Ecography

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Supplementary material

Appendix 1. Historical records of the range expansion of European starling in South Africa.

Table A1. Start and end points of the spread of European starlings in South Africa. The start point is the range edge in year T_1 and the end point is the range edge in year T_2; DIS_1 is the distance (km) between the start and end points; DIS_2 is the distance between the place of introduction (Cape Town) and the end point. Data are from Winterbottom and Liversidge (1954), Liversidge (1962), Harrison et al. (1997) and Hockey et al. (2005).

Start point	End point	T_1	T_2	Duration	DIS_1	DIS_2
Cape Town	Wynberg	1897	1903	6	13	13
Cape Town	Robin Island	1897	1907	10	7	7
Wynberg	Stellenbosch	1903	1908	5	18	50
Stellenbosch	Somerset West	1908	1910	2	18	45
Somerset West	Elgin	1910	1922	12	27	70
Elgin	Hermanus	1922	1938	16	40	120
Elgin	Villiersdorp	1922	1943	11	35	106
Elgin	Riviersonderend	1922	1943	21	94	162
Elgin	Riversdale	1922	1930	7	232	299
Riversonderend	Agulhas	1943	1944	1	71	220
Riversdale	Port Beaufort	1930	1942	12	60	306
Riversdale	Heidelberg	1930	1942	12	30	271
Riversdale	Great Brakriver	1930	1940	10	106	406
Heidelberg	Tradouws Pass	1942	1947	5	36	261
Tradouws Pass	Ladismith	1947	1953	6	89	323
Great Brakriver	Mossey Bay	1940	1953	13	19	388
Great Brakriver	George	1940	1948	8	38	430

Great Brakriver	Knysna	1940	1944	4	100	490
Knysna	Barrington	1944	1953	9	20	475
Knysna	Plettenberg Bay	1944	1951	9	37	520
Cape Town	Darling	1899	1908	9	65	83
Darling	Tulbagh	1908	1920	12	80	120
Tulbagh	Ceres	1920	1928	8	26	125
Ceres	Hoop en Vitkoens	1928	1953	27	42	167
Tulbagh	Worcester	1920	1922	2	58	109
Worcester	Kogmanskloof	1922	1940	18	69	179
Kogmanskloof	Robertson	1940	1945	5	19	158
Darling	Velddrif	1908	1926	16	88	144
Velddrif	Redlinghuis	1926	1928	2	78	174
Redlinghuis	Citrusdal	1928	1943	15	60	175
Citrusdal	Clanwilliam	1943	1950	7	53	229
Clanwilliam	Kleinvlei	1950	1952	2	52	282
Plettenberg Bay	Stormsriver	1951	1955	4	46	579
Stormsriver	Humansdorp	1955	1960	5	86	667
Plettenberg Bay	Port Elizabeth	1951	1954	3	216	748
Port Elizabeth	Uitenhage	1954	1956	2	25	737
Uitenhage	Addo	1956	1961	5	30	799
Uitenhage	Grahamstown	1956	1958	3	154	873
Grahamstown	King William's Town	1958	1961	3	120	993
George	Beaufort West	1948	1967	19	244	461
Grahamstown	Cradock	1958	1970	12	184	802
King Willam's Town	East London	1961	1966	5	62	1045
East London	Kei Mouth	1966	1971	5	100	1126

East London	Umtata	1966	1981	15	235	1229
Kleinvlei	Oranjemund	1952	1970	18	450	802
Umtata	Maclear	1981	1982	1	100	1129

