previo, la edad y el sexo. Las aves que crían múltiples camadas en una temporada pueden dispersarse no sólo entre años, sino también en un mismo año. Se sabe poco acerca de los factores que determinan la dispersión dentro de una temporada o cuán fuerte es ésta comparada con la dispersión sucedida entre años diferentes. Estudiamos la dispersión reproductiva de *Upupa epops* en Valais, Suiza, usando datos de captura-recaptura recolectados por más de 8 años ( $n = 712$  individuos). Analizamos la probabilidad y la distancia de la dispersión reproductiva, en cada año y entre años, en relación con la edad, el sexo y el rendimiento reproductivo mediante modelos multiestado de marca-recaptura y modelos lineales generalizados. Entre años, las hembras se dispersaron más frecuentemente y a lo largo de distancias mayores que los machos (distancia promedio, hembras = 1.98 km; machos = 0.83 km), pero la dispersión sólo fue débilmente afectada por la edad y el éxito reproductivo previo. La dispersión en un año también difirió entre sexos (distancia promedio, hembras = 1.45 km; machos = 0.46 km) y varió poco con la edad y con el éxito reproductivo previo. La probabilidad de dispersión dentro de los años fue menor y la dispersión ocurrió a lo largo de distancias más cortas que la dispersión entre años. Así, las decisiones de dispersarse no parecen depender de pistas diferentes, aunque la dispersión dentro de una temporada reproductiva podría estar restringida por la saturación del hábitat. La dispersión reproductiva fue común en *Upupa epops* en comparación con otras especies de aves. Junto con el hecho de que la inmigración es un componente importante de la dinámica poblacional de esta especie, tales patrones de dispersión sugieren que la conservación exitosa de *Upupa epops* requiere de áreas de reproducción amplias para mantener sus poblaciones viables.

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GAINS AND LOSSES of individuals in a population are the two drivers of changing population size, and dispersal is a demographic mechanism that strongly affects both gain and loss. In organisms that exhibit a high dispersal capacity (e.g., birds; Paradis et al. 1998), there is increasing evidence that the exchange of individuals between populations has a strong effect on local population dynamics and persistence (Newton and Marquiss 1986, Lampila et al. 2006, Schaub and von Hirschheydt 2009, Schaub et al. 2010a) and enhances metapopulation functionality (Hanski 1999, Baillie et al. 2000, Macdonald and Johnson 2001, Kenward et al. 2002). Factors that affect dispersal are therefore potentially important drivers for population change, and their identification increases our knowledge of how population dynamics operates, which is essential in conservation.

Dispersal is an adaptive behavioral strategy that is favored in temporally and spatially variable environments (McPeck and Holt 1992). Dispersing individuals can settle in habitat patches of higher quality and thereby increase their reproductive output, but dispersal may also incur increased probability of mortality. The balance between fitness-related costs and benefits is crucial for the evolution of dispersal (Johnson and Gaines 1990). Dispersal is subdivided into natal 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 events.

Breeding dispersal of birds can be affected by various extrinsic and intrinsic factors, such as sex and age (Lindberg and Seding 1997, Doligez et al. 1999, Oro et al. 1999), personal previous breeding success (Doligez et al. 1999, Travis et al. 1999, Pasinelli et al. 2007), breeding success of conspecifics, presence and density of conspecifics, habitat quality, and nest or mate predation (Haas 1998, Travis et al. 1999, Kim et al. 2009, Schaub and von Hirschheydt 2009). Studies of between-season breeding dispersal dominate the literature. Generally, the probability of dispersal declines with increasing reproductive success and increasing age. It is also typically thought to be lower in males than in females. By contrast, few studies have focused on factors that affect dispersal decisions within a breeding season. Some studies have documented that dispersal movements took place along habitat- or food-availability gradients (e.g., along an altitudinal gradient with changing food availability during the breeding season; Newton 2000, Klemp 2003, Gilroy et al. 2010), whereas others have shown that breeding-season dispersal served to reduce nest predation (Greig-Smith 1982, Jackson et al. 1989) or exposure to nest parasites (Stanback and Dervan 2001).

Dispersal is often difficult to study, for methodological and logistic reasons. For instance, dispersal movements may go undetected because of imperfect detection within the study area (Koenig et al. 1996, Macdonald and Johnson 2001, Kenward et al. 2002) or because dispersers leave the study area. The latter can be overcome by radio- and satellite tracking, but these methods come with high costs in equipment and manpower (Steenhof et al. 2005, Lehnen and Rodewald 2009). Fortunately, probabilistic models that account for imperfect detection can help to address that problem (Lebreton and Pradel 2002, Schaub and von Hirschheydt 2009).

We applied multistate capture–recapture models to study the probability and distance of breeding dispersal in the Eurasian Hoopoe (*Upupa epops*; hereafter “hoopoe”) in relation to previous

reproductive success, age, and sex. Hoopoes are secondary cavity nesters that produce large clutches of  $\leq 12$  eggs (Y. Bötsch et al. unpubl. data). Because hoopoes often lay two clutches a year (Arlettaz et al. 2010b), we studied breeding dispersal between consecutive clutches within the same year and, as is more typically done, between successive breeding seasons. We were particularly interested in knowing whether dispersal events between and within breeding seasons were affected by the same factors. Our study was conducted over a large area that allowed dispersal movements  $\leq 40$  km to be detected. Moreover, our study population bred almost exclusively in nest boxes (Arlettaz et al. 2010b), which enabled surveillance of most dispersal events within the study area. The study population is isolated on a deep alluvial plain in the middle of the Alps, surrounded by high mountain ridges (3,000–4,000 m). Individuals dispersing to another population have to perform movements that are significantly longer than the maximal distance that we can observe within our study area.

## METHODS

*Study site and study species.*—The hoopoe is a secondary cavity-nesting, trans-Saharan migrant (Reichlin et al. 2009, Bächler et al. 2010) that feeds mainly on large arthropods taken on the ground (Fournier and Arlettaz 2001, Schaub et al. 2010b, Tagmann-Ioset et al. 2012). Our study was conducted in the upper Rhône valley in southwestern Switzerland between Sierre and Vernayaz (62 km<sup>2</sup>). The area is intensively farmed and comprises fruit-tree plantations, vineyards, greenhouses, pastures, and arable land. Natural breeding cavities are very scarce in the study area, and hoopoes breed in specifically designed nest boxes that were installed beginning in 1998 (Arlettaz et al. 2010b). Most of these >700 nest boxes were fixed as pairs at  $\sim 380$  sites, on the inside wall of small agricultural shacks, with just the entrance hole visible from outside. The installation of pairs of nest boxes reduced the risk of interspecific competition for nest sites by Tree Sparrows (*Passer montanus*), European Starlings (*Sturnus vulgaris*), and Great Tits (*Parus major*). Because of the high nest-box density, hoopoes typically have alternative breeding sites available nearby. Males defend a nest box but not an extended territory. Both parents contribute to the rearing of the brood, but parental roles differ between the sexes. The female typically broods alone, feeds nestlings until they are nearly fledged, and then often starts a second brood at a new location with a new partner. By contrast, the male feeds the female while she broods and feeds the nestlings until they are independent. Thereafter, the male may also start a second brood, often with a new partner. Extrapair copulations are very uncommon in the study area (K. Berthier et al. unpubl. data).

