

Delayed senescence in a southern population of the pied flycatcher (*Ficedula hypoleuca*)¹

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Abstract: We determined age-specific changes in survival probabilities and reproductive performance of female pied flycatchers, *Ficedula hypoleuca* Pallas, breeding in the southern part of the species' breeding range in central Spain. Our aim was to detect evidence of senescence in the course of a long-term study. A sample of known-age individuals, as well as a larger set of birds of minimum age, was used for analyzing reproductive performance, while only known-age birds were used to estimate age-dependent survival probabilities according to capture-recapture models. Data on laying date, clutch size, number of fledglings, and number of recruits produced were analyzed. Survival probabilities increased from 1-2 years to 3-4 years of age. No decline in reproductive performance was detected before the age of 5 years, and even after that age the evidence for reproductive senescence was weak. Females in our study showed delayed senescence when compared to (i) another population of the species breeding further north, (ii) the closely related collared flycatcher, and (iii) passerines in general. Middle-aged (3-4 years) females in our population seemed to experience a relatively low extrinsic or age-independent mortality, which may favour a delayed ageing process. Low mortality rates may be due to the short migration route and prolonged breeding season of southern pied flycatcher populations.

Keywords: life history, pied flycatcher, reproductive performance, senescence, survival.

Résumé : Nous avons évalué l'effet de l'âge sur la probabilité de survie et la performance reproductrice de femelles de gobemouche noir, *Ficedula hypoleuca* Pallas, nichant dans la partie sud de leur aire de reproduction, dans le centre de l'Espagne. Notre but était de détecter des preuves de sénescence des individus dans le cadre d'une étude à long terme. Un échantillon d'individus d'âge connu, ainsi qu'un plus grand échantillon d'oiseaux d'un âge minimal, fut utilisé pour analyser la performance reproductrice, tandis que seulement l'échantillon d'individus d'âge connu fut utilisé pour estimer les probabilités de survie dépendante de l'âge au moyen de modèles de capture-recapture. Les données sur la date de ponte, la taille de couvée, le nombre de jeunes prenant l'envol et le nombre de recrues ont aussi été analysées. Les probabilités de survie augmentaient de l'âge de 1-2 ans à l'âge de 3-4 ans. Aucun déclin de la performance reproductrice n'a été détecté avant l'âge de 5 ans et les signes de sénescence reproductrice demeuraient faibles chez les plus de 5 ans. Dans notre étude, les femelles ont montré une sénescence retardée en comparaison de celles d'une autre population nichant plus au nord, de même que celles d'une espèce assez semblable, le gobemouche à collier, *Ficedula albicollis*, et des passereaux en général. Les femelles d'âge intermédiaire (3-4 ans) dans notre population ont semblé peu affectées par les causes de mortalité extrinsèques ou indépendantes de l'âge, ce qui peut favoriser un délai dans le vieillissement. Les faibles taux de mortalité peuvent être reliés à la courte route de migration et à la saison de nidification prolongée des populations de gobemouche noir du sud.

Mots-clés : histoire naturelle, gobemouche noir, performance reproductrice, sénescence, survie.

Introduction

Senescence is the age-dependent deterioration in phenotypic performance of individuals leading to a decrease in reproductive value at advanced ages (Rose, 1991; Partridge & Barton, 1993). There is increasing evidence of senescence in wild avian populations (Holmes & Austad, 1995; Ricklefs, 1998), invalidating the assumption that individuals in the wild seldom reach ages at which physiological deterioration can be detected (Nice, 1937; Lack, 1954). This applies both to mortality senescence (McDonald, Fitzpatrick & Woolfenden, 1996) and to reproductive or fecundity senescence (Gustafsson & Pärt, 1990; Komdeur, 1996; Møller & de Lope, 1999). The increasing weakness of the assumption of constant survival rates with age is mostly due to the accumulation of information for many years in long-term studies of individually marked populations (Clutton-Brock, 1988; Newton, 1989). While the literature on changes in reproductive performance with age is vast (Saether, 1990), it focuses mainly on differences between young breeders

and more experienced adult breeders (Harvey, Stenning & Campbell, 1985; Järvinen, 1991). However, from most of these studies, evidence for reproductive senescence can be gleaned in order to determine its prevalence in wild avian populations.