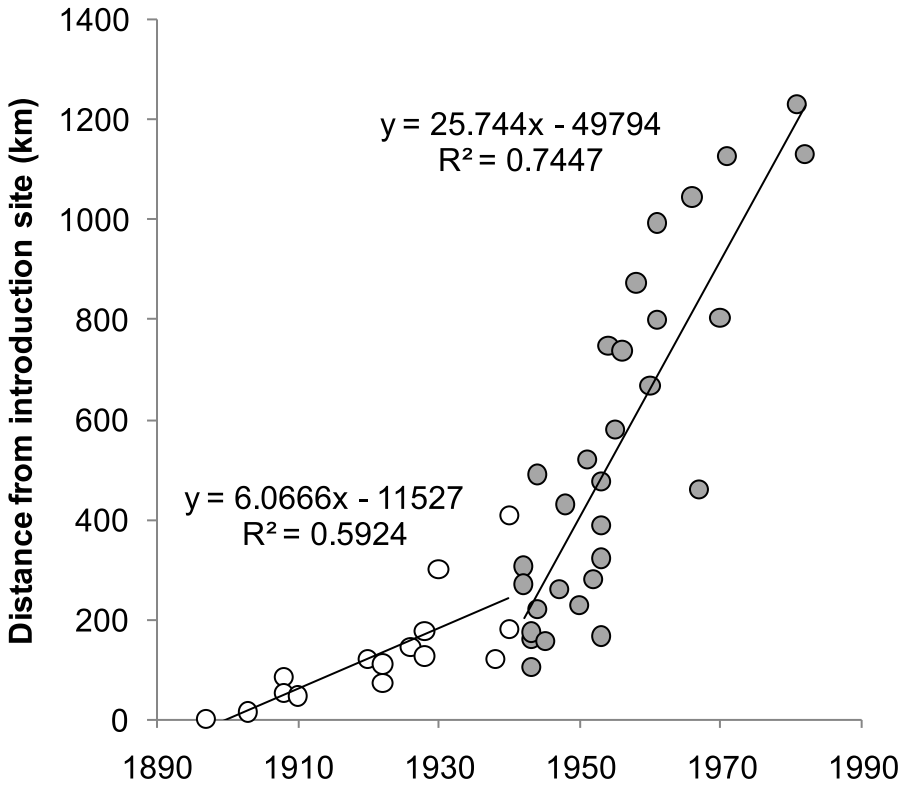

Figure A1. Temporal patterns in European starling's range expansion in South Africa. Data represent the relationship between year of observation and distance from Cape Town of range expansion records using data from Winterbottom and Liversidge (1954), Liversidge (1962), Harrison et al. (1997) and Hockey et al. (2005). Open circles indicate records pre-1940; grey circles indicate records post-1940.

Appendix 2. Calculation of the population growth rate of European starlings.

Okubo's Method

The intrinsic population growth rate r can be estimated according to Okubo (1986) as $r = \ln(N_t/N_0)/t$ (Vandenbosch et al. 1992). This method requires a reliable estimation of the number of individuals in the population (N_t) and also assumes that the population grows exponentially. In the United States, the total number of individuals estimated for the European starling is 71 million in 1939 (Wing 1943, Okubo 1986) and 200 million three decades ago (Feare 1984, Koenig 2003), and thus the estimate of the intrinsic growth rate is $r = 0.224$ yr^{-1} (Okubo 1986, Vandenbosch et al. 1992).

Hui et al. (2009) recommend a Bayesian estimation model and estimate a total of 3.154×10^6 European starlings in South Africa in 1992 according to the southern Africa bird atlas (Harrison et al. 1997). Using these data the intrinsic population growth rate of European starlings in South Africa can be calculated as $r = \ln(N_{1992}/N_{1897})/(1992\text{-}1897) = 0.1271$ yr^{-1}. Using another power law form of the scaling pattern of occupancy, the South African European starling population has been estimated to be around 1.137×10^6 individuals (Hui et al. 2009), from which the intrinsic population growth rate can also be estimated as $r = 0.1164$ yr^{-1}. These two estimates provide a baseline estimate of the intrinsic growth rate of the South African population (0.11~0.13 yr^{-1}).

