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Demography of European Honey Buzzards *Pernis apivorus*

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We set out to explore whether changes in fecundity and survival (or both) of European Honey Buzzards were associated with trends observed in The Netherlands. We used standardized monitoring data on numbers and reproduction from several study plots in The Netherlands over the period of 1974–2005. Survival estimates were based on recoveries of Honey Buzzards ringed throughout Europe (collated by EURING and individual ringing stations). Based on these values we computed the annual population growth rate with a time invariant population model, and used elasticity analysis to detect the parameter with the strongest influence on growth rate. Lambda was smaller than 1, suggesting a population decline, but confidence intervals around lambda were relatively wide. Elasticity of adult survival was much higher than of any other life history parameter, indicating that adult survival has potentially the greatest impact on annual population growth. Because data on reproduction varied strongly we estimated a 95% confidence interval for annual population growth by bootstrapping the reproduction data. Furthermore, we analysed the influence of stochastic food availability (i.e. wasp abundance) on reproduction, and through this demographic factor, on the population trend. The stochastic model suggests a clear population decline, which is consistent with observed declines across much of northern and western Europe (including The Netherlands). For the growth rate λ to reach 1, a reproductive output of 1.16 young per pair was calculated to be necessary, much higher than the 0.53–0.88 found in two study sites in The Netherlands.

Key words: age-specific survival, reproduction, trends, social Hymenoptera, *Pernis apivorus*, population modeling

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The use of persistent pesticides in agriculture in the 20th century negatively affected many rodent- and bird-eating raptor species. The hymenopteran diet of European Honey Buzzards *Pernis apivorus* (hereafter Honey Buzzards), and their forest-dwelling behaviour, precluded prolonged contact with the contaminated part of the food chain in Eurasia (breeding grounds) and tropical Africa (wintering). For want of better information, Honey Buzzard populations are usually referred to as being stable (BirdLife International 2004), but substantial evidence is accumulating that in parts of its European breeding range the species is in

decline (Tjernberg & Ryttman 1994, Cösters *et al.* 2000, Bijlsma 2006, Kjellén 2006, Björklund *et al.* 2008, Mammen & Stubbe 2009a).

Monitoring trends and reproduction of Honey Buzzards, however, is no easy feat. The species arrives late on the breeding grounds (from late April onwards, often after 10 May) and is then difficult to detect. Few birders and raptorphiles employ the required species-specific survey methods to enable reliable monitoring of numbers and breeding success (but see Bijlsma 1997, Hardey *et al.* 2006, Saurola 2008). Counts at migratory bottlenecks are also fraught with bias,

caused by weather impacts on flight behaviour during peak migration (Ulfstrand 1958, Allen *et al.* 1996), differential migration strategies of juveniles and adults (Kjellén 1998, Schmid 2000, Hake *et al.* 2003) and variable counting efforts and methods (Bensusan *et al.* 2007). Notwithstanding the contingencies surrounding census methodology, the decline in Scandinavia and parts of western Europe seems beyond doubt.

In a species that may live as long as 28 years (the maximum age recorded in the EURING files), monitoring necessarily has to rely on standardized surveys spanning several decades at least (Lande *et al.* 2002). Most studies of Honey Buzzards cover shorter time intervals, or make use of small samples and a variety of methods (Rasmussen & Storgård 1989, Kostrzewa 1991, Bijlsma 1993, Tjernberg & Rytman 1994, Gamauf 1999, Cösters *et al.* 2000, van Manen 2000, Voskamp 2000, Wiseman 2012). The present study is also based on too short a time series, i.e. three decades. Our exercise, however, is particularly opportune in the light of recent changes in the phenology of its main prey, social Hymenoptera (Tryjanowski *et al.* 2010, R.G. Bijlsma unpubl.), an increasing predation risk on the breeding grounds (Bijlsma 2004, Hakkarainen *et al.* 2004, Sergio & Hiraldo 2008), and a substantial reduction and degradation of wooded savanna, gallery forest and rainforest in West and Central Africa (Justice *et al.* 2001, Duveiller *et al.* 2008, Zwarts *et al.* 2009), the major wintering grounds of Honey Buzzards (Bijlsma 2002, Hake *et al.* 2003, Gamauf & Friedl 2011, Meyburg & Meyburg 2011, Strandberg *et al.* 2012). These phenomena are likely to impact survival and fecundity in a k-selected food specialist.

Our main objective in this study is to identify the most likely demographic mechanisms driving population change in the Honey Buzzard, based on European ringing data (age-specific survival) and data on reproduction in The Netherlands. Of the ecological mechanisms influencing population change, we tested whether food abundance (social hymenoptera) had an impact on reproduction.

METHODS

Study sites

The breeding biology of Honey Buzzards was studied in two plots in The Netherlands, i.e. south-western Veluwe (52°03'N, 5°40'E, 110 km², 15–21 pairs) and western Drenthe (52°51'N, 6°19'E, 45 km², 5–8 pairs). The Veluwe is a large, continuous woodland in The Netherlands (1230 km²), mainly planted with conifer-

ous trees on Pleistocene soils in the early 1900s. Our study plot of 110 km² comprises of woodland (63%, mostly Scots pine *Pinus sylvestris*), heaths (16%) and farmland (20%). The coniferous forests are fringed with small towns, mixed woodland and riverine valleys, and interspersed with heathland and farmland. The raptor population of the SW Veluwe has been studied from 1974 through 1990, with incomplete surveys pre-dating this series (Bijlsma 1993, Rutz & Bijlsma 2006). From 1991 onwards, attention has been focused on a smaller section of the SW Veluwe (20–38 km², 1–9 pairs). To increase sample size, data on reproductive success from the northern and central Veluwe for 1995–98 have been incorporated (40 km², 8 pairs), collected in the same way as on the south-western Veluwe and involving the same type of habitat (W. van Manen unpubl.). The entire SW Veluwe was surveyed again in 2008–2010, largely by different researchers but deploying methods similar to those used in 1974–90.

One hundred km to the north of the Veluwe, in western Drenthe, another study plot was outlined in 1990. This plot consists largely of woodland (64%) with heaths and farmland on fine loamy sand overlying glacial till (6–12 m above sea level). Woodland consists of Scots pine, Norway spruce *Picea abies*, Douglas fir *Pseudotsuga menziesii* and Larch *Larix leptolepis* planted in the 1940s. To enlarge sample size and duration of the study, data from identical woodlands in central Drenthe, collected from 1985 onwards, have been incorporated (van Manen 2000, unpubl.).

Numbers and reproduction

Three major lines of systematic survey were followed to assess the number of territories, nesting pairs, egg-laying pairs and successful pairs: (a) mapping all observations of Honey Buzzards during near-daily field visits, (b) mapping all nests of all raptor species in the study plots via systematic searching (including winter surveys to find overlooked nests from the previous summer), and (c) tree-topping in July and August (Bijlsma 1997, Hardey *et al.* 2006).