Comparative analyses have revealed that the rate of ageing in natural populations of birds and mammals depends on extrinsic or age-independent mortality independently of taxonomic group and body size (Ricklefs, 1998). Given that life history traits and environmental factors determining extrinsic mortality may vary not only among species, but also among populations within species, Ricklefs' (1998) reasoning can also be applied to comparisons among populations (Partridge & Mangel, 1999). Extrinsic mortality can be estimated from the minimum mortality rates observed at ages at which the benefits of experience have levelled off but before the physiological deterioration due to ageing has begun to act (Ricklefs, 1998). Given the association found by Ricklefs (1998), we should expect at the intraspecific level that populations of the same species with different extrinsic mortality rates should have different rates of ageing, *i.e.*, senescence. Thus, populations breeding in areas with

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marked time or energy restrictions, subjected to high predation or parasitism rates, or whose members are involved in long and hazardous migratory trips may experience accelerated rates of senescence compared to populations breeding in more benign conditions.

In migratory birds, the length of the migration route may affect the probability of survival between years. Increasing latitude of breeding grounds may prolong migration routes (Berthold, 1993). Also, climatic hazards may increase mortality risks for early returning migrants at northern latitudes (Järvinen, 1983) or affect the survival of late migrating individuals. One could therefore expect an increasing gradient with latitude in extrinsic mortality rate, which in turn may determine an acceleration of ageing processes with latitude. There is still no evidence for such latitudinal effects on senescence in birds.

In the present study, we followed trends with age in fecundity and mortality in a population of a migratory passerine, the pied flycatcher (*Ficedula hypoleuca* Pallas), in the southern part of its breeding range. Spanish populations probably have a considerably shorter migration route compared with central European or Scandinavian populations (Lundberg & Alatalo, 1992), a presumably less time-restricted breeding season, and possibly a reduced risk of meeting dangerous climatic conditions (Järvinen, 1983). Our aim was to detect possible symptoms of delayed senescence in our study population in the light of Ricklefs' (1998) demonstration of the link between extrinsic mortality rates and rates of ageing in birds. We have focused on females for which we have more exact information about age-dependent reproductive performance.

Material and methods

SPECIES STUDIED

The pied flycatcher is a small (12-13 g) migratory and hole-nesting passerine of European woodlands. This species shows strong philopatry to breeding sites (Lundberg & Alatalo, 1992). It is a summer visitor overwintering in west Africa (Lundberg & Alatalo, 1992). It returns to the breeding areas during May (Sanz, 1997a). Egg laying in the study population begins in late May, and clutch size ranges from 2 to 8 eggs with a mode of 6 eggs (Sanz, 1997a). The female incubates alone and receives part of her food from her mate (Lundberg & Alatalo, 1992). Young are brooded by the female only to the age of 7 days (Sanz & Moreno, 1995) and both sexes feed the young that fledge within 15-18 days of hatching (Lundberg & Alatalo, 1992).

GENERAL METHODS

The study was conducted in a deciduous forest of *Quercus pyrenaica* Willd. at 1200 m a.s.l. in the vicinity of La Granja, central Spain (40° 54' N, 4° 01' W). From 1991 to 1999, 150-340 nestboxes in the study area were checked for occupation by pied flycatchers. Nestboxes (125 mm × 117 mm bottom area) were erected in a grid with 25 m between adjacent boxes. The nestboxes occupied by pied flycatchers were protected to prevent predation and were cleaned every year after the breeding season. Frequent checks of nestboxes provided data on laying date (defined

as the day when the first egg was laid), clutch size (defined as the number of eggs after the start of incubation) and number of fledglings.