*Data collection.*—All nest boxes were checked every second week. Occupied nest boxes were inspected every third day to gather detailed information about brood phenology and success. Breeding adults were captured at nest boxes, after chicks were at least 4 days old, using three techniques: mist netting close to the nest box, cavity entrance traps (a live trap fixed on the entrance hole that is automatically triggered by an entering bird), and grabbing of brooding females from the nest box. Captured adults were sexed by inspection of the conspicuous uropygial gland (Martín-Vivaldi et al. 2009) and by plumage coloration. We aged birds using plumage as either second-year (SY) or after-second-year (ASY). Each adult was then given a uniquely numbered band.

Nestlings were banded 5–7 days before they fledged, at ~18 days. We considered the number of banded nestlings of a brood a measure of that brood's success.

*Data analysis.*—We performed several analyses to assess the effects of reproductive success, sex, and age on the probability of breeding dispersal and on distance moved within the study area. The analysis of dispersal probability required that we define a dispersal event. For between-year dispersal, breeding dispersal was defined as the movement between the second brood in year 1 and the second brood in year 2. If no second brood occurred in one or in both years, we considered the first brood of the corresponding year. We also evaluated the results when the first brood in both years was used as the reference for all individuals. Dispersal within a year was defined as the movement from the location of the first brood to the location of the second brood in that year. We also deemed those individuals that moved <600 m between successive broods “site faithful” (600 m is the longest movement observed by a radiotracked individual within its home range). The average radius of home ranges in our study was 355 m (Tagmann-Ioset et al. 2012), whereas a French study reported a mean radius of 223 m (Barbaro et al. 2008). Thus, if an individual dispersed >600 m, it is likely that a significant part of its home range had changed.

Dispersal probability between years was modeled with multistate capture–recapture models (Lebreton et al. 2009) and logistic regression models. Multistate capture–recapture models have the advantage that apparent survival is estimated while accounting for imperfect detection, which gives an indication of possible dispersal beyond the study area. The advantage of the logistic regression model is that it allows more flexibility in modeling. If detection probability is high and does not depend on sex, age, and breeding success, we expect similar results from both analyses. We also used a logistic regression model to model within-year dispersal probability. Dispersal distances were analyzed using a linear regression model.

*Dispersal probability: Multistate capture–recapture model.*—We used the multistate model introduced by Schaub and von Hirschheydt (2009) to analyze the capture–recapture data. These models estimate state-transition probabilities, where “state” refers to a combination of classes of reproductive success and of breeding locations. The first step is to create individual capture histories that contain information about observed breeding locations and reproductive success. For each individual that was captured in a year, we calculated the total number of fledglings that it produced over the entire breeding season. We then categorized reproductive success with three levels (no: 0 young fledged; medium: 1–8 young fledged; high: >8 young fledged). The grouping created a strong contrast, although it resulted in unequal sizes of groups. The threshold of 8 chicks was chosen because this was the approximate upper limit of the size of successful single broods (only 19 of 906 observed broods had >8 fledglings). Thus, parents with >8 young usually successfully fledged 2 broods. For each individual we then defined, for each time it was captured, whether or not the actual breeding location was the same (i.e., <600 m away) as the location of its last known breeding event. The reference location was that of the last observed brood in each year. All breeding locations at first capture were assigned to the state “same location.” This choice affects the subsequent coding of the capture history, but not the parameter estimates (Schaub and von Hirschheydt 2009), because the model is written in such a way that the movement probability

from a “same” location to a “different” location is identical to the movement probability from a “different” to a “same” location. The combination of the three classes of reproductive success (no, medium, high) and two types of location (same, different) resulted in six possible states. States 1 and 2, 3 and 4, and 5 and 6 refer to no, medium, and high reproductive success, respectively. Dispersal is defined by the succession of states. If an individual was at the same breeding location at two consecutive occasions (i.e., individual did not disperse), the state numbers at both occasions are either both even or both odd numbers. By contrast, if an individual was at different locations at two consecutive occasions (i.e., individual dispersed), the state numbers change from even to odd, or from odd to even. For example, consider an individual that was unsuccessful in year  $t$ . This hypothetical individual was recaptured in year  $t + 1$  at a site >600 m away from its site in year  $t$ , and here it experienced medium reproductive success. It was then not recaptured in year  $t + 2$ , but in year  $t + 3$  it was again recaptured at the site used in year  $t + 1$  and had high reproductive success. Finally, it was not recaptured in year  $t + 4$ , and the resulting capture history is coded as 14060 (for more details, see Schaub and von Hirschheydt 2009: appendix).

Different parameters can be estimated from the analysis of these capture histories. Conditional on the first observation with a certain reproductive success, individuals may survive and return to the study area (apparent survival probability,  $\phi$ ). If they survive and return, they may (1) disperse within the study area (breeding dispersal probability,  $d$ ), (2) change reproductive success ( $b$ ), and (3) be recaptured (recapture probability,  $p$ ). These parameters can be estimated and modeled as a function of covariates using the multistate 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 fifth years) are overcome by the probabilistic nature of the model.

We used E-SURGE (Choquet et al. 2009) to analyze the multistate capture–recapture data. To test whether model assumptions (identity of probabilities, independence among individuals) were met, we performed a goodness-of-fit test with U-CARE (Choquet et al. 2009). To study the effects 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  $\{\phi(\text{success} * \text{sex} + \text{age}), d(\text{success} * \text{sex} + \text{age}), b(\text{dispersal} * \text{sex}), p(\text{success} + \text{sex} + \text{year})\}$ , we sequentially modeled recapture, change of reproductive success, dispersal, and survival using 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. The candidate models for each parameter were usually constructed in such a way that they contained a combination of the factors sex, age, and reproductive success. We additionally considered models in which the change in reproductive success was either Markovian (i.e., change of success depended on success in preceding year) or random (i.e., change of success did not depend on success in preceding year). For breeding dispersal ( $d$ ), we considered the potential effects of reproductive success either only in males or only in females. All candidate models are shown in Table S2 (online supplement; see Acknowledgments). To make inferences, we model averaged across all models that were within 3 AIC values of the last step (models with  $\Delta\text{AIC} > 3$  received low support from the data; Akaike weight < 0.05).

*Dispersal probability: Logistic regression models.*—For these models, we considered only cases in which an individual was captured either in two consecutive years (for dispersal between years) or in two consecutive broods within a year (for dispersal within year). We then defined and analyzed this Boolean variable with a logistic regression model. For individuals with data from multiple years, we randomly selected one year for analysis so that all individuals were considered only once. 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 multistate model, we included reproductive success as a continuous variable. For the analysis of dispersal between years, reproductive success was the total number of fledglings produced in the first year; for the analysis of dispersal within a year, reproductive success was the number of fledglings in the first brood. We also included models with the two-way interactions sex\*reproductive success and age\*reproductive success to test whether potential effects of reproductive success were consistent between sexes and age classes. We calculated for each model the predictions for desired values of the explanatory variables. We ranked the models according to the AIC and averaged the model predictions over all candidate models weighted by the AIC weights. The candidate models for the analyses of dispersal probability between and within years were identical. Goodness-of-fit was evaluated with a Hosmer-Lemeshow test (Hosmer and Lemeshow 2000).