Surveys on the SW Veluwe in 1974–1990 by RGB encompassed 22,661 field hours, of which 49% in May–August (and another 1910 hours in the summers of 1991–2005). Similar surveys in Drenthe in 1990–2005 took 15,567 field hours (60% in May–August). Over the years, hundreds of raptor nests were located and checked annually for occupancy until their downfall. Areas where Honey Buzzards were seen posting in tree tops, in low-level wing-clapping display (especially when involving two birds), and heard calling (notably

cycle-wheel call, indicating display, prey transfer or incubation shift), were checked for newly built nests. Tree-topping was employed to overlook woodland (view of several km in all directions in flat country, under fine weather conditions). In July and August, observations from tree-tops, lasting 3–6 h per day between 09:00–17:00 h summer time, were undertaken from carefully chosen trees across the study area. Flight behaviour was recorded, mapped and timed, especially regarding prey transportations and straight-line departures from the forest (directly or indirectly – via triangulation – leading to occupied nests), and prolonged soaring and wing-clapping display at high altitudes (i.e. no nest with chicks to attend, hence not breeding, or already having failed). If possible, each bird was sexed and aged, and notes and sketches/photographs were made to describe plumage, stage of moult and anomalies. This information was used to identify individual birds and delineate territories and putative home ranges. Over the years, RGB annually spent on average 50 hours in surveys from tree-tops (range 18–93 h, depending on weather, wasp abundance and breeding success). All methods combined reliably reflect the number of territories in the study area, as well the breeding status of pairs in July–August (having an active nest, or not), as tested against detailed information obtained via birds equipped with a datalogger (van Manen & van Diermen 2010).

A reliable assessment of the number of non-breeding territorial and failed breeding pairs is particularly relevant, as up to 100% of the pairs may refrain from breeding, or fail to raise fledglings, in any one year (Schubert 1977, Göttingen 1984, Kostrzewa 1991, Bijlsma 1998a, van Manen 2000). Non-breeding was hard to prove unequivocally, as Honey Buzzards are particularly unobtrusive during the pre-laying, laying and incubation periods.

Occupied nests were checked frequently until well after fledging to collect data on clutch and egg size, biometrics and food remains (Bijlsma 1997), unless the pair was particularly vocal. Alarm-calling tends to attract Northern Goshawks *Accipiter gentilis*, a predator of adult and nestling Honey Buzzards, especially since the 1990s when Goshawks started facing food shortage and diversified their diet (Bijlsma 2004, Rutz & Bijlsma 2006). Honey Buzzards are tolerant of human disturbance, and regular nest checks are possible without adverse effects (R.G. Bijlsma in Batten & Ogilvie 1999).

Monitoring food availability

Larvae of social wasps are the main food of Honey Buzzards, supplemented with bumblebee broods,

amphibians and nestling birds (especially thrushes and pigeon squabs) when wasps are in scarce supply (Bijlsma 1993, Bijlsma *et al.* 1997, Bijlsma 1998a, Gamauf 1999). Annual wasp abundance was monitored by recording active and depredated wasp nests that were incidentally encountered during fieldwork from May up to and including August. In order to account for annual variations in field work intensity, the number of encountered wasp nests was converted into number of wasp nests found per 100 field hours. This index of wasp abundance (a) covers the period 1974–2005 for Veluwe and Drenthe combined (for 14 years of overlapping data since 1992, the correlation was highly significant; Spearman rank correlation, $r_s = 0.895$, $df = 12$, $P < 0.001$).

We tested the reliability of the wasp index against several other measures of wasp abundance, viz. (b) number of nests on a wooden house with reed-thatched roof in the study site in Drenthe, (c) qualitative assessment of wasp abundance in July–August by the local greengrocer in Diever, Drenthe-plot (scored as 0–3, respectively none, few, moderate numbers, abundant), (d) number of foraging workers observed during one minute in tree tops in July–August, and (e) number of colonies in two woodland transects of 1000 × 10 m. The indices of wasp abundance showed high concordance for both study sites (Pearson correlations, 2-tailed, with level of significance (* at 0.05, ** at 0.01): (b) versus (c), (d) and (e) respectively 0.621**, 0.479* and 0.673**).

Ring recoveries and survival analysis

For the survival analysis, recoveries of Honey Buzzards ringed in seven European countries, covering nine ringing schemes, were used (Table 1). Only recoveries from birds that were found freshly dead (within a week, Condition code 2, EURING) were used.

We used the so-called Seber recovery model in the software program MARK to estimate annual survival and recovery probabilities. We selected recoveries of dead birds with known age (i.e. ringed as nestlings) and of birds ringed as adults, which is a prerequisite to assess estimates of juvenile survival in Mark (White & Burnham 1999). Sex-independent survival and recovery probabilities in the MARK analysis were assumed, as few Honey Buzzards had been sexed and sexual size dimorphism is small (female wing length/male wing length = 1.03; Cramp & Simmons 1980). According to Cooch & White (2005), the most general model should include all relevant important data. In our analysis Honey Buzzards are assumed to be adults when they are two years or older; the majority of first-year birds

stay in Africa during their first summer, which excludes ringing of this age class. Our most general model has 20 survival parameters for birds ringed as juveniles and 19 for those ringed as adult (in MARK code: $S(a1-20, a2-20)r(y)$). Here, S stands for survival, $a1-20$ for birds ringed as juveniles in year classes, $a2-20$ for birds ringed as adult in year classes, and r for recovery probability that is dependent on year y . Birds older than 20 years are pooled because of the small number of recoveries. A bootstrap goodness-of-fit test was applied to see whether the general model fitted the data. We checked for overdispersion by calculating \hat{c} . In case of death, recovery models \hat{c} can be calculated by (1) \hat{c} = observed deviance divided by the mean deviance of the simulated data, or by (2) \hat{c} = observed model \hat{c} divided by mean \hat{c} from the bootstraps. A value of $\hat{c} > 1$ indicates a certain degree of overdispersion in the data (Cooch & White 2005).

Comparing the relative fit of the general model with different models with a reduced number of parameters provides good inference only if the more general model adequately fits the data (Cooch & White 2005). Models differing less than two units in the value for the Akaike's Information Criterion (AIC) or the modified AIC (QAIC) are not considered different (Cooch & White 2005) and the parameters of such models have been averaged.

Statistical analysis

Data on reproduction were not normally distributed for Veluwe (Kolmogorov–Smirnov = 0.327, $df = 380$, $P < 0.001$) or Drenthe (Kolmogorov–Smirnov = 0.430, $df = 273$, $P < 0.001$). Therefore, data comparisons were carried out with the Mann–Whitney U-test. Spearman rank correlations (ρ) were used to obtain trends in reproduction for variables that were not normally

distributed. We tested the wasp indices for autocorrelation in SPSS 11.0 (ACF, lags of 1 to 16 years), and fitted a linear regression model to the number of young per pair and the logarithm of food availability.