To calculate the intrinsic growth rate of starlings in the native region of Britain, we used an extended version of Okubo's method. The above method assumes an exponentially growing population. In contrast, a more widely used model for population dynamics is the logistic equation: $dN/dt = rN(1\text{-}N)/K$, where K stands for the carrying capacity. Annual estimates of the starling's abundance index from 1966 to 2008 were used in a nonlinear regression of the solution to the logistic equation with 5000 maximum iterations and the Levenberg-Marquardt method (Mathematica 8.0; Wolfram Research Inc.), which gave an estimate of the intrinsic population growth rate $r = 0.0335\ \text{yr}^{-1}$ in Britain (S.E. = 0.0014, t = 23.4, $P < 0.01$, Adusted $R^2 = 0.98$). We use this value of intrinsic growth rate for transforming diffusion rates (D) calculated from the ringing records to the rate of spread (v) in Britain.

Caswell's Method

When an estimate of population size is not available, Caswell's (2001) matrix population model can be applied to estimate the population growth rate (Clark and Martin, 2007). Specifically, Clark and Martin (2007) have developed the following three-stage matrix population model:

$$\begin{bmatrix} N_J \\ N_1 \\ N_+ \end{bmatrix}_{t+1} = \begin{bmatrix} \varphi_J A_1 \frac{C_1}{2} S_1 & \varphi_1 A_+ \frac{C_+}{2} S_+ & \varphi_+ A_+ \frac{C_+}{2} S_+ \\ \varphi_J & 0 & 0 \\ 0 & \varphi_1 & \varphi_+ \end{bmatrix} \times \begin{bmatrix} N_J \\ N_1 \\ N_+ \end{bmatrix}_t ,$$

where the subscript J, 1 and + indicate the juveniles, adults that are one-year old and adults that are more than two years old; φ, A, C and S represent the stage-specific annual survival rate, number of nesting attempts, clutch size and nest success. The asymptotic finite rate of population change can be calculated by the dominant eigenvalue (λ) of the matrix (Caswell 2001, Clark and Martin 2007), which yields:

$$\lambda = \frac{1}{2}\left(A_1 C_1 S_1 \varphi_J R_1 + \varphi_+ + \sqrt{A_1^2 C_1^2 S_1^2 \varphi_J^2 R_1^2 + 4A_+ C_+ S_+ R_+ \varphi_J \varphi_1 - 2A_1 C_1 S_1 R_1 \varphi_J \varphi_+ + \varphi_+^2} \right)$$

The contribution of each life-history parameter (or process) can be estimated as the partial derivative of the eigenvalue (sensitivity and elasticity; Caswell 2001, Clark and Martin 2007).

Parameterization

The survival rate of the European starling has been reported for some populations (Deevey 1947, Stewart 1978, Flux and Flux 1981), from which we reconstructed the survival rate of starlings in different countries (see Fig. A2). The survival rates followed a negative exponential form, $\Phi_t = \exp(-\alpha t)$, and therefore the probability-transition (annual) survival rates, φ_1 and φ_+, were constant (i.e. stage insensitive; Clark and Martin, 2007), $\varphi = \Phi_{t+1} / \Phi_t = \exp(-\alpha)$, where the coefficient α ranged from 1.099 (Switzerland) to 0.436 (New Zealand). The annual survival rate was thus estimated as 0.333 in Switzerland, 0.455 in UK, 0.523 in US and 0.647 in New Zealand. We took φ = 0.647 as the annual survival rate of adult birds in South Africa (Cooper and Underhill 1991). The annual survival rate for juveniles was set as 50% of the adult rate, φ_J = 0.324 (Ricklefs 1973).

Although second breeding attempts (i.e. double brooding) are common in North America and Europe (A = 1.61 in the US; Feare 1984, Clark and Martin 2007), they are rare in South Africa, where approximately 4% of mature adults raise two broods (Cooper and Underhill 1991). We thus assumed that A_+ = 1.04 and, assuming that the probability that first year adults raised two broods is 0.02 (i.e. half the probability of mature adults), A_1 = 1.02.