*Dispersal distance: Linear regression models.*—We analyzed log-transformed dispersal distances using linear regression models. As before, we considered only cases in which an individual was captured either in two consecutive years (for dispersal between years) or in two consecutive broods within a year (for dispersal within year). We considered distances that were >0 m (i.e., we modeled distance provided that individuals changed 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). We tested for normality of residuals with Kolmogorov-Smirnov tests. All analyses using logistic and linear regression models were performed with R, version 2.10.0 (R Foundation for Statistical Computing, Vienna). Standard errors of differences were calculated with the delta method. Results are presented as means  $\pm$  SE.

## RESULTS

In total, 712 adult hoopoes (367 females, 345 males) were captured between 2002 and 2009, of which 187 were recaptured at least once in another year (89 males, 98 females). Of 985 captures (507 females, 478 males), 44 (26 females, 18 males) had no, 727 (353 females, 374 males) had medium, and 214 (128 females, 86 males) had high reproductive success. We used data from 158 individuals (76 males, 82 females) for the analysis of dispersal between years with the logistic regression models and 247 individuals (98 males, 149 females) for the analysis of dispersal within years.

*Dispersal probability and apparent survival: Multistate capture–recapture models.*—The goodness-of-fit test of the most general multistate model was not significant (overall:  $\chi^2 = 33.38$ ,  $df = 63$ ,  $P > 0.99$ ; for details, see Table S1 [online supplement; see Acknowledgments]), indicating neither overdispersion nor violation of homogeneity assumptions. The best model for recapture contained no explanatory variable (for complete model list, see Table S2). Models that included sex ( $\Delta AIC = 1.85$ ), year ( $\Delta AIC = 3.25$ ), or reproductive success ( $\Delta AIC = 3.40$ ) were ranked lower. In the best model for the second step, a change in reproductive success depended only on whether or not the individuals dispersed and the change was Markovian. The next-best models, which also contained sex or age effects or that considered random transitions, had almost no support ( $\Delta AIC > 8.36$ ). The best model for breeding dispersal included an effect of reproductive success in males, but not in females. The next-best models had either no effect at all (constant dispersal probability) or a sex effect only ( $\Delta AIC > 1.11$ ). Finally, the top 24 models for apparent survival all contained an effect of reproductive success ( $\Delta AIC < 8.35$ ). Nonetheless, there was some uncertainty about the association of sex and age with apparent survival (best model with sex and age:  $\Delta AIC = 1.09$ ; Table 1).

TABLE 1. Model selection results for apparent survival ( $\phi$ ), breeding dispersal ( $d$ ), change of reproductive success ( $b$ ), and recapture probability ( $p$ ) using a multistate capture–recapture model for Eurasian Hoopoes (2002–2009). The best 10 models from the last modeling step are shown; the other fitted models are presented in Table S2 (online supplement; see Acknowledgments). Results include difference in Akaike's information criterion (AIC) of the current and the best model ( $\Delta AIC$ ), the AIC weight of the given model ( $w_i$ ), the number of estimated model parameters ( $K$ ), and the model deviance. Model notation: disp = dispersal; period (.) = constant; success = reproductive success (3 classes); + = additive effect; \* = interactive effect.

| Model                                                                                             | $\Delta AIC$ | $w_i$ | $K$ | Deviance  |
|---------------------------------------------------------------------------------------------------|--------------|-------|-----|-----------|
| $\phi(\text{success}), d(\text{male: success; female: .}), b(\text{disp}), p(.)$                  | 0.000        | 0.173 | 20  | 1,878.166 |
| $\phi(\text{success}), d(.), b(\text{disp}), p(.)$                                                | 1.076        | 0.101 | 17  | 1,885.242 |
| $\phi(\text{success+sex+age}), d(\text{male: success; female: .}), b(\text{disp}), p(.)$          | 1.090        | 0.100 | 22  | 1,875.256 |
| $\phi(\text{success}), d(\text{sex}), b(\text{disp}), p(.)$                                       | 1.691        | 0.074 | 18  | 1,883.857 |
| $\phi(\text{success}), d(\text{male: success; female: .}), b(\text{disp}), p(\text{sex})$         | 1.807        | 0.070 | 21  | 1,877.973 |
| $\phi(\text{success+sex+age}), d(.), b(\text{disp}), p(.)$                                        | 2.146        | 0.059 | 19  | 1,882.312 |
| $\phi(\text{success*sex+age}), d(\text{male: success; female: .}), b(\text{disp}), p(.)$          | 2.704        | 0.045 | 25  | 1,870.870 |
| $\phi(\text{success+sex+age}), d(\text{sex}), b(\text{disp}), p(.)$                               | 2.759        | 0.044 | 20  | 1,880.925 |
| $\phi(\text{success}), d(.), b(\text{disp}), p(\text{sex})$                                       | 2.879        | 0.041 | 18  | 1,885.045 |
| $\phi(\text{success+sex+age}), d(\text{male: success; female: .}), b(\text{disp}), p(\text{sex})$ | 2.963        | 0.039 | 23  | 1,875.129 |



Model-averaged breeding-dispersal probability of females was relatively high ( $0.70 \pm 0.02$ ) and did not differ among classes of reproductive success or with age (Fig. 1A). Males with medium ( $0.68 \pm 0.02$ ) or high ( $0.58 \pm 0.10$ ) reproductive success had higher dispersal probabilities than males with no reproductive success ( $0.28 \pm 0.44$ ; Fig. 1A). Model-averaged apparent survival was nearly identical for both sexes and age classes but differed with reproductive success (Fig. 1B; ASY females: no =  $0.22 \pm 0.03$ ; medium =  $0.44 \pm 0.03$ ; high =  $0.60 \pm 0.01$ ; SY females: no =  $0.19 \pm 0.02$ ; medium =  $0.40 \pm 0.03$ ; high =  $0.56 \pm 0.04$ ; ASY males: no =  $0.20 \pm 0.02$ ; medium =  $0.43 \pm 0.02$ ; high =  $0.60 \pm 0.02$ ; SY males: no =  $0.18 \pm 0.02$ ; medium =  $0.40 \pm 0.03$ ; high =  $0.57 \pm 0.04$ ). The recapture probability was constant across years, sexes, ages, and classes of reproductive success ( $0.71 \pm 0.05$ ). Because recapture probability did not depend on any of the factors that we included in the models, dispersal

modeling without considering imperfect capture should not have induced spurious patterns about factors that affected dispersal. However, modeling without accounting for detection provides only relative estimates of dispersal probability.

The probability of changing class of reproductive success for individuals that initially had no reproductive success differed between site-faithful and dispersing individuals (Fig. S1 [online supplement; see Acknowledgments]). Individuals with no reproductive success that did not disperse achieved medium reproductive success, whereas individuals that dispersed could achieve either medium or high reproductive success. Thus, on average, dispersal was advantageous in terms of future reproductive success. For individuals that initially had medium or high reproductive success, the probability of changing classes of reproductive success did not depend on dispersal status.