Life history graph and matrix population model

We grouped the life cycle of Honey Buzzards into juveniles (J_t), birds aged one to two years old (B_t), sub-adults, i.e. birds aged two to three years (S_t) and adults, birds exceeding three years of age (A_t) (Figure 1). The annual survival in these four age classes is denoted by P_i ($i = 1, \dots, 4$) and the reproduction (females per female) by F_i ($i = 3, 4$), where i indicates the age class.

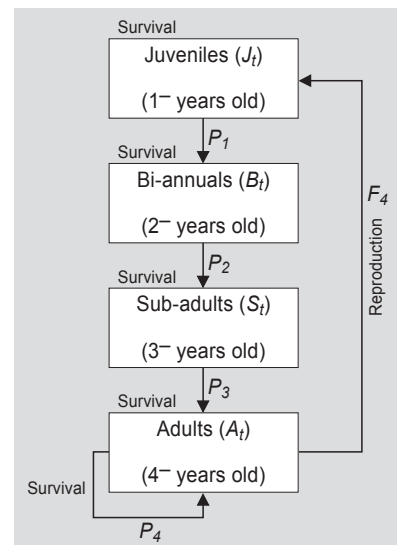


Figure 1. Life-cycle of the Honey Buzzard, with age categories starting just before the breeding season (hence minus sign in superscript, e.g. 3⁻).

Table 1. A total of 6895 ringed Honey Buzzards from nine ringing schemes (7 European countries) provided 235 dead recoveries.

Country	Number ringed as nestling (adult)	Number recoveries of ringed juveniles	Number recoveries of ringed adults	Years
Belgium	150 (0)	5	0	1974–1985
Denmark	352 (0)	10	0	1969–1999
Finland	3265 (70)	99	5	1968–2005
Germany (Helgoland)	220 (0)	5	0	1976–1982
Germany (Hiddensee)	555 (49)	15	2	1977–2002
Germany (Radolfzell)	292 (45)	10	0	1962–2004
Netherlands	868 (0)	38	0	1957–2005
Sweden	936 (76)	42	3	1969–2005
Switzerland	17 (0)	1	0	1976–1982

The life history is presented in mathematical form as a stage-structured matrix population model (Caswell 2001) (Eqn. 1). The pre-breeding census moment of the model was set at the beginning of July, just before the eggs hatch, which is halfway the census moments for survival calculation based on ring recoveries (January). We assumed that (a) the population grows density-independent, (b) survival of female Honey Buzzards is equal to that of males, (c) sex ratio is 1:1, and (d) breeding takes place in a pulse in early July. This last assumption is motivated by the synchronised onset of laying within years, with 75% of the laying in 1973–2006 starting between 20 May and 3 June (unpubl. data Dutch Raptor Group & R.G. Bijlsma, $n = 559$). Eggs normally hatch late June or early July. Age of first breeding was estimated at the third calendar-year (based on Tjernberg & Rytman 1994, Roberts & Lewis 2008, and Roberts 2011). The matrix model that matches the life history in Figure 1 is given in Eqn. 1 and explained in Appendix 1.

$$\begin{bmatrix} J_{t+1} \\ B_{t+1} \\ S_{t+1} \\ A_{t+1} \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0 & F_4 \\ P_1 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 \\ 0 & 0 & P_3 & P_4 \end{bmatrix} \begin{bmatrix} J_t \\ B_t \\ S_t \\ A_t \end{bmatrix} = \mathbf{C} \begin{bmatrix} J_t \\ B_t \\ S_t \\ A_t \end{bmatrix} \quad \text{Eqn. 1.}$$

The values for annual survival in the four age classes are based on the MARK analysis of dead recoveries (see Appendix 1 and last line in Table 4). Three reproductive values are used: a high based on the average number of young per pair calculated over all pairs of the Veluwe region, a low based on the Drenthe area and an average based on all data. With these survival and reproductive values the annual growth rate (the dominant eigenvalue λ) of the population model is computed, and elasticity analysis is used to detect the parameter with the largest influence on annual population growth. Because reproductive output strongly varied over the years, we estimated a 95% confidence interval for the annual population growth by bootstrapping the data on reproduction. Furthermore, we analysed the influence of stochastic food availability (i.e. wasp abundance) on reproductive output and, via this demographic factor, on population trend. Food availability is modelled by drawing a random food availability from the normal distribution of $\ln(\text{wasp nests}/100\text{hour})$ with a mean of 1.97 and a standard deviation of 1.20. With this food availability, realised reproduction (the number of young Y) is drawn from a prediction-interval around the regression line (Moore & McCabe 2003; Ott & Longnecker 2001; Eqn 2).

$$Y = 0.116 \ln(W) + 0.481 \quad \text{Eqn 2.}$$

For a population trend of the Honey Buzzard with stochastic reproduction, either by directly drawing the fertility or by indirectly drawing one via wasp availability, we simulated the trend of 1000 populations over a period of 100 years, starting with an arbitrary initial population size of 20,000 female birds distributed across the four life stages in the proportions that we know from the stable stage distribution for the model based on the average reproductive success.

RESULTS

Trends and reproduction

On the Veluwe, the number of territorial pairs remained more or less stable throughout the 1970s, 1980s and early 1990s (Figure 2). The density in Drenthe has been lower overall than on the Veluwe, with a slight tendency towards decline after the early 1990s.

Honey Buzzards in Drenthe produced significantly fewer young than in the Veluwe region ($U_{380,273} = 41611.5$, $P < 0.001$, Table 2, Figure 3). The Veluwe showed a significant decrease ($\rho = -0.167$, $P = 0.001$), and in Drenthe a stable – and already low – reproduction was found ($\rho = -0.028$, $P = 0.645$). These regions combined showed a significant decrease in the number of young produced per pair in 1973–2005 ($\rho = -0.231$, $P < 0.001$).

Annual wasp abundance (Figure 4) was not autocorrelated, according to an autocorrelation function

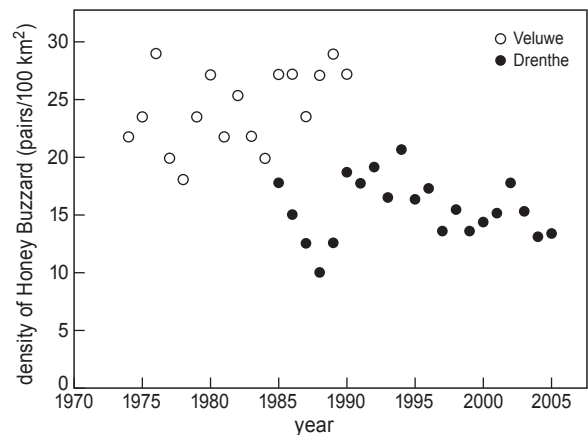


Figure 2. Density of Honey Buzzards (pairs/100 km² of woodland) on the Veluwe (1974–1990, 15–21 pairs/year) and in Drenthe (1985–2005, 4–24 pairs/year, including data collected by W. van Manen in a variable number of plots in central Drenthe).