Most of the breeding females (91.7%, $n = 950$) were caught and identified (or ringed if they had not been encountered previously) during incubation or when they were feeding the nestlings. Nestlings were ringed at 13 days of age just before fledging (hatching date = day 0). The data analyzed in this study are mainly based on females with exact known age, since they had been ringed as nestlings in a previous year ($n = 39$ birds for the cohorts born in 1991-1994, see below). In addition, immigrant females could be aged as yearlings or older (at least 2 years old) on their first capture following the criteria in Karlsson, Persson & Walinder (1986), Potti (1993) and Potti & Montalvo (1991). For females with unknown age on the first capture (at least 2 years old) as breeders in our study area, we have used a conservative estimated minimum age of 2 years. Because this nestbox area was used for many other studies (Moreno *et al.*, 1995; Sanz & Moreno, 1995; Sanz, 1997b), we used only unmanipulated clutches to calculate number of fledglings and recruits. The number of recruits was observed through recapture of individuals banded as nestlings.

The subsequent local survival of the females and the number of recruits was observed through recapture in the following breeding seasons. Age-dependent female local survival rate was calculated according to the Cormack-Jolly-Seber capture-recapture model (Lebreton *et al.*, 1992) as presented in the program MARK (White & Burnham, 1999). Only females of known age which could potentially have reached 5 years of age during the study years were included in the analysis. We have thus excluded from this analysis all females born after 1994. Survival after 5 years was not considered, given the sample sizes for females attaining 6 or more years.

STATISTICAL PROCEDURES

For analyses of reproductive performance comparing female age classes, we used two separate data sets:

(i) Birds of known age, because they were ringed as nestlings or were captured on their first year of life in our study area. To examine reproductive performance at the five stages of breeding, we combined birds that were 5 or more years old to increase sample sizes for the oldest age classes. Given the possibility of bias due to non-random sampling of ages through cohorts (old age classes only from early years of study), we limited the analyses to early cohorts from which birds of 5 years of age could be found (cohorts born in the years 1991-1994). Another potential source of bias is that the sample of known age individuals comes from an increasingly smaller number of years of the study as age increased. To avoid possible effects of systematic temporal changes during the course of the study, we also analyzed data from the last 5 years of the study (1995-1999).

(ii) Birds with an estimated minimum age of 2 years at first capture in our study area. To examine reproductive performance, we combined birds that were 6 or more years old to increase sample sizes for the oldest age classes. We assigned females to cohorts according to their estimated minimum age. Thus, we included females which were at least 2 years old in the years 1992-1995 (presumably from cohorts born in 1990-1993).

At the population level, breeding parameters (laying date, clutch size, number of fledglings, and recruits) varied among years. Because we were interested in the consequences of variation in the breeding parameters among different female age classes, we transformed them into a standard normal distribution (standardized value = [original value - mean value]/standard deviation), on the basis of means and standard deviation within each year. Thus, when referring to, for example, laying date or clutch size in this paper we refer to standardized laying date and clutch size, unless stated otherwise.

To determine changes with female age in breeding parameters, we used regression analyses using linear and quadratic models. The statistically significant model giving the highest r^2 was used. Mean values are reported with standard errors. All significance levels are two-tailed.

Results

FEMALE SURVIVAL PROBABILITY

For the 65 females of known age which could potentially attain 5 years in 1999 (cohorts 1991-94), there was an increase in survival probability estimates from 1 to 4 years according to the Cormack-Jolly-Seber model (Figure 1). The probability of female local survival was clearly higher for females of 3-4 years than for those of 1 and 2 years (Figure 1). Given the small sample of females attaining 5 years, the standard error was very high for the survival probability estimate of 4 year-old females. However, the increase in survival probability estimates between the ages of 2 and 3 years appears statistically robust.

