

## Stabilising selection on wing length in reed warblers *Acrocephalus scirpaceus*

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The size of an animal is of utmost importance for its overall success and each species is thought to have its own optimal size. If this is true, size traits ought to be under stabilising selection unless the animal is living in a highly unstable environment. Wing length is a standard measurement of the size of birds, but up to date there have been few indications of stabilising selection on wing length. In this study we analyse recovery data for reed warblers *Acrocephalus scirpaceus* ( $n = 771$ ) ringed as juveniles in Sweden from 1981 until 2001. The data showed a significant relationship between juvenile wing length and survival time, with median juvenile wing lengths (66–67 mm) being the most favourable. The estimated stabilising selection differential ( $C = -0.094$ ) supports that wing length of the reed warblers in our study is under stabilising selection. The reed warbler is a long-distance migratory species and we suggest that opposing selection pressures may act on wing length during different life history stages, and that this might explain the rather broad peak of favourable wing lengths found.

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An animal's size is determined by several factors such as the parents' genes and the availability of energy during growth (cf. Alatalo and Lundberg 1986, Thessing 1999). Body size is of utmost importance for the overall success of an animal and Brown et al. (1993) suggested the existence of an optimal body size due to energetic constraints for birds, mammals and fish, respectively. This optimal size, though, would only be optimal in a situation without competition from similar species and, since this is very seldom the case, each species may be expected to have its own optimal size in relation to other species. This optimal size would then be the best trade-off between opposing selection pressures working on different parts of the body, or during different periods in

the life history of an organism (Roff 1981, Brown et al. 1993). Size measures are highly heritable (cf. Boag and Grant 1978, Price and Grant 1984, Alatalo and Lundberg 1986, Thessing 1999, Grant and Grant 2002) and have been shown to affect survival (cf. Bumpus 1899, Gibbs and Grant 1987, Brown and Bomberger Brown 1998). Thus, estimating survival of individuals differing in size measurements might give an estimate of the optimal size of a certain species.

The reed warbler *Acrocephalus scirpaceus* is a small passerine bird and reed warblers belonging to the Swedish population are long-distance migrants, spending the winter in tropical West Africa (Stolt 1999). Size in birds is traditionally estimated from wing length, a

standard measurement collected during bird ringing activities (cf. Cornwallis and Smith 1960, Spencer 1972, Svensson 1992, Bairlein 1994). Whether wing length is a good measurement of body size or only of the flight apparatus in reed warblers is unclear but Wyllie and Newton (1994) showed that wing length was the single best measure, of six measures investigated, of overall body size in sparrowhawks *Accipiter nisus*. Wing length has also been shown to correlate with tarsus length (Craig and Villet 1998), and heritability of wing length has been shown to be high in, for example, Darwin's medium ground finches *Geospiza fortis* (Boag and Grant 1978, Price and Grant 1984). Up to date, there have been few indications of stabilising selection on wing length although this is not unknown for other size traits in birds (cf. Alatalo and Lundberg 1986, Monaghan and Metcalfe 1986, Lindén et al. 1992, Björklund and Senar 2001). The aim of the present study was to investigate the optimal wing length of reed warblers, and to establish whether stabilising selection pressure on wing length occurs.

## Material and methods

The study was based on recovery data of reed warblers ringed in Sweden from 1981 until 2001. The birds were ringed during the ordinary ringing activity at bird observatories, by ringing groups and private bird ringers. Birds were trapped from the end of June until early October when the last individuals are about to depart from Sweden on autumn migration (Hall 1996, Nielsen and Rhönnsstad 1996). When trapped, all birds were individually marked, aged and wing length was measured as the maximum length of the flattened and straightened wing (Svensson 1992). Reed warblers attain a fully grown wing shortly (within days) after they have left the nest, and only birds with the growth of wing feathers completed (c.f. Ginn and Melville 1983, Bensch and Lindström 1992) were included. In the statistical analysis the juvenile wing length from the ringing occasion is the wing length used.

All recoveries of reed warblers ringed as juveniles during their first autumn that had data on wing length from the ringing occasion, were included ( $n = 771$ ). This includes all kinds of recoveries such as re-traps by ringers, birds killed by hunters and other individuals found recently dead, but the larger part of the available recoveries apply to re-traps of birds that were still alive. Both recoveries in Sweden and abroad were included. The majority of the birds (82.3%) were recovered more than 100 km from the ringing site, 13.2% were recovered 10–100 km away and only 1.6% within 10 km from the ringing site ( $n = 752$ , distance data were missing for 19 birds). If a bird was recovered more than once only the latest recovery was considered.