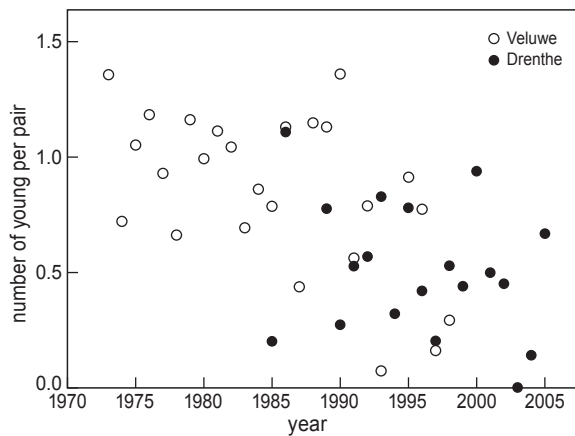


Figure 3. Average number of young per territorial pair for Honey Buzzards breeding on the Veluwe (1974–92: 7–21 pairs, and 1995–98: 6–20 pairs) and in Drenthe (1985–86: 9–10 pairs, and 1990–2005: 6–21 pairs). See also Methods.

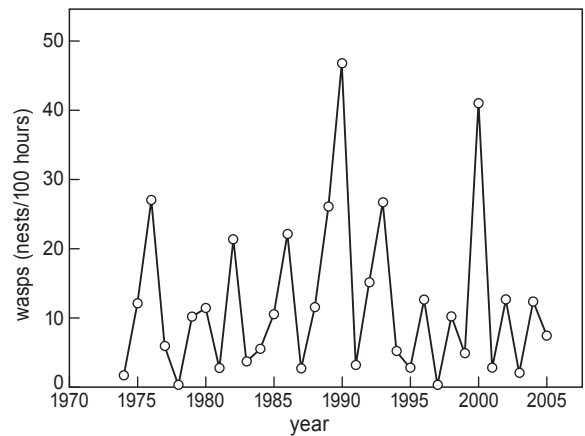


Figure 4. Average number of wasp nests encountered per 100 hours of fieldwork combined for Veluwe (1974–2005) and Drenthe (1990–2005). Intensity of fieldwork in May–August in 1974–2005 averaged 755 ± 157 hours per year (range 458–1143 hours).

Table 2. Summary of reproductive parameters for two study sites in The Netherlands. The percentage breeding is given as fraction of the total number of pairs in the area that have produced at least one egg. The number of young per pair is averaged over all territorial pairs.

Area	Years	Percentage breeding	Mean number young/pair \pm SD	<i>n</i>
Veluwe	1973–1998	63	0.88 ± 0.935	380
Drenthe	1985–2005	41	0.53 ± 0.836	273
Total	1973–2005	54	0.74 ± 0.911	653

Table 3. The four best-fitting models and the general model used for parameter estimation in MARK ($\hat{c} = 1.171$). Model coding as follows: *S* = survival rate, *r* = recovery rate, *a* = age structured, *y* = difference over years and (.) = constant survival or recovery rate. Between brackets after *S* or *r* there are two terms, separated by a comma. The first term shows the parameter structure for birds ringed as juveniles and the second term for birds ringed as adults. In age-structured models the numbers after a show how many age classes were used in the model. For example in the model $S(a1-4,a4)r(.)$ the survival rate of birds ringed as juveniles were different over 4 classes; first-year survival, second-year survival, third-year survival, and survival of older. The birds ringed as adults have a constant survival rate that is equal to the fourth survival parameter of birds ringed as juveniles. NP = number of parameters.

Model	QAICc	Delta QAICc	QAICc weight	Model likelihood	NP	QDeviance
$\{S(a1-4,a4)r(.)\}$	2613.225	0.0000	0.2332	1.0000	5	496.002
$\{S(a1-2,a2)r(.)\}$	2614.238	1.0131	0.1405	0.6026	3	501.020
$\{S(a1-4,a4)r(a1-2,a2)\}$	2614.724	1.4999	0.1102	0.4724	6	495.498
$\{S(a1-4,a2-4)r(.)\}$	2614.901	1.6762	0.1009	0.4325	5	497.678
$\{S(a1-20,a2-20)r(y)\}$	2691.974	78.7495	0.0000	0.0000	111	359.085

with lags 1–16. The linear regression of the number of young produced per Honey Buzzard pair (Y) on the natural logarithm of the average number of wasp nests encountered per 100 hours of fieldwork (W) was highly significant (Eqn 2; $F = 13.65, P < 0.001$).

MARK analysis

The bootstrap goodness-of-fit test ($P < 0.05$) of the general model ($S(a1-20, a2-20)r(y)$) with 20 (19) age classes for Honey Buzzards ringed as juveniles (adults) indicated relatively small overdispersion (first approach: $\hat{c} = 1.171$; second approach: $\hat{c} = 1.028$). We used the adjusted \hat{c} ($= 1.171$) and the QAICc for further model selection and estimates of variance.

Table 3 shows the four best fitting models out of 12 models with two to four age classes for survival and the general model. Recovery rates were either set constant ($r(\cdot)$) or different for juveniles and adults ($r(a1-2, a2)$). Parameter estimates of the four best models with DQAICc <2 were averaged (Table 4) and used in the matrix model. Juvenile survival was 62.6%, then increased to 83.7–87.0% during the subsequent subadult and early adult stages, to slightly decrease again and remain constant at some 80% during the adult stages of life.

Population growth rate

Based on the estimated survival rates and three different reproductive rates for Honey Buzzard, Table 5 shows the results for the deterministic population model, assuming that sub-adult birds do not yet repro-

duce. The dominant eigenvalue λ is less than 1 for all three scenarios, implying an intrinsic growth rate $r < 0$ ($\lambda = e^r$), and, consequently, population decline. Even when assuming that reproduction of subadult birds equals that of older birds ($n = m$), the dominant eigenvalue is still below 1 for all three scenarios (low, average, and high reproduction $\lambda = 0.93, 0.97$ and, 0.99 , respectively).

Elasticity and variance in lambda

The annual survival of adult birds showed the highest elasticity of all age classes (d , in Table 5), indicating that the population growth rate of Honey Buzzards is most sensitive to changes in adult survival. The variance of λ is calculated from the survival estimates (Table 4, see also Appendix 1), the elasticities (Table 5), and the variances in reproduction (0.699, 0.830, and 0.874 for respectively low, average and high reproduction). For low, average and high reproductive success the confidence intervals are 0.66–1.18, 0.72–1.18 and 0.74–1.20. Thus, for all three scenarios $\lambda = 1$ falls within the 95% confidence interval, indicating that the probability of values of the growth rate being lower than 0.66 or higher than 1.20 is less than 5%.