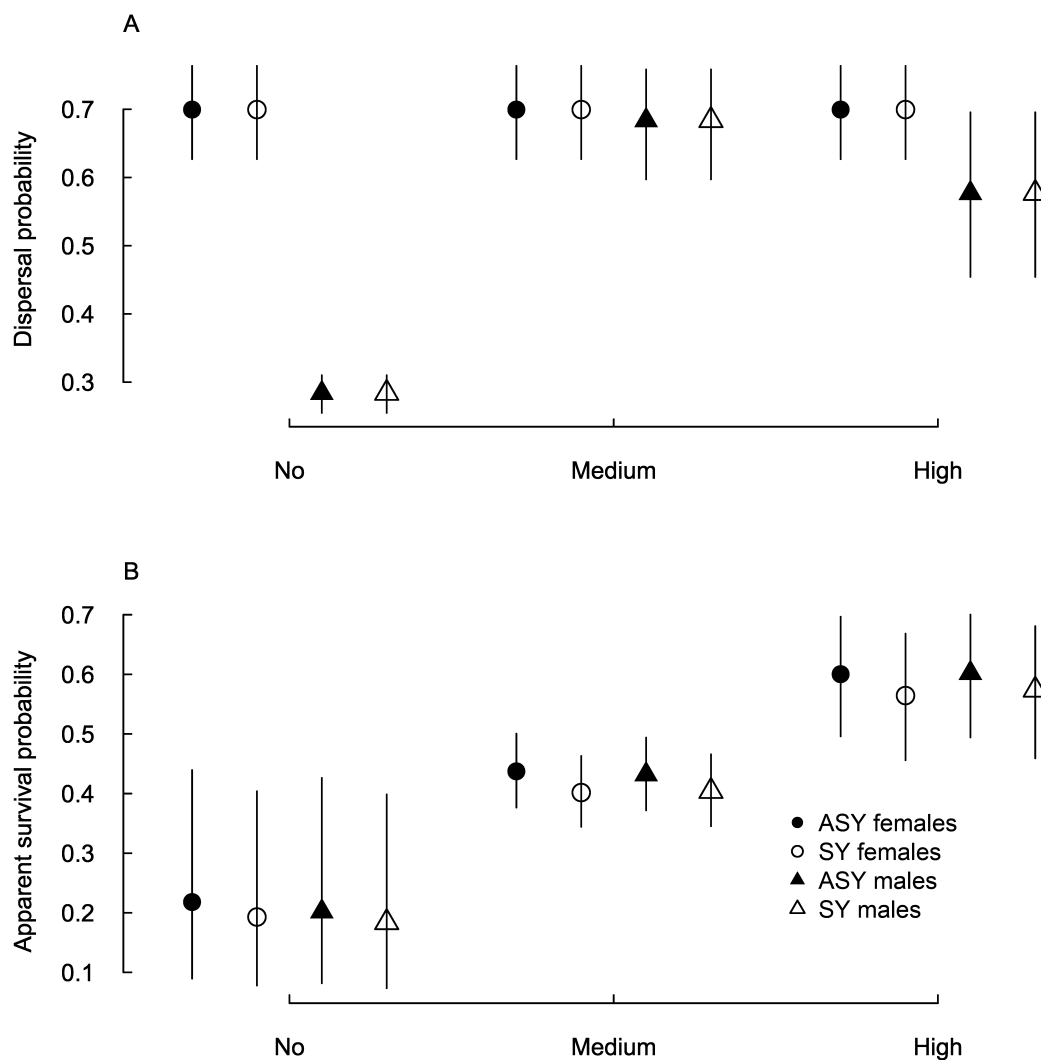


FIG. 1. Model-averaged probabilities of (A) dispersal between years and (B) apparent survival of Eurasian Hoopoes in relation to previous reproductive success (x-axis: null, medium, and high), age, and sex, estimated with a multistate capture–recapture model (2002–2009; ASY = after-second-year; SY = second-year). Error bars are 95% confidence intervals.

### DISPERSAL PROBABILITY: LOGISTIC REGRESSION MODELS

*Dispersal between years.*—The Hosmer-Lemeshow test indicated no lack of fit for the most complex model ( $\chi^2 = 8.64$ ,  $df = 8$ ,  $P = 0.37$ ). Model selection revealed that many models achieved similar support from the data (Table 2). The best model included an age effect only, whereas the next-best models also had a sex effect ( $\Delta AIC = 0.05$ ). The model without any effect still received some support by the data ( $\Delta AIC = 1.26$ ), whereas the best model that included an effect of reproductive success was ranked lower ( $\Delta AIC = 1.51$ ). Although the model-averaged predictions suggested that females had a higher probability of dispersal than males, that SY individuals were more likely to disperse than ASY individuals, and that dispersal probability changed with increasing reproductive success, large confidence intervals (Fig. 2) weakened the strength of all these effects. The mean dispersal probabilities for individuals with the median number of fledglings ( $= 6$ ) were 0.58 (95% CI: 0.45–0.70) for SY females, 0.49 (0.33–0.66) for ASY females, 0.51 (0.36–0.66) for SY males, and 0.40 (0.23–0.59) for ASY males. Similar results were obtained from an analysis that considered the first (instead of the second) brood in a year as reference (Table S2 and Fig. S2), indicating that the choice of the reference brood had a negligible influence on our conclusions.

*Dispersal within year.*—The Hosmer-Lemeshow test indicated no lack of fit of the most complex model ( $\chi^2 = 12.98$ ,  $df = 8$ ,  $P = 0.11$ ). In contrast to the modeling of dispersal between years,

TABLE 2. Model selection results for Eurasian Hoopoe breeding-dispersal probability between years (2002–2009), obtained from logistic regression models ( $n = 158$  individuals). The models are ordered by their support, with the best model at the top. Results include the difference in Akaike's information criterion (AIC) of the current and the best model ( $\Delta AIC$ ), the AIC weight of the given model ( $w_i$ ), the number of estimated model parameters ( $K$ ), and the model deviance. Model notation: period (.) = constant; success = reproductive success; + = additive effect; \* = interactive effect;  $\nabla$  = Hosmer-Lemeshow goodness-of-fit test ( $\chi^2_8 = 8.64$ ,  $P = 0.37$ ).