The elapsed time between ringing and recovery provides a measure of survival since it indicates a minimum life span of the bird. This minimum life span (from here on called "survival") was estimated in days and we transformed the date of ringing to an assumed date of birth appointed to be the 1st of July for all individuals except one that was ringed on 20 June. If the bird was alive when recovered the actual life span may be much longer. The shortest interval between ringing and recovery was 29 days and the oldest bird in our material was controlled alive after 3700 days, i.e. over 10 years old.

The recovery frequency of reed warblers is about 0.7% (of 316211 reed warblers ringed in Sweden between 1911–1999 a total of 2144 were recovered; Fransson et al. 2001), i.e. the 771 recoveries analysed in this study equals 113712 ringed reed warblers. Thus, it was not possible to use traditional mark-recapture statistical methods for analysing the data. A flexible technique to investigate selection is the cubic spline analysis (cf. Schluter 1988, Lindén et al. 1992). This is a non-parametric method especially suitable to analyse non-normal distribution patterns (Schluter 1988). We performed a spline analysis and, as suggested by Schluter (1988), followed up on this by a parametric model analysis. The relative survival ( $w$ ) of each wing length category (Table 1) was calculated in relation to the mean survival time of all recovered birds. A stabilising selection differential, defined as  $C = \text{Cov}(w, z^2)$ , was estimated by the methods described by Lande and Arnold (1983;  $z$  = the standardised normal distribution of the juvenile wing lengths). To investigate if mean juvenile wing length changed with increasing age the birds were divided into three age categories: I =  $\leq 365$  days, II = 366–730 days, III =  $\geq 731$  days.

All statistical analyses were performed with the statistical program JMP (SAS Inst. Inc. 1989). Measurements are presented  $\pm$  standard deviation (SD) if nothing else is indicated. The data was provided to us by the Bird Ringing Centre, Swedish Museum of Natural History. Biometrical data of birds ringed at Falsterbo, South Sweden, was provided by Falsterbo Bird Observatory.

Table 1. Average age at recovery (in days) and relative survival per juvenile wing length category,  $n$  = sample size.

Wing length	n	Average age	Relative survival
$\leq 63$ mm	24	252.9	0.725
64 mm	72	256.1	0.734
65 mm	130	297.3	0.853
66 mm	183	346.5	0.994
67 mm	167	348.7	1
68 mm	106	270.0	0.774
69 mm	66	237.3	0.681
$\geq 70$ mm	23	199.3	0.572

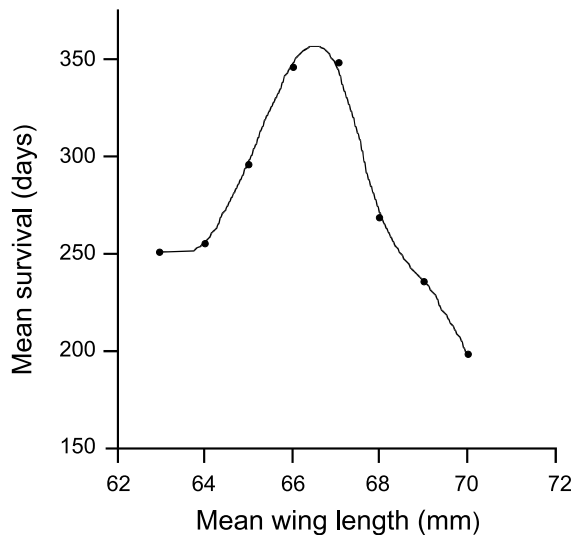


Fig. 1. Spline analysis of mean survival time per mean wing length ( $r^2 = 0.999$ , sum of squared errors = 0.083,  $\lambda = 0.001$ ).

## Results

The wing length of recovered juvenile birds varied between 61 and 71 mm ( $n = 771$ ) with a mean wing length of  $66.4 \pm 1.7$  mm. Mean survival time was  $303.1 \pm 15.3$  (SE) days with a range between 29 and 3700 days. Neither juvenile wing length, nor survival time differed between birds recovered alive and birds found dead (juvenile wing length of birds found alive:  $66.4 \pm 1.7$  mm,  $n = 711$ , found dead:  $66.6 \pm 1.6$  mm,  $n = 60$ ,  $t = 0.91$ ,  $P = 0.37$ ; survival of birds found alive:  $298.3 \pm 427.8$  d,  $n = 711$ , found dead:  $356.5 \pm 377.5$  d,  $n = 60$ ,  $t = 1.07$ ,  $P = 0.28$ ), so both categories were pooled in all analyses.