Stochastic simulations with different reproductive values

In the simulations we either used a resampling of the reproductive data or a resampling of the data on food availability, together with the prediction interval

Table 4. Estimated parameter values and their standard errors as estimated in the best fitting MARK models for the Honey Buzzard in percentages per year; $S_{juv}(i)$ ($i = 1, \dots, 4$) is the % survival of Honey Buzzards ringed as juvenile between year ($i-1$) and i ; $S_{ad}(i)$ is the % survival of Honey Buzzards ringed as adult between year ($i-1$) and i ; $r_{juv}(i)$ are the % recovery of Honey Buzzards ringed as juvenile during the first year ($i = 2$), whereas r_{ad} is the % recovery of Honey Buzzards ringed as adults. The last row shows the notation of the different survival estimates in the matrix model (see Appendix 1).

Parameter from	S_{juv1}	S_{juv2}	S_{juv3}	S_{juv4}	S_{ad2}	S_{ad3}	S_{ad4}	r_{juv1}	r_{juv2}	r_{ad2}
{ $S(a1-4, a4) r(\cdot)$ }	65.3	84.3	88.5	80.0	80.0	80.0	80.0	3.8	3.8	3.8
SE	3.4	3.2	3.1	2.3	2.3	2.3	2.3	0.3	0.3	0.3
{ $S(a1-2, a2) r(\cdot)$ }	65.5	82.7	82.7	82.7	82.7	82.7	82.7	3.8	3.8	3.8
SE	3.4	1.8	1.8	1.8	1.8	1.8	1.8	0.3	0.3	0.3
{ $S(a1-4, a4) r(a1-2, a2)$ }	50.7	84.3	88.5	80.1	80.1	80.1	80.1	2.6	4.8	4.8
SE	17.6	3.2	3.1	2.3	2.3	2.3	2.3	1.0	1.6	1.6
{ $S(a1-4, a2-4) r(\cdot)$ }	65.3	83.0	87.7	80.6	83.0	87.7	80.6	3.8	3.8	3.8
SE	3.4	3.2	3.1	2.3	3.2	3.1	2.3	0.3	0.3	0.3
Weighted average	62.6	83.7	87.0	80.8	81.2	82.0	80.8	3.0	4.0	4.0
SE	6.1	2.8	2.8	2.2	2.3	2.3	2.2	0.4	0.5	0.5
Notation	p	b	c	d			d			

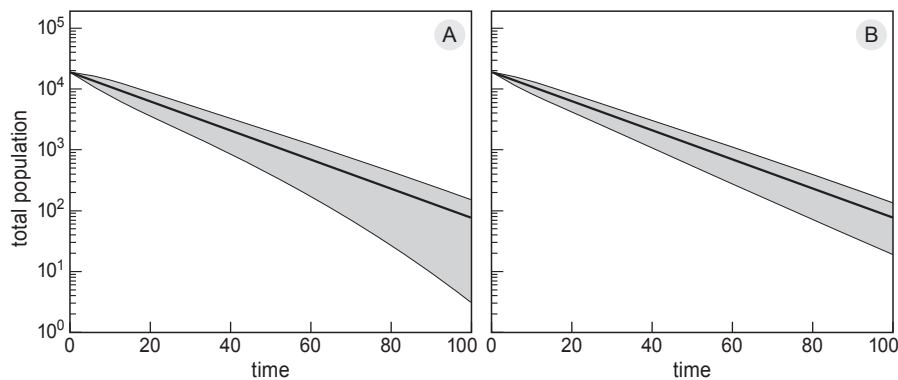


Figure 5. (A) Development of the Honey Buzzard population using resampling of the realised yearly reproduction per pair in Veluwe and Drenthe as input for the matrix model. (B) Reproduction is assumed to depend on food availability using the regression line $\# \text{ young} / \text{ pair} = 0.116 \times \ln(\text{wasp} / 100\text{hour}) + 0.481$. The solid lines show the average population trend for 1000 simulations, with 95% confidence intervals (thin lines).

around the relationship as depicted in Eqn. 2. In all 1000 simulations the population is declining (Figure 5A). Also, when reproductive output is modeled through food availability, all simulated populations show a decline (Figure 5B).

DISCUSSION

Survival of juveniles and immatures

First-year survival was estimated at 62.6%, significantly lower than in any other age group (no overlap between confidence intervals of first-years and birds older than one year). However, it was substantially higher than the 48.8% (all causes of mortality, includ-

ing shooting) and 58.1% (only birds found dead) found in Swedish Honey Buzzards for which ring recoveries were used up to and including 1991 (Tjernberg & Rytman 1994). Our analysis incorporates the Swedish data, but covers a longer time span and a wider range of ringing schemes from across western and northern Europe. The better survival of first-year birds in our analysis, as compared to the Swedish exercise, may have several explanations, not necessarily mutually exclusive.

First of all, our analysis not only includes data from populations that migrate in a southwesterly direction and leave Europe via the Iberian Peninsula (Table 1, Bijlsma 1993, www.euring.org). The Swedish birds use a wider corridor in an arc between SW and S (small

Table 5. Matrix models (C) based on values of the survival analysis with MARK and the reproduction data. The C matrices only differ in the upper-right element, because different reproduction values were used. The elasticity of adult survival is $e(d)$; the other elasticities are equal and therefore represented by $e(m)$. The yearly population growth rate is given by the dominant λ .

	C	E(parameters)	λ
Low reproduction ($m = 0.53$) Drenthe	$\begin{bmatrix} 0 & 0 & 0 & 0.152 \\ 0.853 & 0 & 0 & 0 \\ 0 & 0.838 & 0 & 0 \\ 0 & 0 & 0.808 & 0.808 \end{bmatrix}$	$e(d) = 0.78$ $e(m) = 0.09$	0.92
Average reproduction ($m = 0.74$)	$\begin{bmatrix} 0 & 0 & 0 & 0.212 \\ 0.853 & 0 & 0 & 0 \\ 0 & 0.838 & 0 & 0 \\ 0 & 0 & 0.808 & 0.808 \end{bmatrix}$	$e(d) = 0.74$ $e(m) = 0.10$	0.95
High reproduction ($m = 0.88$) Veluwe	$\begin{bmatrix} 0 & 0 & 0 & 0.252 \\ 0.853 & 0 & 0 & 0 \\ 0 & 0.838 & 0 & 0 \\ 0 & 0 & 0.808 & 0.808 \end{bmatrix}$	$e(d) = 0.72$ $e(m) = 0.11$	0.97