| Model                                  | $\Delta AIC$ | $w_i$ | $K$ | Deviance |
|----------------------------------------|--------------|-------|-----|----------|
| 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  |
| Male: age; female: success + age       | 1.509        | 0.063 | 4   | 213.260  |
| Success + age                          | 1.802        | 0.054 | 3   | 215.554  |
| Male: success + age; female: age       | 2.047        | 0.048 | 4   | 213.798  |
| Sex + success                          | 2.430        | 0.040 | 3   | 216.182  |
| Male: .; female: 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  |
| Male: success * age; female: age       | 2.870        | 0.032 | 5   | 212.621  |
| Male: success; female: .               | 3.017        | 0.030 | 3   | 216.768  |
| Male: age; female: 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 $\nabla$ | 5.133        | 0.010 | 6   | 212.884  |

modeling of dispersal between the first and second broods in the same year produced three models that had more support from the data than the other candidate models (Table 3;  $\Delta AIC < 3.9$ ). However, all factors were included in these three top models. Model-averaged probabilities of dispersal between first and second broods were relatively higher in females (model-averaged dispersal probability for individuals with median number of fledglings, SY: 0.40 [95% CI: 0.30–0.52], ASY: 0.53 [0.40–0.65]) than in males (model-averaged dispersal probability for individuals with median number of fledglings, SY: 0.28 [0.16–0.44], ASY: 0.09 [0.03–0.25]; Fig. 2). The patterns of dispersal probability within years were similar to the patterns of dispersal between years, and the confidence intervals were again large. Males and SY females with the median number of fledglings tended to have higher between-year than within-year dispersal probabilities (differences, SY males:  $0.23 \pm 0.11$ ; ASY males:  $0.31 \pm 0.15$ ; SY females:  $0.17 \pm 0.09$ ), whereas dispersal probabilities within and between years were very similar in ASY females (difference =  $-0.04 \pm 0.11$ ).

### DISPERSAL DISTANCE: LINEAR REGRESSION MODELS

*Dispersal distance between years.*—The frequency distribution of dispersal distances showed that females more often dispersed over longer distances than males (Fig. 3; females: mean =  $1.98 \pm 0.41$  km, median = 0.67 km, range: 0–32.7 km,  $n = 118$ ; males: mean =  $0.83 \pm 0.18$  km, median = 0.51 km, range: 0–19.4 km,  $n = 115$ ).

Modeling dispersal distances revealed that the best model included all variables considered (breeding success, sex, and age), but also that many candidate models with fewer variables or a different combination of them were similarly well supported by the data (Table 4). The null model was the least supported ( $\Delta AIC = 5.60$ ), which indicates that dispersal distance was affected by the variables considered. Model-averaged dispersal distance declined with increasing reproductive success (ASY males: from 0.70 km [95% CI: 0.36–1.38 km] when no young fledged to 0.54 km [0.36–0.82 km] when 10 young fledged; SY males: from 0.79 km [0.49–1.28 km] when no young fledged to 0.73 km [0.48–1.11 km] when 10 young fledged; ASY females: from 1.14 km [0.59–2.20 km] when no young fledged to 0.80 km [0.53–1.22 km] when 10 young fledged; SY females: from 1.29 km [0.75–2.22 km] when no young fledged to 1.10 km [0.73–1.65 km] when 10 young fledged). Model-averaged dispersal distance was lower, on average, in older than in younger individuals (model-averaged dispersal distance for individuals with median number of fledglings, ASY males: 0.60 km [95% CI: 0.40–0.90 km], SY males: 0.75 km [0.54–1.06 km], ASY females: 0.92 km [0.64–1.33 km], SY females: 1.17 km [0.83–1.65 km]; Fig. 4). The most obvious difference was related to sex: females within both age classes dispersed greater distances than males. The same pattern was observed if only first broods were considered (Table S4 and Fig. S3 [online supplements; see Acknowledgments]).

*Dispersal distance within year.*—The frequency distribution of dispersal distances between first and second broods showed that females dispersed longer distances than males (Fig. 3). Mean dispersal distance of females was  $1.45 \pm 0.24$  km (median = 0.45 km, range: 0–26.2 km,  $n = 184$ ), and that of males was  $0.46 \pm 0.07$  km (median = 0.29 km, range: 0–5.6 km,  $n = 114$ ).

As for dispersal distance between years, modeling of dispersal distance between first and second broods revealed that many

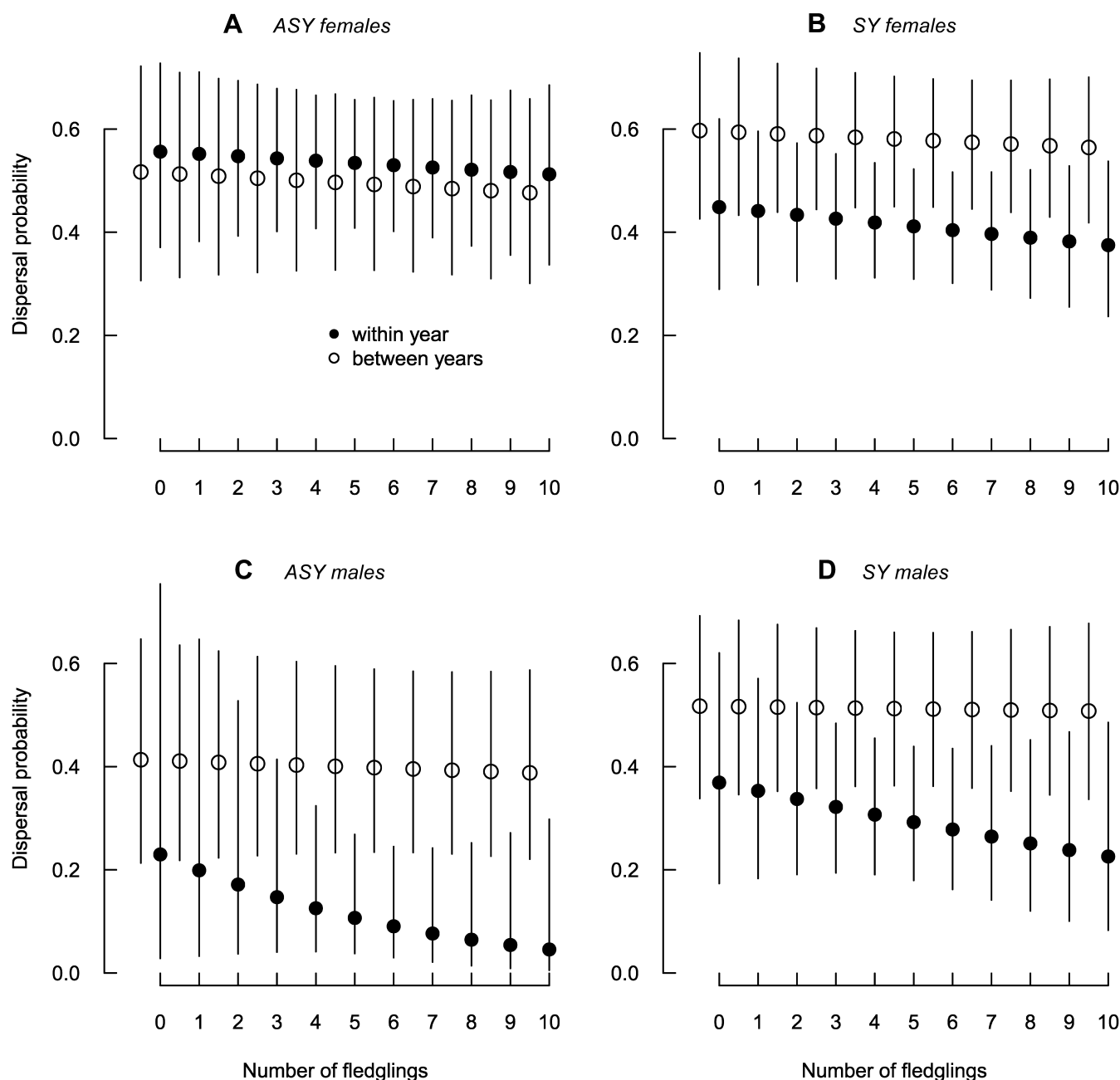


FIG. 2. Model-averaged probabilities of Eurasian Hoopoe dispersal between and within years in relation to the number of fledglings (sum of fledglings of the whole breeding season for dispersal between years; number of fledglings of first brood for dispersal within years), separated for both sexes and age classes (2002–2009; ASY = after-second-year; SY = second-year). Error bars are 95% confidence intervals.

