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Appendix B from M. van de Pol et al., "Variation in Habitat Choice and Delayed Reproduction: Adaptive Queuing Strategies or Individual Quality Differences?"

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Estimation of Annual Values of Population and Life-History Parameters

Table B1

Annual counts of high- and low-quality territories (T_H and T_L), nonbreeder counts (T_N), total population size, and annual fecundity in high- and low-quality territories (F_H and F_L)

	Population numbers				Fecundity	
Year	T_H	T_L	T_N	Total	F_H	F_L
Period 1:						
1984	60[a]	148[a]	123	331[a]	.153	.048
1985	60[a]	151[a]	110	321[a]	.177	.017
1986	69[a]	149[a]	110	328[a]	.088	.025
1987	69[a]	126[a]	64	259[a]	.138	.084
1988	69[a]	139[a]	75	282[a]	.155	.059
1989	57[a]	136[a]	112	305[a]	.159	.051
1990	62[a]	136[a]	114	312[a]	.014	.009
1991	67[a]	144[a]	99	309[a]	.082	.000
1992	60	133	88	281	.085	.026
1993	65	124	53	243	.048	.037
1994	65	132	76	273	.188	.024
Period 2:						
1995	65	118	112	295	.020	.000
1996	56	76	64	196	.108	.038
1997	57	60	43	160	.255	.071
1998	60	63	58	181	.054	.000
1999	60	59	97	216	.000	.000
2000	59	61	59	179	.000	.000
2001	55	61	62	178	.000	.000
2002	53	54	106	213	.001[b]	.002[b]
2003	50	48	113	211	.015[b]	.005[b]
2004	48	45	117	210	.003[b]	.000[b]
Means:						
Period 1	64	138	93	295	.117	.035
Period 2	56	65	83	204	.045	.011
All years	61	106	87	248	.084	.024
EWD	26	56	37	119	.670[c]	.190[c]

Note: Estimates are based on areas A, B, C, D, and O (see Heg et al. 2000 for a map) and are derived from the annual census of population numbers at the start of each breeding season and intensive monitoring during the whole breeding season. Annual fecundity was defined as the annual number of offspring per territory that survived until adulthood. EWD refers to the values used by Ens et al. (1995) based on areas A and C from 1984 to 1992. The number of nonbreeders represents half the number of counted individuals because we are interested in tracking only females in our models (we assumed an adult sex ratio of 50 : 50).

[a] Territory numbers for areas B, D, and OBK from 1984 to 1991 were imputed because not all breeders were color ringed in those areas until 1992.

[b] Values of F_H and F_L in 2002–2004 could not be determined exactly because we do not know yet how many offspring survived until adulthood. Reported are the annual number of fledglings per territory times the probability that they survived until adulthood based on average survivorship from 1984 to 2001.

[c] Fecundity values in EWD were too high because they (1) did not account for the fact that not all offspring survive from fledging to adulthood and (2) used the total number of fledglings produced, while population models account for only female offspring.

Table B2

Annual state transition and mortality probabilities (%) estimated using multistate capture-recapture models and the number of color-ringed individuals on which estimates were based

	High-quality territory owner (H)					Low-quality territory owner (L)					Nonbreeder (N)				
	Ringed	m_{HH}	m_{HL}	m_{HN}	μ_H	Ringed	m_{LL}	m_{LH}	m_{LN}	μ_L	Ringed	m_{NN} (m^*_{NN})	m_{NL}	m_{NH}	μ_N (μ^*_N)
Period 1:															
1984–1985	37	83.4	2.8	11.1	2.7	103	88.3	2.2	4.3	5.3	4	100 (100)[a]	0[a]	0[a]	0 (0)[a]
1985–1986	39	89.5	.0	2.8	7.7	156	91.6	2.6	4.6	1.2	12	73.5 (76.5)	9.1	9.1	8.3 (5.3)
1986–1987	63	63.3	5.8	13.5	17.5	189	76.8	6.0	2.7	14.5	17	46.5 (59.0)	9.1	9.1	35.3 (22.8)
1987–1988	65	92.2	1.6	3.2	3.1	168	94.9	1.8	1.8	1.4	43	73.0 (75.5)	12.5	7.5	7.0 (4.5)
1988–1989	80	87.2	2.6	6.5	3.8	189	90.5	1.1	4.5	3.8	78	90.8 (92.3)	5.3	.0	3.8 (2.4)
1989–1990	73	94.5	1.4	2.8	1.4	179	86.7	2.9	7.6	2.7	134	83.8 (85.5)	8.7	2.4	5.2 (3.4)
1990–1991	93	93.5	2.2	3.3	1.1	185	90.2	3.9	5.0	1.0	165	82.9 (85.4)	9.7	.6	6.7 (4.3)
1991–1992	101	93.0	1.0	1.0	5.0	193	94.2	1.1	2.1	2.6	162	87.3 (88.8)	5.8	2.6	4.3 (2.8)
1992–1993	120	91.5	.9	1.8	5.8	226	88.6	1.9	4.7	4.9	167	77.9 (81.8)	6.8	4.1	11.3 (7.3)
1993–1994	124	95.1	.8	3.3	.8	226	91.0	.9	5.9	2.2	145	77.9 (80.7)	11.9	2.2	8.0 (5.2)
1994–1995	123	93.4	.8	3.4	2.4	234	89.9	1.4	3.7	5.1	133	68.4 (74.8)	9.0	4.5	18.1 (11.7)
Period 2:															
1995–1996	127	51.6	2.4	13.0	33.0	209	51.3	12.1	12.2	24.4	113	31.5 (44.0)	17.3	16.0	35.2 (22.7)
1996–1997	112	78.7	2.0	7.1	12.2	130	69.9	9.3	10.1	10.7	90	59.3 (68.1)	8.7	7.3	24.7 (15.9)
1997–1998	109	94.4	1.0	1.0	3.7	100	91.0	4.1	2.5	2.4	89	71.0 (74.1)	11.9	8.6	8.4 (5.4)
1998–1999	117	84.0	1.9	5.7	8.5	105	88.7	4.1	4.1	3.1	77	71.1 (75.4)	12.6	4.2	12.1 (7.8)
1999–2000	113	91.9	.0	6.4	1.7	90	87.0	2.5	5.0	5.5	92	61.5 (69.1)	17.2	.0	21.2 (13.7)
2000–2001	110	93.5	.0	2.0	4.4	111	85.0	2.4	6.8	5.8	115	81.4 (84.5)	7.8	2.3	8.4 (5.4)
2001–2002	110	89.8	2.0	1.2	7.0	109	78.4	5.6	12.2	3.7	109	84.3 (86.5)	5.5	4.1	6.1 (3.9)
2002–2003	105	84.3	1.0	4.1	10.6	96	79.4	3.6	12.4	4.5	85	68.1 (76.5)	5.0	3.3	23.6 (15.2)
2003–2004	100	90.0	3.1	2.0	4.9	82	76.1	3.4	6.7	13.8	64	63.1 (71.2)	10.1	4.0	22.8 (14.7)
Means:															
Period 1	83	88.8	1.8	4.8	4.6	186	89.3	2.3	4.3	4.1	96	76.2 (80.0)[a]	8.8[a]	4.2[a]	10.8 (7.0)[a]
Period 2	111	84.3	1.5	4.7	9.6	115	78.5	5.2	8.0	8.2	97	65.7 (72.2)	10.7	5.5	18.1 (11.6)
All years	96	86.7	1.7	4.7	6.9	154	84.5	3.6	6.0	5.9	97	71.5 (76.5)[a]	9.6[a]	4.8[a]	14.1 (9.1)[a]
EWD	46	90.2	1.9	3.1	4.9	82	88.4	2.6	3.9	5.1	47	72.4	13.8	5.4	8.4