numbers even SE), indicating that part of the Scandinavian population departs via Italy, a higher-risk route compared to Spain (more shooting, a longer crossing over the Mediterranean Sea, and a central Saharan passage; Fransson & Pettersson 2001, Hake *et al.* 2003, Strandberg *et al.* 2010). Finnish Honey Buzzards migrate to Africa in a S-SE corridor, leaving Europe via the Balkan, Italy, Greece and western Turkey, and crossing the full width of the Mediterranean Sea and Sahara (www.luomus.fi/elaintide/mehilaishaukat/, accessed 2 January 2012). Juvenile Honey Buzzards are known to depart later from the breeding grounds than adults (Kjellén 1998, Bijlsma *et al.* 2001), and hence migrate under less favourable thermal conditions, are more prone to wind drift than adults (Thorup *et al.* 2003), and generally take the more direct and dangerous route to sub-Saharan Africa via the Central Mediterranean (Schmid 2000, Hake *et al.* 2003) and the Sahara (Strandberg *et al.* 2010). Juvenile satellite-tracked raptors crossing the Sahara (including Honey Buzzards) were found to suffer much higher mortality (31% per crossing attempt) than adults (only 2%; Strandberg *et al.* 2010). Despite the higher risk for juveniles and for birds following the route via Italy, the Balkan and Greece, a decline in mortality among first-year birds in recent decades may reflect a real change for the better (Tjernberg & Rytman 1994 compared to this study). Bird protection throughout southern Europe, where shooting used to be – and locally still is – an important mortality factor (Woldhek 1979, Magnin 1991), has improved both legally and in practice, leading to improved survival rates in many long-distance migrants (Saurola 1985, McCulloch *et al.* 1992, Giordano *et al.* 2005, Zwarts *et al.* 2009).

Secondly, the number of Honey Buzzards ringed annually has been stable since the 1950s (Sweden, Fransson & Pettersson 2001) or may even have increased. Non-reporting has a positive impact on calculated survival rates, especially when hunters in southern Europe increasingly refrain from reporting shot (protected) birds (Robinson *et al.* 2009, Guillemain *et al.* 2011). However, the number of Honey Buzzard rings reported within the Euring scheme did not change over time (www.euring.org). First-year survival may therefore really have improved over the decades.

Survival of second- and third-year old birds was higher than in any other age category (Table 4). The majority of Honey Buzzards remain in Africa during their first year(s) of life before returning to the breeding grounds (Bijlsma 1993, Roberts & Lewis 2008,

Roberts 2011, Gamauf & Friedl 2011, Strandberg *et al.* 2012). These birds roam widely across tropical Africa, with a south-shifting tendency in the northern summer to occupy the wintering sites at latitudes between 4.4°N and 8.8°N that have been vacated by adults in spring (Strandberg *et al.* 2012). The latter band of tropical forest may represent the preferred wintering habitat. The colony cycle of Old World polistine wasps, notably of the genera *Polistes*, *Ropalidia*, *Parapolybia*, *Polybioides* and *Belonogaster*, is generally annual with nesting periods shorter than 6–8 months. In the (sub)tropics, where high and rather constant air temperatures prevail, social wasps may start new colonies at any time of the year (Akre & Davis 1978, Yamane 1996). Abundance, species richness and colony size (from tens to 10,000s of cells) of social wasps and bees vary considerably in the (sub)tropics, depending on local variations in humidity, floristic diversity and flowering phenology (Roubik 1989, Turillazzi & West-Eberhard 1996). Although information on food and feeding of Honey Buzzards in tropical Africa is lacking, the relatively high survival rate of immatures suggests an advantage of staying in Africa during the northern summer.

Survival of adults

In our study, we arbitrarily assigned Honey Buzzards in their third year of life as adults, largely based upon the evidence of a prolonged stay in Africa in early life (Gamauf & Friedl 2011, Strandberg *et al.* 2012), delayed acquisition of fully adult soft parts (i.e. grey cere and yellow/orange iris; Bijlsma 1998b) and anecdotal evidence from the breeding quarters (Roberts 2011). Annual survival of adults was 80.8–82.0%, much lower than the 91.7% of an earlier analysis of Swedish birds (Tjernberg & Rytman 1994). Among age classes, adult survival showed the highest elasticity, which is probably a trait typical of long-lived species (Heppell *et al.* 1996, Klok *et al.* 2009), including raptors (Imperial Eagle *Aquila heliaca*: Katzner *et al.* 2006; White-tailed Eagle *Haliaeetus albicilla*: Sulawa *et al.* 2010). However, in an analysis for Black Kite *Milvus migrans*, Sergio *et al.* (2011) found a higher elasticity for younger adults (up to seven years old, i.e. the age when most survivors had entered the breeding population) than for older birds. This apparently contradicting outcome partly arises from which age-class definitions are used by researchers. Most modellers only make a distinction between juveniles and adult birds. A reanalysis of the Black Kite data, using the underlying parameters, then also shows a higher elasticity for adults, albeit higher for the younger adults than for the

oldest age categories (see Figure 2 and online appendix, both in Sergio *et al.* 2011).

The apparent decline in adult survival, as perceived from the comparison between this study (which includes the data from Sweden) and the Swedish one by Tjernberg & Rytman (1994), may reflect the rapidly changing conditions on the breeding grounds, in the African wintering quarters or in both at the same time. Substantial evidence is accumulating that predation risk on the breeding grounds has increased (Hakkarainen *et al.* 2004, Sergio & Hiraldo 2008), with Honey Buzzard among the species being particularly vulnerable (Bijlsma 2004). In the Veluwe plot, for example, nest failure in Honey Buzzards caused by predation (Northern Goshawks, to a lesser extent Pine Marten *Martes martes*, mostly targeted at nestlings but frequently also involving adults) was absent in 1970–75 (a total of 20 nests under observation), then gradually increased to 10.3% in 1976–89 (184 nests), 15.8% in 1990–99 (57 nests) and 40.7% in 2000–09 (27 nests). In the Drenthe study plot, nest predation was already high in the 1990s and increased in the years to follow, i.e. 25% in 1990–95 (16 nests), 18.2% in 1996–99 ($n = 11$), 40% in 2000–04 ($n = 15$) and 45.4% in 2005–09 ($n = 18$) (Bijlsma 2004, and unpubl.).

The sparse data from satellite-tracked adult Swedish and German birds (Hake *et al.* 2003, Meyburg & Meyburg 2011), adult Dutch birds equipped with a datalogger (J. van Diermen, W. van Manen & W. Bouten, unpubl.) and visual observations in rainforest in SE Nigeria (Bijlsma 2002) suggest that adult Honey Buzzards, once settled in the wintering quarter, have single or several small and fixed home ranges which are used nonstop or successively during the northern winter. Although the African wintering quarters may seem a land of milk and honey, the surface area (in km²) of suitable wintering habitat in West- and Central Africa is less than 25% of the size of the breeding area (Bijlsma 2002), and its extent is declining at a fast pace. The annual decline in the forested area in Liberia, Ivory Coast, Ghana, Nigeria, Cameroun, Central African Republic, Equatorial Guinea, Democratic Republic of Congo, Congo-Brazzaville and Gabon, i.e. the countries where the majority of Honey Buzzards spend the northern winter, varied between 0.6 and 2.1% per annum since the 1970s, depending on region and time frame (Dixon *et al.* 1996, Justice *et al.* 2001, Mayaux *et al.* 2005). The remaining fragments of woodland are often seriously degraded and fragmented (Duveiller *et al.* 2008); this is particularly true for West Africa. The strong decline in size and quality of forests must have

further limited the size of the wintering area for Honey Buzzards. A negative impact of forest loss and forest degradation on population size is likely, perhaps via increased competition for high-quality territories (see also Strandberg *et al.* 2012).