candidate models were similarly well supported by the data (Table 5). By contrast, the null model received no support ( $\Delta AIC = 16.78$ ), which indicates that dispersal distance was affected by the variables considered. Model-averaged dispersal distances between first and second broods showed similar pattern as dispersal distance between years (Fig. 4). Males dispersed over shorter distances than females (model-averaged dispersal distance for individuals with median number of fledglings, ASY males: 0.32 km

[95% CI: 0.22–0.45 km], SY males: 0.38 km [0.27–0.55 km], ASY females: 0.67 km [0.52–0.87 km], SY females: 0.71 km [0.55–0.92 km]) and, especially for males, the distances tended to decline with increasing reproductive success (ASY males: from 0.54 km [95% CI: 0.23–1.25 km] when no young fledged to 0.22 km [0.12–0.41 km] when 10 young fledged; SY males: from 0.63 km [0.32–1.27 km] when no young fledged to 0.27 km [0.13–0.56 km] when 10 young fledged; ASY females: from 0.78 km [0.49–1.23 km]

TABLE 3. Model selection results for Eurasian Hoopoe breeding-dispersal probability within years (2002–2009) between first and second broods, obtained from logistic regression models ( $n = 247$  individuals). The models are ordered by their support, with the best model at the top. Given are the difference in Akaike's information criterion (AIC) of the current and the best model ( $\Delta\text{AIC}$ ), the AIC weight of the given model ( $w_i$ ), the number of estimated model parameters ( $K$ ), and the model deviance. Model notation: period (.) = constant; success = reproductive success; + = additive effect; \* = interactive effect;  $\nabla$  = Hosmer-Lemeshow goodness-of-fit test ( $\chi^2_8 = 12.98$ ,  $P = 0.11$ ).

| Model                                  | $\Delta\text{AIC}$ | $w_i$ | $K$ | Deviance |
|----------------------------------------|--------------------|-------|-----|----------|
| Male: age ; female: 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  |
| Male: success * age; female: age       | 3.973              | 0.045 | 5   | 295.481  |
| Male: .; female: 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  |
| Male: age; female: 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  |
| Male: success; female: .               | 8.975              | 0.004 | 3   | 304.483  |
| Sex + age                              | 9.415              | 0.003 | 3   | 304.923  |
| Age * success + sex * success $\nabla$ | 10.089             | 0.002 | 6   | 299.597  |
| Success * age + sex                    | 10.377             | 0.002 | 5   | 301.885  |
| Male: success + age; female: 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   |

when no young fledged to 0.61 km [0.39–0.95 km] when 10 young fledged; SY females: from 0.82 km [0.53–1.28 km] when no young fledged to 0.64 km [0.41–0.99 km] when 10 young fledged). Overall, dispersal distances between first and second broods were shorter than dispersal distances between years (difference between model-averaged dispersal distances between vs. within years for individuals with median number of fledglings, ASY males:  $0.28 \pm 0.14$  km; SY males:  $0.37 \pm 0.15$  km; ASY females:  $0.25 \pm 0.19$  km; SY females:  $0.46 \pm 0.22$  km).

## DISCUSSION

Our results show that (1) the probability of breeding dispersal and (2) the distance dispersed between and within breeding seasons were affected by the same factors in Eurasian Hoopoes. Both forms of dispersal differed strongly between sexes, but the effects of age and reproductive success on either form of dispersal were weak and poorly estimated. Generally, dispersal between years was more likely and occurred over longer distances than dispersal within years.

Our analyses of dispersal probability between years using the multistate capture–recapture model and the logistic regression model yielded similar results, especially for females; dispersal probabilities in both analyses were weakly affected by previous reproductive success and age. In males, some differences between the two analyses emerged. The multistate analysis

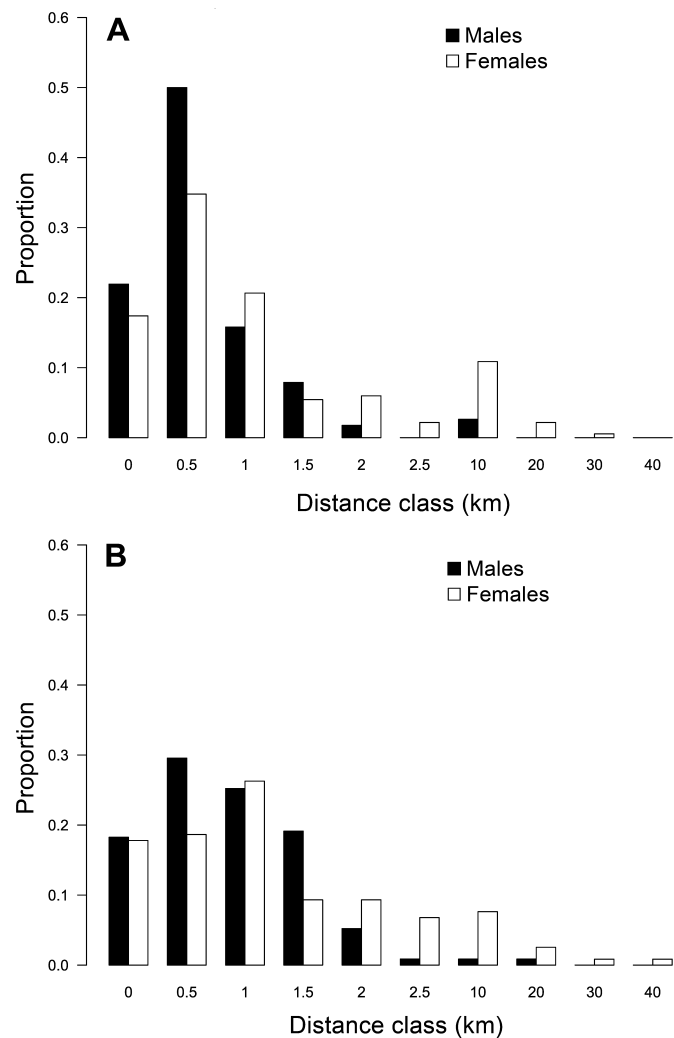


FIG. 3. Distribution of the proportion of observed dispersal distances of male and female Eurasian Hoopoes (A) within years and (B) between years. Sample sizes: dispersal between years: 115 males and 118 females; dispersal within year: 114 males and 184 females (2002–2009).

showed, for instance, that males with low reproductive success were highly site faithful, whereas the logistic regression model suggested that dispersal probability did not depend on previous reproductive success. Because site fidelity of individuals with no reproductive success is contrary to expectations (Haas 1998, Doligez et al. 1999, Blakesley et al. 2006, Schaub and von Hirschheydt 2009), we think that small sample sizes produced spurious results in the multistate model. We think that reproductive success had a weak effect on dispersal decisions in males. Overall, the probabilities of dispersal between years obtained with the multistate model were higher than those obtained with the logistic regression models, which is to be expected because the former accounted for detection probability. However, capture probabilities were generally high and did not vary with any of the factors that we included in our analyses. Therefore, imperfect detection is unlikely to have affected those analyses that did not include this parameter.