The clutch size in South Africa is C_+ = 4.40 (Hockey et al. 2005), which is much smaller than the clutch sizes in Europe and North America (e.g. C = 5.36 in US; Martin 1995), suggesting an evolutionary (or physiological) mechanism behind the smaller clutch size in warmer areas (Martin et al. 2000). The clutch size of one-year adults was estimated according to $C_1 = 1.01C_+ - 0.515$ (Clark and Martin, 2007), and thus we assumed that C_1 = 3.93 in South Africa.

Nest success is higher in South Africa (S_+ = 0.74; Cooper and Underhill, 1991) than in the USA (S = 0.65; Martin 1995). The nest success for the one-year adult was assumed to be slightly less, $S_1 = 0.85 \times S_+$. The contribution of these life history parameters to the population growth can be quantified by the matrix elasticity (Caswell 2001).

According to the eigenvalue of the matrix population model, we have λ = 1.122 and thus r = 0.115 yr^{-1} in South Africa, which compares to r = 0.224 yr^{-1} in USA (Okubo 1986). Two parameters in Caswell's model contributed to the lower intrinsic growth rate in South Africa than in the USA, i.e. fewer second broods and a smaller clutch size (Cooper and

Underhill 1991). The estimate from Caswell's method for the South African population r = 0.115 yr^{-1} is very similar to that obtained using Okub's method (0.11~0.13 yr^{-1}). We use the former estimate in this study as our focus is on dispersal strategy and we assume that fecundity is physiologically determined and stable during the invasion process.

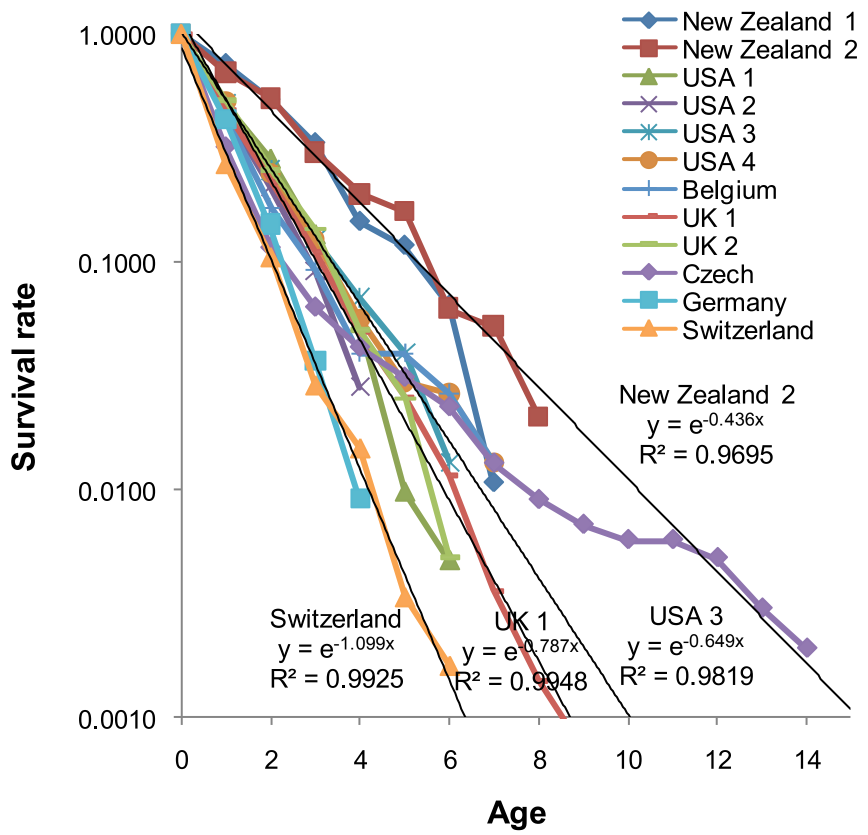

Figure A2. The survival rate of European starling in different countries. Data from life tables published in Deevey (1947), Stewart (1978) and Flux and Flux (1981).

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