Reproduction

For a species whose range of reproductive output *de facto* varies between 0 and 2, productivity (number of chicks raised per nest) shows wide annual variations within and between sites, from 0 in some years to 1.88 in others (review in Schmid 2000). In a species as notoriously difficult to study as the Honey Buzzard, it is almost impossible to assess the validity of published reproductive values. Large regional and temporal variations seem in order, either in line with differences in habitat or based on large annual variations in wasp abundance (the latter, in The Netherlands, by a factor of 40; R.G. Bijlsma unpubl., close to that found in England; Archer 2001). Non-breeding is difficult to prove unequivocally, and any failure to detect non-breeding has a 'positive' effect on estimated reproductive success. For The Netherlands, we show that (1) reproductive output of Honey Buzzards on the Veluwe has declined in the 1990s and 2000s as compared to the 1970s and 1980s, (2) reproductive performance of Honey Buzzards in Drenthe has been consistently low since at least the mid-1980s, and (3) number of young raised per pair is significantly correlated with wasp availability ($F = 13.651$, $P < 0.001$, Eqn. 2). However, despite large fluctuations in wasp indices between 1974 and 2005, wasp abundance overall did not change (slope = -0.073 , $P = 0.636$). This suggests that wasp abundance per se is not involved in the declining reproductive performance on the Veluwe. Increased predation on chicks and adults may further reduce reproductive output (Bijlsma 2004). An average reproductive output of 0.8–1.0 young/pair in Europe, as summarised by Schmid (2000) for Europe, is well above Honey Buzzard performance in a Dutch setting where non-breeding is common and predation frequent. For the growth rate λ to reach 1, the reproductive output per pair should be 1.16, much higher than the 0.53–0.88 found in the present study but not altogether impossible given the modal clutch size of two.

European trends

The trend assessment for European Honey Buzzards by BirdLife International (2004) reads 'overall stable', meaning less than 20% change between 1990 and 2000. Disregarding the fact that a period of ten years is

too short to assess a trend in this species, it highlights the problems surrounding a species of which half the population is estimated to live in Russia, a country for which reliable census data for common raptor species including Honey Buzzard are scarce. When using data from specialists and well-studied countries, Honey Buzzards in Europe show mixed fortunes with a negative overtone. Indirect evidence for a decline first came from standardized counts of southbound Honey Buzzards at Falsterbo, showing a significant decrease between 1973 and 1992, most notably in 1973–81 (Tjernberg & Rytman 1994). Numbers here have been more or less stable since the early 1990s, at some 35% of the 1970s-level (Kjellén 2006, www.skof.se), although a local study in Dalsland suggests an ongoing decline (Södergren 2011). Since then, several schemes in Europe, specifically designed for monitoring breeding raptors, have corroborated the Swedish data, notably in Finland (highly significant decline between 1982 and 2008, of -2.8% annually for territories and -4.2% for nests, using TRIM to calculate trends; Björklund *et al.* 2008), in Nordrhein-Westfalen in western Germany (lower numbers in 1980s, and especially in mid-1990s, with almost a halving of numbers between 1972 and 1998; Cösters *et al.* 2000), in Germany overall (significant decline by $-3.1 \pm 1.4\%$ annually between 1988 and 2002, using TRIM; Mammen & Stubbe 2009a), but with some recovery in 2003–06 (Mammen & Stubbe 2009b), and in The Netherlands (-20% between 1980s and early 2000s, but stable since then; Bijlsma 2006). In contrast, stable figures have been recorded for France (Thiollay & Bretagnolle 2004), also reflected in stable autumn passage numbers at Organbidexka in the western Pyrenees (on average 10,738, 11,383 and 10,736 passage migrants per autumn in the 1980s, 1990s, and 2000s respectively; www.organbidexka.org). Similarly, autumn passage in northern Israel, reflecting passage migrants from NE-Europe and Russia, has been stable in the 1980s and 1990s, with respectively 334,000 and 323,000 migrants per autumn (Shirihai *et al.* 2000). Spring migration numbers at Eilat, in southern Israel, indicated a small decline of 12% for the same decades (but with fewer years covered; Shirihai *et al.* 2000), which lies within the margins of error for this type of monitoring (Bednarz *et al.* 1990).

In stark contrast to the rest of Europe, numbers in Serbia were supposed to have steeply increased since the mid-1980s (Puzović 2000), as in the Czech Republic (Reif *et al.* 2006), but both datasets are based on small sample sizes and inadequate census methods. Trends at migration hotspots around the Mediterranean showed

mixed fortunes, with a steep decline in numbers during spring passage at Gibraltar (-54% in post-1980s years as compared to pre-1980s, based on 7 years in each period; Bensusan *et al.* 2007), a decline during spring passage at Cap Bon, Tunisia (-56% between 1970s and early 1990s; de Jong *et al.* 2009), and an increase of passage migrants during spring migration in the central Mediterranean (Corso 2001, Agostini *et al.* 2007).

Outlook

In our deterministic models for reproduction and survival, irrespective of whether Honey Buzzards started breeding in their third year of life or one year later, the dominant eigenvalue λ was always smaller than 1. As the elasticity of adult survival is approximately seven times that of reproduction, a change in adult survival is likely to have the greatest impact on population dynamics. In all scenarios $\lambda = 1$ lies within the confidence intervals, and therefore the suggested population decline is not significant. However, as a consequence of variance in the survival estimates, the confidence intervals around λ are relatively wide, reducing the likelihood of detecting a decline. In contrast, our stochastic model, where reproduction depends on wasp abundance, shows a clear population decline, even more so when real data for wasp availability (in contrast to resampled wasp abundances from real data) were used. A decline would be consistent with the trend in northern and parts of western Europe. The decline in Europe has been particularly steep in Sweden and Finland, where reproductive output – as in The Netherlands – has declined (Kjellén 2006, Björklund *et al.* 2008, Södergren 2011). As a matter of fact, the well-studied Veluwe population has been surveyed again in 2008–10, using methods similar to the one employed in 1974–90 (data collected by W. van Manen, P. van Geneijgen & R.G. Bijlsma). The number of territorial pairs had dropped to 12–13, i.e. a decline of 20–40% as compared to the 1970s and 1980s, and reaching the lower density of Drenthe that prevailed throughout 1985–2010. The declines in northern and western Europe are cause for concern, as they seem to be the result of multiple bottlenecks in the life cycle of the species, notably poor adult survival but also poor reproduction. Clearly, reproductive rates, and the factors influencing mortality risks and survival, vary substantially across regions in Europe. The present set of ringing data is, however, too small to allow a geographically stratified analysis of survival, although such an approach is much needed to understand the complex changes happening as we speak.