TABLE 4. Model selection results for Eurasian Hoopoe breeding-dispersal distance between years (2002–2009), obtained from linear regression models ( $n = 132$  individuals). The models are ordered by their support, with the best model at the top. Results include the difference in Akaike's information criterion (AIC) of the current and the best model ( $\Delta\text{AIC}$ ), the AIC weight of the given model ( $w_i$ ), the number of estimated model parameters ( $K$ ), and the model deviance. Model notation: period (.) = constant; success = reproductive success; + = additive effect; \* = interactive effect;  $\nabla$  = Kolmogorov-Smirnov test for normality of residuals ( $D = 0.13$ ,  $P = 0.04$ ).

| Model                                  | $\Delta\text{AIC}$ | $w_i$ | $K$ | Deviance |
|----------------------------------------|--------------------|-------|-----|----------|
| Success * age + sex                    | 0.000              | 0.135 | 6   | 142.062  |
| Sex + age                              | 0.025              | 0.133 | 4   | 146.461  |
| Male: age; female: success + age       | 0.546              | 0.103 | 5   | 144.828  |
| Sex + success                          | 1.138              | 0.076 | 4   | 147.700  |
| Male: success + age; female: age       | 1.672              | 0.058 | 5   | 146.069  |
| Age * success + sex * success $\nabla$ | 1.769              | 0.056 | 7   | 141.814  |
| Sex                                    | 1.874              | 0.053 | 3   | 150.794  |
| Male: age ; female: 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  |
| Male: .; female: success               | 2.194              | 0.045 | 4   | 148.886  |
| Sex * age + success                    | 2.298              | 0.043 | 6   | 144.557  |
| Male: success; female: .               | 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  |
| Male: success * age; female: 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  |

Sex had a strong effect on dispersal between years; females were more likely to disperse and move longer distances than males. In this respect, dispersal of hoopoes is similar to dispersal of many other bird 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, Zuberogitia et al. 2009). Within years, females also dispersed more often and over longer distances.

Age did not have a strong effect on dispersal probability and distance in hoopoes, both within and between years. Still, the effect size was in the expected direction, in that younger individuals were more likely to disperse than older individuals. In long-lived species such as the Black Kite (*Milvus migrans*; Forero et al. 1999), Audouin's Gull (*Larus audouinii*; Oro et al. 2004), and Lesser Kestrel (*Falco naumanni*; Calabuig et al. 2008), age had a stronger effect on dispersal than in short-lived species such as the Barn Swallow (*Hirundo rustica*; Schaub and von Hirschheydt 2009), Pied Flycatcher (*Ficedula hypoleuca*; Eeva et al. 2008), or Eurasian Hoopoe (present study).

Many studies have reported a strong influence of an individual's personal previous reproductive output on dispersal (Haas 1998, Doligez et al. 1999, Calabuig et al. 2008, Schaub and von Hirschheydt 2009). This response is expected because dispersal is adaptive only if fitness increases (Johnson and Gaines 1990). Our data indicated no relationship between reproductive success and

dispersal, either between or within years, for either sex (Figs. 2 and 3). In hoopoes, females usually leave their brood before the chicks fledge (Arlettaz et al. 2010a) and, therefore, have little knowledge about final reproductive success. In males, even with full knowledge of reproductive success, dispersal was only weakly affected by reproductive success. Dispersal of individuals that had no reproductive success was beneficial: they achieved, on average, higher reproductive success when they dispersed than when they remained site faithful. However, the vast majority of individuals had medium or high reproductive success, and the probability of changing reproductive class was independent of their dispersal decision. This may explain why the relationship between current reproduction and the dispersal decision in hoopoes was relatively weak. Theoretical models show that dispersal can be beneficial, irrespective of reproductive success, if territory quality is subject to high temporal variability (Paradis et al. 1998). Territory quality of hoopoes in the study area varies spatially (M. Tschumi et al. unpubl. data), but whether it is also temporally variable is unknown.

Apparent survival of both sexes and age classes was the same and increased with previous reproductive success. Because permanent emigration and mortality are confounded, it is impossible to determine whether individuals with low reproductive success experienced higher mortality or more often dispersed beyond the study area than individuals with high reproductive success. However, some evidence exists to support the hypothesis that differential mortality is likely to account for most of the difference. First, if dispersal to another population was the reason, we would have expected a stronger dependence of dispersal within the study area on reproductive success. For example, in female Barn Swallows, apparent survival increased with reproductive success (albeit not as 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 in reproductive success was Markovian (i.e., it depended on previous reproductive success; Fig. S1), pointing toward large intraspecific variation in individual performance. Thus, individual differences in survival are not unexpected.

Few studies have focused on dispersal between the first and second breeding attempts of the same year. Our results showed that within-year dispersal was affected by the same factors as dispersal between years, which suggests that similar functional relationships existed. Overall, probability of within-year dispersal was slightly lower than dispersal between years, possibly because of habitat saturation and constraints set by the low availability of either mates or nest site (Skrade and Dinsmore 2010). Breeding dispersal seems to be very common in hoopoes compared with many other bird species (Greenwood and Harvey 1982). In many species with low breeding dispersal, current reproductive success is often the main driver for dispersal (Pasinelli et al. 2007, Schaub and von Hirschheydt 2009). Thus, individuals that have low reproductive success presumably attempt to disperse to a territory of higher quality in the next year to increase reproductive output. The situation seems to differ in hoopoes because breeding dispersal is very common, the decision to disperse is only weakly influenced by current reproduction, and dispersal is no more likely than site fidelity to lead to increased reproductive success. Thus, the decision to disperse is unlikely to be motivated by an attempt to acquire a territory of higher quality. Frequent changes of breeding sites may be a strategy to avoid parasite infestation (Fitz