Note: Column headings indicate status in year *t*. Estimates were derived from intensive observations in areas A, B, C, D, and O and nearby roosts (see Heg et al. 2000 for a map). Parameters were estimated using one statistical model that simultaneously estimates transitions between states, mortality, and resighting probabilities per state (fig. 3). This model makes corrections for the fact that we have overlooked some individuals in certain years. The resighting probability of breeders was >0.99 in all years; annual resighting probabilities of nonbreeders varied between 0.6 and 1. Estimates did not differ between the sexes and were therefore combined. All model parameters were allowed to vary between years (fully time-dependent model; for more details on the analysis, see van de Pol et al. 2006). We studied a nonclosed population; in particular, nonbreeders were not completely site faithful. By comparing patterns of local observations with dead recoveries from a larger area (northwestern Europe), we estimated that annual emigration (E_N) of nonbreeders was on average 5%, with emigration most pronounced in years with high mortality (M. van de Pol, unpublished data). Furthermore, annual immigration of nonbreeders was difficult to quantify; therefore, we assumed that immigration equaled emigration. Because emigration of nonbreeders out of the study area results in an overestimation of (local) nonbreeder mortality (μ_N), we corrected μ_N in a specific year t downward proportionally by $\mu^*_N(t) = (1 - E_N/\bar{\mu}_N)\mu_N(t)$. Consequently, m_{NN} was also adjusted by $m^*_{NN}(t) = 1 - m_{NH}(t) - m_{NL}(t) - \mu^*_N(t)$. Corrected estimates (in parentheses) were used in all calculations. EWD refers to values used by Ens et al. (1995) based on areas A and C from 1984 to 1992 for breeders and from 1987 to 1992 for nonbreeders.

[a] Nonbreeder parameters in 1984–1985 were not included in means because they were based on few individuals.

Table B3

Variance-covariance matrix of the model parameters used in the calculation of the confidence intervals around point estimates of model predictions

	m_{HH}	m_{HL}	m_{HN}	m_{LL}	m_{LH}	m_{LN}	μ_N	F_H	F_L	T_H	T_L
m_{HH}	.0083										
m_{HL}	−.0013	.0002									
m_{HN}	−.0032	.0006	.0016								
m_{LL}	.0036	−.0006	−.0014	.0023							
m_{LH}	−.0010	.0002	.0004	−.0006	.0002						
m_{LN}	.0005	−.0001	−.0001	−.0001	.0000	.0003					
μ_N	−.0063	.0009	.0018	−.0035	.0010	−.0005	.0093				
F_H	.0000	−.0002	.0002	.0002	−.0002	.0000	−.0005	.0032			
F_L	.0001	.0000	.0002	.0001	−.0001	.0000	−.0005	.0006	.0006		
T_H	−.1363	.0274	.0415	.0025	−.0025	−.0524	.1511	−.0297	.0197	18.7	
T_L	−.4927	.0535	.1822	−.1747	.0638	−.0255	.1409	.1219	−.0885	−5.6	83.6

Note: Variances (underscored diagonal elements) are based on between-year variation in life-history parameters or number of breeders. Covariances (below-diagonal elements) are based on between-year covariations between all combinations of number of breeders and life-history parameters. Variances and covariances are calculated using the annual values in period 1 (1984–1994; $n = 11$), which are given in tables B1 and B2, along with the parameter definitions. The variance-covariance matrix was used to generate a multivariate-normal distribution of all parameters, from which 1,000 random samples were taken. These 1,000 random samples were used as input parameters of the queue models and were used to generate confidence intervals and standard errors around model predictions to assess their reliability.