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SAMENVATTING

De Europese populatie van de Wespendif *Pernis apivorus* staat te boek als stabiel, maar er zijn sterke aanwijzingen dat de soort in verschillende landen, zoals in Finland, Zweden, Duitsland en Nederland, achteruitgaat. In deze studie proberen we te achterhalen of de afname kan worden geassocieerd met veranderingen in overleving, reproductie of beide. Hiertoe maken we gebruik van terugmeldingen van vers dood gevonden geringde Wespendifven uit zeven landen (1957–2005). De jaarlijkse overleving was significant lager voor eerstejaars vogels (62,6%)

dan voor oudere vogels. De overleving was het hoogst voor tweede- en derdejaars (83,7–87,0%) en nog oudere (80,8–82,0%) Wespendifven. Voor de reproductiecijfers putten we uit langlopende studies op de Veluwe (vanaf 1974) en Drenthe (vanaf 1985). De Veluwse Wespendifven waren succesvoller (63% van de paren bracht één of meer jongen groot, gemiddeld 0,88 jong/paar) dan die in Drenthe (41%, 0,53 jong/paar). Al deze cijfers ingebracht in een tijdsonafhankelijk matrixmodel maken het mogelijk de jaarlijkse populatiegroei (= λ) te berekenen voor verschillende scenario's (lage, hoge en gemiddelde jongenaanwas). De resultaten vormen een sterke aanwijzing voor een populatieafname, al zijn de betrouwbaarheidsintervallen rond λ ruim. De populatiegroei blijkt vooral gevoelig te zijn voor de overleving van de adulte vogels: het effect van de overleving is bijvoorbeeld zeven keer sterker dan dat van reproductie. Dit betekent dat de populatieafname het snelst kan worden omgebogen door de overleving van volwassen vogels te verbeteren. Deze uitkomst is niet verrassend voor een langlevende vogel als de Wespendif. Het voedselaanbod (in casu: stand van sociale wespen) liet voor Nederland geen duidelijke langetermijnverandering zien, maar toch bleek deze stochastische variabele in combinatie met reproductiecijfers te leiden tot een populatieafname indien doorgerekend voor de lange termijn. Dat komt overeen met de werkelijkheid, zowel in Nederland als daarbuiten. De huidige reproductie van 0,53–0,88 jongen/paar haalt het niet bij de 1,16 jongen/paar die nodig zijn om een stabiele populatie te garanderen. Het lijkt er op dat Wespendifven meerdere problemen hebben: een te lage overleving van adulte vogels en een te geringe jongenaanwas. Helaas zijn er onvoldoende ringgegevens om te berekenen of de overleving is veranderd in de loop van de tijd, dan wel verschilt binnen Europa. Dat bemoeilijkt ook de beantwoording van vragen over het hoe en waarom van deze bottlenecks in het leven van Wespendifven. Daar komt nog bij dat onze kennis beperkt is met betrekking tot wat er in het overwinteringsgebied in subtropisch Afrika plaatsvindt, al kunnen we ons daar wel een voorstelling van maken (in het bijzonder: habitatvernietiging). Kortom, sombere vooruitzichten voor Wespendifven.

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APPENDIX 1.

Some matrix entries in Eqn. 1 are composite parameters (Eqn. A.1), F_4 equals the number of fledged pulli produced by an adult ($m/2$) female times p (the survival of ringed pulli from July to January next year) times the probability to survive the next 0.5 year from January to July ($b^{0.5}$). Here, b equals the survival of marked birds aged 0.5 to 1.5 years (census time for survival is in January). Survival is assumed constant within a year, meaning that survival per half year equals the square root of the survival during the full year. Also P_1 and P_2 are composite parameters, P_1 including survival of birds aged 0.5 to 1.5 years (b) from July to January and birds aged 1.5 to 2.5 (c) from January to July. And P_2 survival of birds aged 1.5 to 2.5 (c) from July to January and adult survival (d) from January to July. Written in full, matrix \mathbf{C} (Eqn. 1) looks like:

$$\mathbf{C} = \begin{bmatrix} 0 & 0 & 0 & \frac{m}{2} \cdot p \cdot b^{0.5} \\ b^{0.5} \cdot c^{0.5} & 0 & 0 & 0 \\ 0 & c^{0.5} \cdot d^{0.5} & 0 & 0 \\ 0 & 0 & d & d \end{bmatrix} \quad \text{Eqn. A.1.}$$

The dynamics of the population are governed by the dominant eigenvalue λ of matrix \mathbf{C} , if $\lambda > 1$ the population grows unlimited, if $\lambda = 1$ the population is stable and if $\lambda < 1$ the population decreases and ultimately goes extinct. After some time of transient dynamics the population can reach the stable stage distribution, where the proportion of birds in the four age classes is constant. The stable stage vector is equivalent to the right eigenvector of the matrix corresponding with λ .

Elasticity and variance in lambda

The composite matrix from Eqn. A.1 is used to perform an elasticity analysis for each of the parameters. We have calculated the elasticities with implicit differentiation of the characteristic equation. The characteristic equation is

$$f(\lambda) = \lambda^4 - d \cdot \lambda^3 - c \cdot b \cdot d \cdot \sqrt{d} \cdot \frac{m}{2} \cdot p = 0.$$

From these the partial derivatives with respect to b , c , d , p and m are derived to give their sensitivities, denoted as $s(\text{parameter})$: for instance, the sensitivity of λ with respect to b , $s(b) = \partial\lambda/\partial b$ is derived from

$$4\lambda^3 \frac{\partial\lambda}{\partial b} - 3d \cdot \lambda^2 \frac{\partial\lambda}{\partial b} - c \cdot d \cdot \sqrt{d} \cdot \frac{m}{2} \cdot p = 0.$$

Therewith the elasticity of b is calculated as

$$e(b) = b s(b) / \lambda.$$

All the other elasticities are derived in the same way (see Eqn A.2).

$$e(b) = e(c) = e(p) = \frac{b}{\lambda} \frac{c \cdot d \cdot \sqrt{d} \cdot \frac{m}{2} \cdot p}{4\lambda^3 - 4d\lambda^2}$$

$$e(m) = e(p) = e(b) = e(c) = \frac{0.5b \cdot c \cdot d \cdot \sqrt{d} \cdot m \cdot p}{\lambda(4\lambda^3 - 3d \cdot \lambda^2)} \quad \text{Eqn. A.2.}$$

$$e(d) = \frac{d}{\lambda} \frac{\lambda^3 + 0.75c \cdot b \cdot m \cdot p \cdot \sqrt{d}}{4\lambda^3 - 3d \cdot \lambda^2}$$

The contribution to the variance in λ of a parameter can be calculated as the product of the variance and the squared sensitivity of that parameter (variance(parameter) * [s(parameter)]²) (see Lande 1988). The total variance in λ is the sum of all these contributions.