FEMALE AGE EFFECTS ON REPRODUCTIVE PERFORMANCE

For females of known age of the cohorts of 1991-94, laying date decreased linearly with age (Figure 2a). For all females (including those with an estimated minimum age), laying date showed a quadratic relationship with age (Figure 3a). Laying date showed a weak tendency to

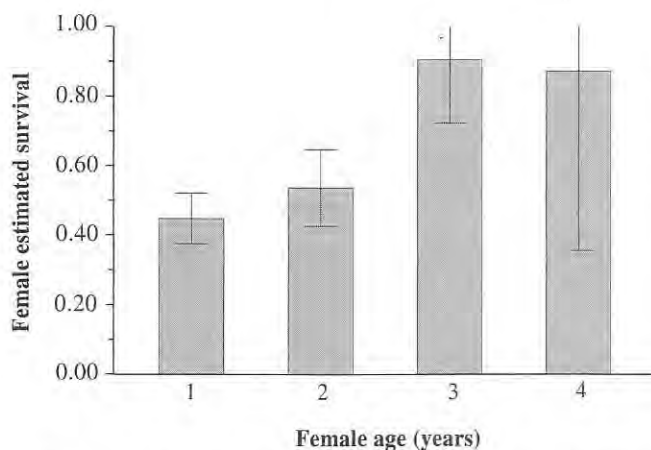


FIGURE 1. Estimated survival probability of female pied flycatchers of known age (cohorts born in 1991-1994, $n = 65$). The error bars represent the standard errors of the mean estimates according to the Cormack-Jolly-Seber capture-recapture model as estimated by program MARK (White & Burnham, 1999).

increase again after the age of 5 years (Figure 3a). For females of known age, clutch size increased linearly with age (Figure 2b). For all females, clutch size showed a quadratic association with age (Figure 3b), with clutch size decreasing after the age of 5 years. For females of known age, number of fledglings increased linearly with age (Figure 2c). The same trend was apparent when including all females in the analysis (Figure 3c). For females of known age, the number of recruits did not differ among age classes (Figure 2d). The same was true in the analysis of all females (Figure 3d). The same trends resulted when only data from 1995-1999 was included in the analyses, so we have not presented these results.

One problem with studies of age-dependent trends in breeding performance is that increases with age can be due to selection, which operates by removing the less efficient individuals from older age groups. If that were the case, we should expect that individuals surviving to old ages (5 or more years) would already be the most proficient at younger ages. However, we performed an ANCOVA on clutch size at ages 2-4 years for the estimated minimum age sample, comparing females reaching old age with those not attaining 5 years, while using age as a covariable. No difference between the two groups of females was found (Factor: $F_{1,385} = 0.02$, $p = 0.89$), whereas age was significant for the two groups (Covariable: $F_{1,385} = 4.41$, $p = 0.036$; Interaction $F_{2,385} = 0.33$, $p = 0.56$; Model: $F_{3,385} = 2.69$, $p = 0.046$). Thus, we can discard the selection hypothesis as an explanation for our age-dependent increases in performance.

Discussion

We found evidence for high survival probabilities at advanced ages in a population of a short-lived migratory passerine breeding in the southern part of the species' breeding range. This assertion is based on a comparison of our southern European population of the pied flycatcher with data from central Europe (Sternberg, 1989), where survival probability is highest for 1 year-old females and declines steadily afterwards. In our population, survival estimates for 3 and 4 year-old females are higher than for younger females, and they are higher than for 1-year old females in the German study (0.53; Sternberg, 1989). The pattern we found is in agreement with Ricklefs' (1998) contention that mortality rates should reach a low point some time after the effects of improvements with experience become unimportant, but before ageing processes begin to operate. No such valley in mortality rates is observed in the central European population (Sternberg, 1989). A Scandinavian population of the closely related collared flycatcher (*Ficedula albicollis* Temminck) shows a constant age-dependent survival probability which is clearly lower than for our 3-4 year-old age group and similar to the mortality observed for our 1-2 year-old age group (Gustafsson & Pärt, 1990). Mortality senescence also seems to be delayed in our population compared with similar-sized passerines like the barn swallow (*Hirundo rustica* L.; Møller & de Lope, 1999) or larger species like the Florida scrub jay (*Aphelocoma coerulescens* Bosc; McDonald, Fitzpatrick & Woolfenden, 1996), where declines in survival