A spline analysis of the present material showed that the data was approximately normally distributed (Fig. 1). The relationship between juvenile wing length and survival was analysed using a non-linear regression analysis. The regression equation for the normally distributed curve was:

$$Y = 194.0 + 0.390 X \text{ where}$$

$$X = 394.1 \times e^{-\left(\frac{(\text{Wing length} - 66.4)^2}{2 \times 2.75}\right)}$$

In this equation  $Y = \text{age at recovery}$ , 66.4 is the mean juvenile wing length and 2.75 the variance of the juvenile wing lengths of the recovered birds.

The equation for the normally distributed curve describes the relationship between age at recovery and juvenile wing length well (Lack of fit:  $P = 0.999$ ,  $n = 771$ ). One bird was over ten years old and an extreme outlier compared to the rest of the recovered birds, but the exclusion of this bird did not change the result (Lack of fit:  $P = 0.998$ ,  $n = 770$ , Equation:  $Y = 200.2 + 0.796 X$ ,

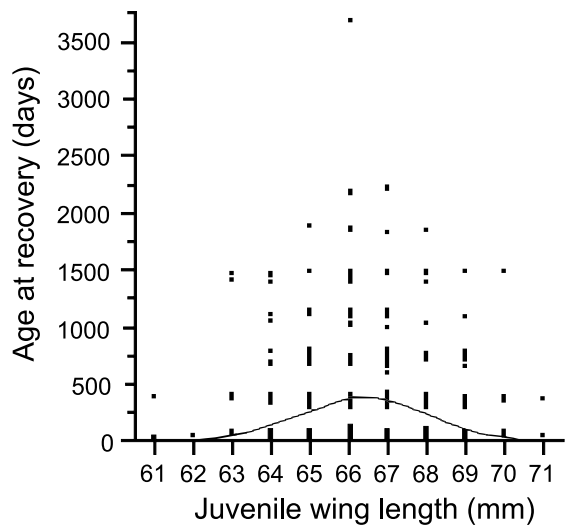


Fig. 2. The relationship between juvenile wing length (mm) and age at recovery (days) in recovered reed warblers *Acrocephalus scirpaceus* ( $n = 771$ ). The curve is based on a non-linear regression analysis.

$P_b = 0.007$ ). The same estimation by years of survival instead of days corroborated the result (Lack of fit:  $P = 0.995$ ,  $n = 771$ , Equation:  $Y = 1.3 + 0.002 X$ ,  $P_b = 0.005$ ). The curve shows that relative survival was highest for birds with an average juvenile wing length (Fig. 2). The relative survival was thus highest for a juvenile wing length of 67 mm, almost as high for 66 mm (0.994) and declined towards more extreme wing lengths (Table 1).

Mean juvenile wing length did not differ between age categories ( $\bar{X}_I = 66.5 \pm 1.7$  d,  $\bar{X}_{II} = 66.2 \pm 1.6$  d,  $\bar{X}_{III} = 66.4 \pm 1.4$  d, Welch-test:  $F = 1.245$ ,  $P = 0.275$ ), but the variances decreased with age ( $s_I^2 = 2.91$ ,  $n = 527$ ;  $s_{II}^2 = 2.64$ ,  $n = 145$ ;  $s_{III}^2 = 2.05$ ,  $n = 99$ ; Levenes test:  $P = 0.034$ ).

The stable average wing lengths, in combination with decreasing variances with increasing age, indicate a stabilising selection pressure on wing length (Endler 1986, Brodie et al. 1995). To investigate this further we estimated a stabilising selection differential ( $C$ ). The stabilising selection differential estimates the difference between variances (of the character in focus) before and after selection, and a negative value of  $C$  indicates stabilising selection (Schluter and Smith 1986). In this case  $C$  was significantly negative both with the extreme outlier included ( $C = -0.094$ ,  $P = 0.013$ ) and excluded ( $C = -0.087$ ,  $P = 0.017$ ). An overall stabilising selection might be the consequence of both stabilising and disruptive selection pressures if the stabilising selection pressure is more common, or stronger, over time than disruptive selection pressures. To investigate the occurrence of stabilising selection over time we estimated  $C$  for all years with more than 45 ringed birds. In eight of eleven years  $C$  indicated stabilising selection, although

Table 2. The stabilising selection differentials (C) with P-values for all years with more than 45 ringed birds. Age = average age (in days) at recovery for birds ringed during the same calendar year (the lower values for 1998–2000 reflects the shorter time these birds have had to be recovered), Wing = mean wing length (in mm) for birds ringed the same calendar year, n = sample size.