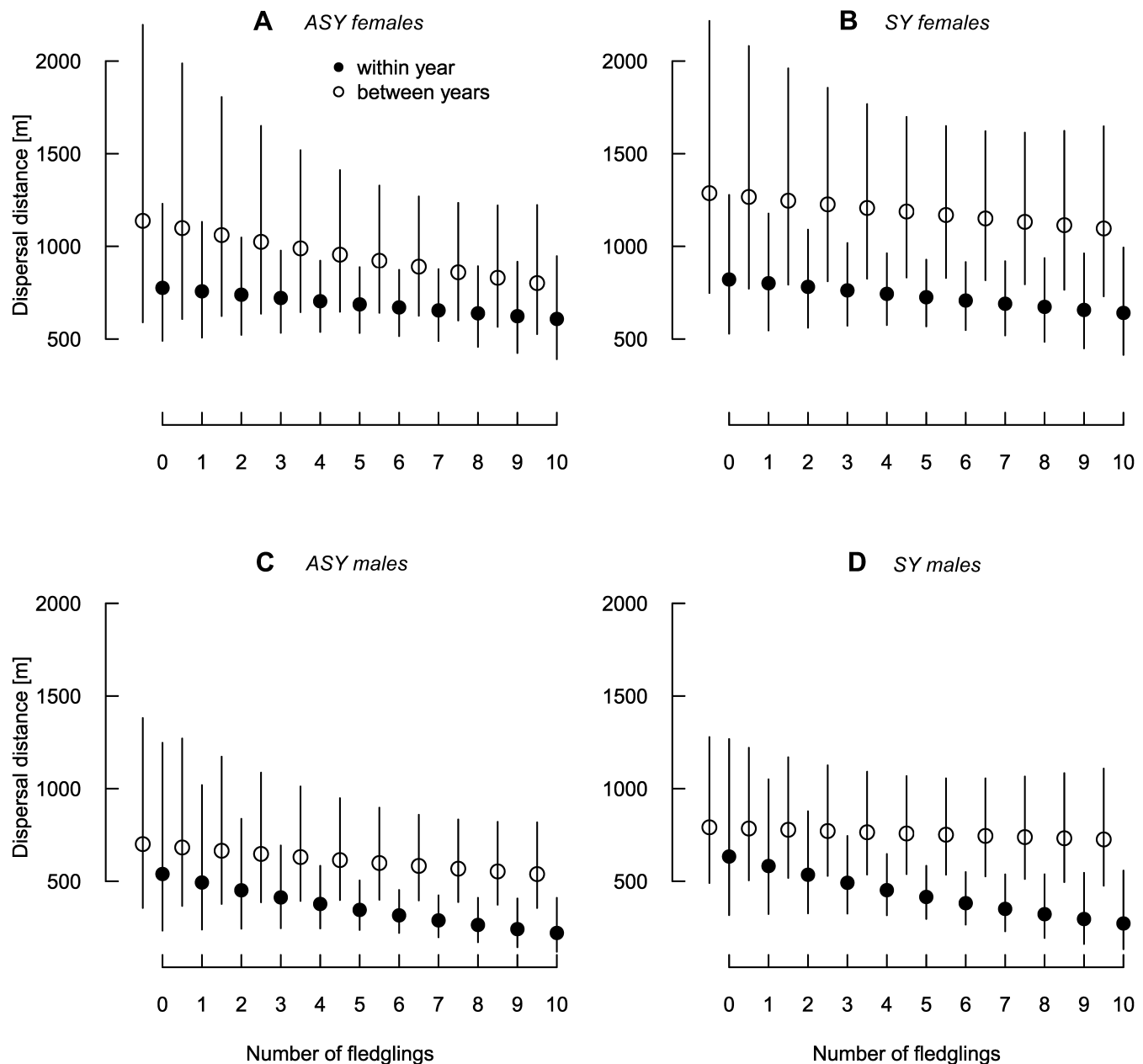


FIG. 4. Model-averaged distances of Eurasian Hoopoe dispersal between and within years in relation to the number of fledglings (sum of fledglings of the whole breeding season for dispersal between years; number of fledglings of first brood for dispersal within years), separated for both sexes and age classes (2002–2009; ASY = after-second-year; SY = second-year). Error bars are 95% confidence intervals.

et al. 2004). However, we have never found ectoparasite-infested nests in our study area (Y. Bötsch unpubl. data). Because within-year breeding-dispersal distances of females are longer than the maximum home-range radii (Tagmann-Ioset et al. 2012), we believe that the main reason for within-year dispersal is the need to find a new mate for the second brood. The current male mate provisions food to the chicks until they fledge, whereas the female usually abandons her first brood to start a second brood before the first fledges (Arlettaz et al. 2010a), and an early start for the second brood is no doubt beneficial. Parental behavior in male birds is associated with a sharp drop

in testosterone and a rise of prolactin (Deviche et al. 2000, Foerster et al. 2002, Schmid et al. 2011); conceivably, it is impossible for males to return to a fully sexual state while being responsible for all parental care. Females may thus be forced to disperse to find suitable males, which may primarily include males that have not yet bred in that year. In addition, multiple male partners allow females to produce young of greater genetic diversity within a single breeding season. Breeding dispersal appears to be strong in the hoopoe, at least compared with other short-lived birds studied so far. A generally high dispersal potential of hoopoes has been demonstrated by demographic and

TABLE 5. Model selection results for Eurasian Hoopoe breeding-dispersal distance between years (2002–2009) between first and second broods, obtained from linear regression models ( $n = 208$  individuals). The models are ordered by their support, with the best model at the top. Results include the difference in Akaike's information criterion (AIC) of the current and the best model ( $\Delta\text{AIC}$ ), the AIC weight of the given model ( $w_i$ ), the number of estimated model parameters ( $K$ ), and the model deviance. Model notation: period (.) = constant; success = reproductive success; + = additive effect; \* = interactive effect;  $\nabla$  = Kolmogorov-Smirnov test for normality of residuals ( $D = 0.05$ ,  $P = 0.21$ ).

| Model                                  | $\Delta\text{AIC}$ | $w_i$ | $K$ | Deviance |
|----------------------------------------|--------------------|-------|-----|----------|
| Male: success; female: .               | 0.000              | 0.189 | 4   | 273.051  |
| Male: success + age; female: 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  |
| Male: success * age; female: 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 $\nabla$ | 4.164              | 0.024 | 7   | 270.652  |
| Sex + success                          | 4.823              | 0.017 | 4   | 279.457  |
| Male: age; female: success + age       | 5.025              | 0.015 | 5   | 277.051  |
| Male: age; female: 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  |

genetic studies of the same Valais population, which showed that immigration and emigration are important drivers of hoopoe population dynamics (Schaub et al. 2012). Such wide-ranging dispersal patterns suggest that successful hoopoe conservation may require that large areas of suitable breeding habitat exist to maintain functional and sustainable populations.

#### ACKNOWLEDGMENTS

Supplementary online material is available at [dx.doi.org/10.1525/auk.2012.11079](http://dx.doi.org/10.1525/auk.2012.11079). Many thanks to the people who sampled data in this hoopoe project in the Valais: M. Bermann, F. Biollaz, C. Bueno, L. Dafond, S. Ehrenbold, K. Falsone, S. Geiser, J. Hellmann, J. Laesser, F. Leippert, M. Mermoud, S. Mettaz, P. Mosimann-Kampe, P. Portner, T.S. Reichlin, M. Schaad, B. Schmid, A. Sierro, A. Tagmann-Ioset, M. Tschumi, N. Weisshaupt, and S. Zingg. M. Lindberg and an anonymous reviewer provided constructive comments on previous versions of the manuscript, and A. Hadley helped with language polishing.

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Associate Editor: M. Lindberg