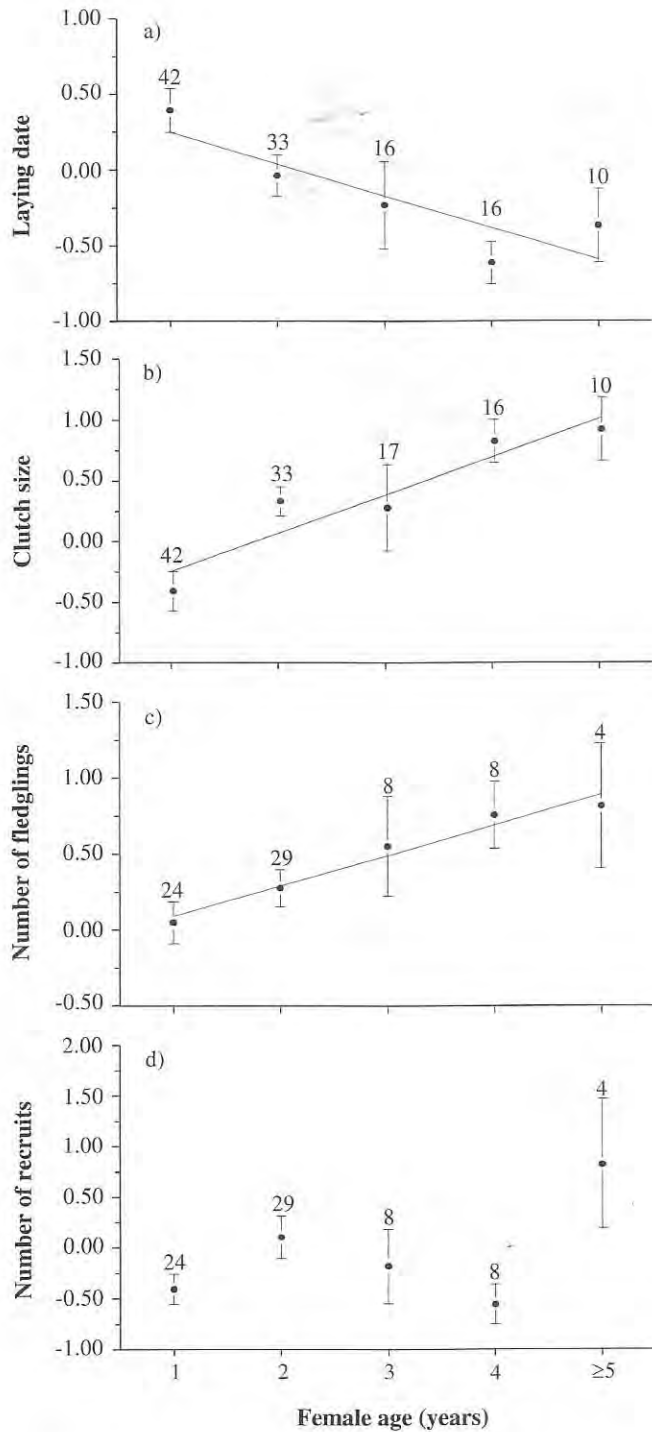


FIGURE 2. Laying date, clutch size, number of fledglings and number of recruits of female pied flycatchers of known age of the cohorts of 1991-1994 breeding between 1992 and 1999. The regression equations are: a) Laying date = 0.56 - 0.25 female age, $F_{1,115} = 16.56$, $p < 0.001$, $r^2 = 0.12$ (test of significance of coefficients: constant $t = 3.43$, $p < 0.001$; female age $t = 4.07$, $p < 0.001$), b) clutch size = -0.62 + 0.34 female age, $F_{1,116} = 24.51$, $p < 0.001$, $r^2 = 0.17$ (test of significance of coefficients: constant $t = 3.34$, $p = 0.001$; female age $t = 4.95$, $p < 0.001$), and c) number of fledglings = -0.16 + 0.22 female age, $F_{1,71} = 9.86$, $p = 0.002$, $r^2 = 0.12$ (test of significance of coefficients: constant $t = 0.94$, $p = 0.35$; female age $t = 3.14$, $p = 0.002$). All data were standardized for each year. Numbers above bars are sample sizes. The error bars represent the standard error of the mean.