Year	Age	Wing	C	P (for C)	n
1990	287.5	66.5	-0.28	0.04	51
1991	414.3	67.0	-0.06	0.81	46
1992	257.6	66.3	-0.11	0.14	91
1993	286.1	66.2	-0.19	0.19	74
1994	386.1	66.5	-0.23	0.37	54
1995	398.1	66.6	+0.01	0.88	65
1996	373.4	66.5	-0.06	0.77	54
1997	309.6	66.3	-0.01	0.94	87
1998	190.3	66.2	+0.08	0.42	58
1999	197.9	66.5	-0.08	0.15	72
2000	91.2	66.4	+0.04	0.13	64

Table 3. The directional selection differentials (S) with P-values for all years with more than 45 ringed birds, n = sample size.

Year	S	P (for S)	n
1990	-0.07	0.71	51
1991	+0.12	0.68	46
1992	+0.05	0.72	91
1993	+0.06	0.72	74
1994	-0.16	0.56	54
1995	-0.05	0.77	65
1996	-0.07	0.75	54
1997	+0.37	0.01	87
1998	-0.02	0.85	58
1999	+0.04	0.63	72
2000	-0.03	0.32	64

only significantly so in one year (Table 2). Neither the wing length ( $F = 1.12$ ,  $P = 0.34$ ), nor the survival time for the period 1990–1997 ( $F = 1.23$ ,  $P = 0.28$ , the years 1998–2000 were excluded from this analysis due to the shorter time these birds had had to be recovered) did differ between these years.

There was no evidence of directional selection on juvenile wing length in the complete data set ( $S = +0.026$ ,  $P = 0.80$ ,  $n = 771$ ), and a significant directional selection was observed only in one year out of eleven (Table 3). No direction of the selection was indicated more than the other (positive sign 5 years, negative sign 6 years).

## Discussion

This study indicates that stabilising selection pressures act on wing length in reed warblers and that the optimal wing length of juvenile reed warblers is 66–67 mm. Birds with this average juvenile wing length had a significantly better chance for survival than individuals with shorter or longer juvenile wings (Fig. 2, Table 1). If the observed difference in survival is related to wing length alone, or a

combination of correlated traits, for example overall body size, is not possible to judge from these results (cf. Lande and Arnold 1983). Since flight performance is of utmost importance for birds, and especially so in migratory species, we assume that wing length is a trait that affects survival, and hence, is under selection. The variation in relative survival between individuals with different juvenile wing lengths is not very large and this may be explained by different selection pressures acting on different parts of the body, and by the fluctuation of environmental influences over time (Price et al. 1984, Gibbs and Grant 1987, Grant and Grant 1989, Alatalo et al. 1990, Peach et al. 1991). For example, Grant and Grant (2002) showed that natural selection favoured different size traits in Darwin's medium ground finches and cactus finches *Geospiza scandens* during periods of differing environmental conditions. The influence of environmental factors on tarsus length in the collared flycatcher *Ficedula hypoleuca* has been shown to be as large as the genetic influence (Kruuk et al. 2001). The relative influence of the genetic and environmental components on juvenile wing length is not known.

Selection pressures vary in strength and direction in different phases of an animal's life and may differ for different parts of the population (cf. Price and Grant 1984, Gibbs and Grant 1987, Schluter et al. 1991, Björklund and Senar 2001, Pérez-Tris and Telleria 2001). It is reasonable to believe that migrating birds, like the reed warbler, do encounter different selection pressures during migratory and non-migratory periods. The annual migration includes about 10 000 km and covers in total about five months. The breeding habitat is dense reed beds, which also is a habitat preferred during winter. Longer and pointed wings are more efficient during long-distance migration, while shorter and rounder wings enhance manoeuvrability (cf. Alatalo et al. 1984, Nilsson 1992, Norman 1997), which is of utmost importance in dense vegetation. Thus, a migratory life can result in opposing selection pressures during migratory and non-migratory periods, and this might explain why we see a rather broad peak of favourable wing lengths.