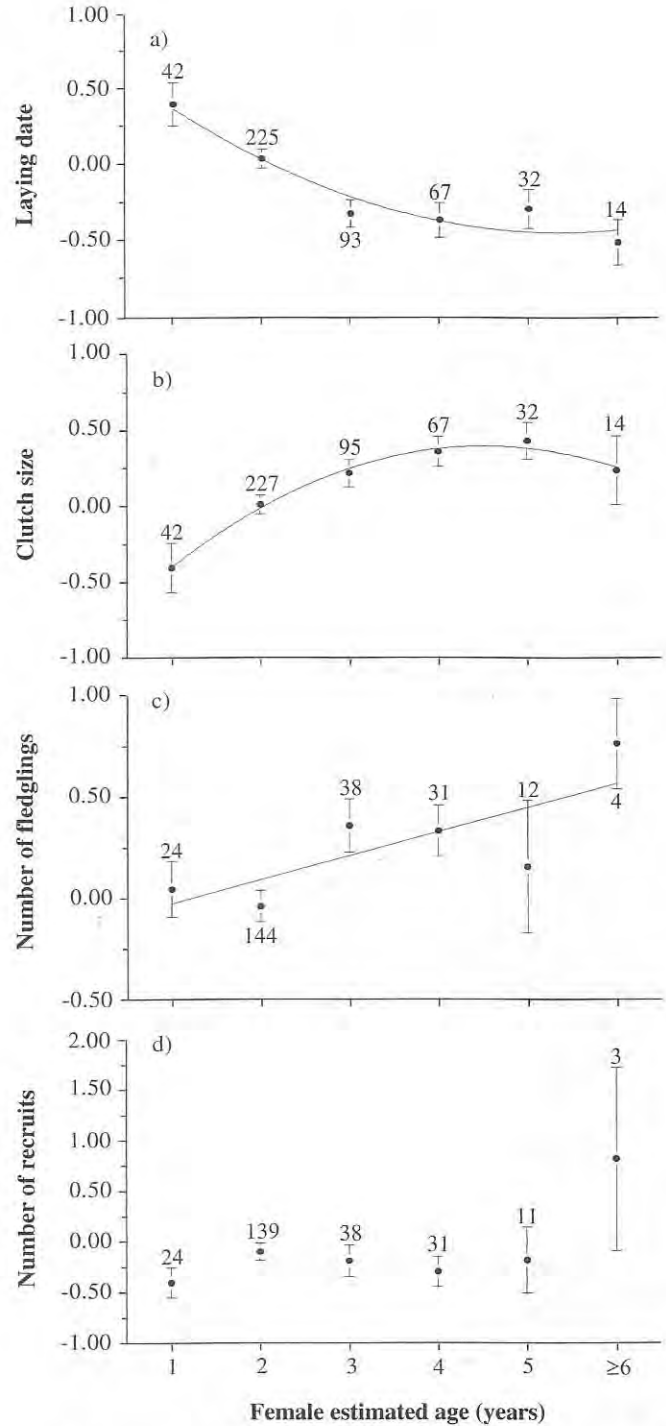


FIGURE 3. Laying date, clutch size, number of fledglings and number of recruits of female pied flycatchers of estimated age which were at least 2 years old in the years 1992-1995 (presumably from cohorts born in 1990-1993) breeding between 1992 and 1999. The regression equations are: a) laying date = 0.90 - 0.59 female age + 0.06 square female age, $F_{2,470} = 15.69$, $p < 0.001$, $r^2 = 0.06$ (test of significance of coefficients: constant $t = 3.70$, $p < 0.001$; female age $t = 3.39$, $p < 0.001$; square female age $t = 2.36$, $p = 0.018$), b) clutch size = -0.80 + 0.50 female age - 0.05 square female age, $F_{2,474} = 11.53$, $p < 0.001$, $r^2 = 0.05$ (test of significance of coefficients: constant $t = 3.35$, $p < 0.001$; female age $t = 3.12$, $p = 0.002$; square female age $t = 2.27$, $p = 0.024$), and c) number of fledglings = -0.24 + 0.13 female age, $F_{1,251} = 6.62$, $p = 0.011$, $r^2 = 0.02$ (test of significance of coefficients: constant $t = 1.68$, $p = 0.09$; female age $t = 2.57$, $p = 0.011$). All data were standardized for each year. Numbers above bars are sample sizes. The error bars represent the standard error of the mean.

probabilities set in after the ages of 3 or 2 years, respectively. The pattern appears similar to that found in the great tit (*Parus major* L.), where a peak in survival probability for females is detected at the age of 4 years (McCleery & Perrins, 1988). We cannot ascertain if survival probabilities of our females peak at 4 years or continue to rise, given our small samples for females attaining 5 or more years. Unfortunately, the other studies cited have not calculated survival probabilities according to capture-recapture models, so our comparison rests on the assumption that proper estimates for these populations would not substantially change the patterns found. In any case, females in our study population seem to have comparatively high survival probabilities at intermediate ages and a comparatively late onset of ageing symptoms.

Evidence of reproductive senescence has been found in 11 passerine species, and we found deterioration of performance in some reproductive trait with age in 9 of them (Table I). According to these studies, there is a trend for senescence in some reproductive variable that sets in at the age of 3-4 years in passerines (Table I). Two exceptions to this pattern are the insular, tropical, and cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*), and the relatively large and also cooperatively breeding Florida scrub jay, in which senescence sets in at the ages of 5 and 7 years, respectively (Table I). In our study, we found no evidence of deterioration in reproductive performance before the age of 5 years for females of known age, but instead a monotonic increase for most variables. This increase in performance is apparently not due to selection that removes inefficient individuals before they reach old age (Forslund & Pärt, 1995), but to improvements with age operating on the average individual in the population. For the larger data set which included females of estimated minimum age, a weak tendency towards a decline in performance with respect to laying date and clutch size was detected after the age of 5 years. With regard to the number of recruits, no trend was apparent with relation to age. In any case, senescence seems to be delayed in our study population when compared with related species of roughly the same body size. The house martin and the indigo bunting, which show no reproductive senescence until the ages of 4 and 6 years, respectively (Table I), are the species most similar to our pied flycatcher population. We may conclude from our survey of the passerine literature that

fecundity senescence in our study population, which is still not discernible at the age of 5 years, appears comparatively late.

Can this delay in reproductive senescence be associated with the increase in survival probabilities until the ages of 3-4 years detected in our population? We may deduce from our survival data that no decline in residual reproductive value is expected for females before the age of at least 5 years. There is increasing evidence that life history traits such as timing of reproduction and clutch size are optimized with respect to condition (Tinbergen & Daan, 1990; Daan, Dijkstra & Tinbergen, 1990; Aparicio, 1998). Any age-specific deterioration in general physiological performance, which would not set in until extrinsic mortality rates weaken selection against ageing (Ricklefs, 1998), would clearly affect reproductive variables and the capacity for parental care. Both phenomena may be linked, presumably through a general physiological deterioration of the organism (Partridge & Mangel, 1999). From Table I, it is clear that reproductive senescence is a common and important aspect of avian life histories, and that individuals in most populations in the wild may reach ages at which they can be considered senescent, even in short-lived species.