The range of profitable wing lengths may also be wider if the two sexes have different wing length optima (Monaghan and Metcalfe 1986, Nilsson 1992, Pérez-Tris and Telleria 2001). We have found no indications that this should be the case in the reed warbler, but since sexing is difficult in this species (Svensson 1992), this source of variation should not be ignored. Forty-seven birds in this study had been sexed (on shape of the cloacal region, or the occurrence or lack of an incubation patch; Svensson 1992) when re-trapped, 28 females and 19 males. The wing lengths among these birds did not differ between the sexes (Females: mean wing length = 66.1 mm, males: mean wing length = 66.5 mm,  $t = 0.99$ ,  $P = 0.33$ ).

Four factors, although not independent, indicated stabilising selection on wing length in the present data, i.e. (1) the spline analysis (Fig. 1), (2) the exceptional good fit of the recovery data to a normally distributed curve (Lack of fit:  $P = 0.999$ ; Fig. 2), (3) the decreasing variance with age ( $P = 0.034$ ), and (4) the stabilising selection differential ( $C = -0.094$ ,  $P = 0.013$ ). The stabilising selection differential has been criticised for sometimes indicating stabilising selection in the absence of an intermediate fitness optimum (cf. Lindén et al. 1992), but a brief look at the distribution of the recovered birds (Figs. 1 and 2) indicates that this was not the case in the present study.

The statistical analyses of the data supported a stabilising selection pressure on wing length in the reed warblers. This has been difficult to show earlier (cf. Price and Grant 1984, Schluter and Smith 1986, Nilsson 1992, Barbraud 2000), although stabilising selection is well known from other size traits (cf. Alatalo and Lundberg 1986, Monaghan and Metcalfe 1986, Schluter and Smith 1986, Lindén et al. 1992, Barbraud 2000, Björklund and Senar 2001, Kruuk et al. 2001). The evidence available so far is Bumpus' (1899) descriptive study on house sparrows *Passer domesticus* during a severe snow storm, and Craig and Villet's (1998) indirect evidence by estimating that inter-population variation was lower than expected by genetic drift alone in the genus *Euplectes*. Evidence of directional (Gibbs and Grant 1987, Brown and Bomberger Brown 1998, Björklund and Senar 2001) disruptive (Wiggins 1991, Björklund and Senar 2001), and oscillating (Gibbs and Grant 1987) selection on wing length have, however, been found. The lower repeatability in measurement of wing length compared to other size estimations (Price and Grant 1984, Hasselquist et al. 1995) require that selection must be stronger, or sample sizes larger, than for other size traits for any selection to be detected. Selection via survival might also be hard to detect since it tends to be weaker than selection via fecundity or mating success (Kingsolver et al. 2001), at least when measured over longer time periods (Hoekstra et al. 2001).

The time scale is an important factor when interpreting results from selection studies and it may influence the conclusions drawn (cf. Hoekstra et al. 2001, Grant and Grant 2002). Kingsolver et al. (2001) pointed out that the magnitude of directional selection was significantly greater for selection episodes measured over shorter than longer time intervals, and Hoekstra et al. (2001) showed that viability selection, similarly, was stronger when measured over short compared to longer time periods. In the present study there was statistically significant support for stabilising selection only in one of the eleven years with at least 45 ringed birds (Table 2). However, in eight of the remaining ten years the stabilising selection differential was negative, and the wing length remained fairly stable during these years. There was support for

directional selection in only one year (Table 3), and the stabilising selection found may thus, not be the result of oscillating selection. It is, however, possible that the result found in this study, covering more than 20 years, has to be seen as a long-term selective regime shaping the wing length values.

Our study indicates that the optimal size for juvenile reed warblers corresponds to a wing length of 67 mm. In passerine birds, wing length normally increases by about one mm during the first moult, when the juvenile wing feathers are exchanged for the first adult set (cf. Alatalo et al. 1984, Nilsson 1992, Norman 1997, Hall and Fransson 2000, Hall 2002). In this case, the adult wing length would then be 68 mm. Whether the two age categories have different wing length optima, or the wing length of juveniles is a consequence of the optimal wing length of adults, or vice versa, remains to be investigated.

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