Individuals in our study population probably have a much shorter migration route compared with central European birds or Scandinavian collared flycatchers. This is based on the fact that both central and northern European populations (and presumably southern as well) of the pied flycatcher have their wintering grounds in the same area of West Africa, whereas collared flycatchers winter in central Africa (Lundberg & Alatalo, 1992). Although the importance of migratory route length for mortality risks during migration has not been fully explored (Cuadrado & Hasselquist, 1994), it may be determinant for explaining the high survival probabilities for our middle-aged females, which may have accumulated experience about the best stopover sites or the best flight itineraries across the Sahara desert (Berthold, 1993). Another source of mortality associated with breeding range may be climatic hazards in spring for early-arriving birds (Järvinen, 1983), or the risk of starvation on the breeding grounds during unfavourable weather in the post-breeding period (Järvinen, 1987; Lindström *et al.*, 1990). Time restrictions at high latitudes may induce an overlap between moult and premigratory fattening (Lindström, Daan & Visser, 1994). The time

TABLE I. Evidence of senescence in reproductive performance in birds. Performance variables are only presented when significant evidence of senescence has been found ($\rightarrow +$ indicates increases, $\rightarrow =$ represents no change and $\rightarrow -$ are decreases)

Species	Trends with age (years)			Performance variables	Reference
<i>Hirundo rustica</i> L.	1 $\rightarrow +$	3 $\rightarrow -$	≥ 5	number of fledged young	(1)
<i>Delichon urbica</i> L.	1 $\rightarrow +$	2 $\rightarrow =$	≥ 4		(2)
<i>Anthus spinoletta</i> L.	1 $\rightarrow +$	4 $\rightarrow -$	≥ 5	clutch size in second clutches	(3)
<i>Acrocephalus sechellensis</i>	2 $\rightarrow +$	5 $\rightarrow -$	≥ 8	hatching success, number of fledged young	(4)
<i>Ficedula albicollis</i> Temminck	1 $\rightarrow +$	3 $\rightarrow -$	≥ 5	lay. date, clutch size, number of fledged young, number of recruits	(5)
<i>Parus caeruleus</i> L.	1 $\rightarrow +$	3 $\rightarrow -$	≥ 4	brood size, offspring survival	(6)
<i>Parus major</i> L.	1 $\rightarrow +$	4 $\rightarrow -$	≥ 5	laying date, brood size, offspring survival	(6)
<i>Pica pica</i> L.	1 $\rightarrow +$	4 $\rightarrow -$	≥ 5	clutch size	(7)
<i>Aphelocoma coerulescens</i> Bosc	2 $\rightarrow +$	7 $\rightarrow -$	≥ 12	number of fledged young, offspring survival	(8)
<i>Passerina cyanea</i> L.	1 $\rightarrow =$	6			(9)
<i>Melospiza melodia</i> Wilson	1 $\rightarrow +$	3 $\rightarrow -$	≥ 4	number of fledged young	(10)

References: (1) Møller & de Lope, 1999; (2) Bryant, 1988; (3) Askenmo & Unger, 1986; (4) Komdeur, 1996; (5) Gustafsson & Pärt, 1990; (6) Dhondt, 1989; (7) Birkhead & Goodburn, 1989; (8) Fitzpatrick & Woolfenden, 1988; (9) Payne, 1989; (10) Nol & Smith, 1987.

constraint and the costs of overlapping reproduction and moult (Hemborg & Lundberg, 1998) may explain why birds from northern areas migrate with unmoulted feathers more often than more southerly birds (Hyytiä & Vikberg, 1973; Jenni & Winkler, 1994; Hedenström, Lindström & Pettersson, 1995). The costs of migrating without having a fully moulted plumage are unknown. Individuals in Mediterranean populations arrive at the breeding grounds on the same dates as those of populations breeding further north (Sanz, 1997a). Although Spanish pied flycatchers breed in montane habitats where they may also incur risks due to weather (Sanz, 1995), early birds may still move to lower altitudes when confronted with late spring storms. The possibility of a swift evasion from deleterious meteorological conditions may be precluded for individuals in northern populations. Finally, birds breeding in the southern part of the breeding range may have a longer period in which to moult after breeding and to accumulate the necessary reserves for migration (Veistola, 1997). All these advantages of breeding in the south may explain the delayed senescence found in Spanish pied flycatchers. The prevalence of intraspecific variation associated with latitude and migratory route in avian ageing patterns remains to be explored, but appears as a tantalizing possibility.

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