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Age at first reproduction and longest-lived individuals in the Pallid Swift *Apus pallidus*

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Abstract - Swifts are long living birds with delayed maturation; however, the age at first reproduction and their maximum life span is known for a few species. We discuss here some data about these parameters, using observations collected during our long-standing study on Pallid Swift *Apus pallidus* in Northern Italy. The longest-lived bird in our dataset was still recovered breeding 19 calendar years after maturity, and the youngest confirmed age at first breeding was 3 years (i.e., bird in 4th calendar year). No breeding attempts have been verified for individuals in their second and third calendar year.

Keywords: Pallid Swift, age first reproduction, longevity, senescence

INTRODUCTION

The demographic traits of organisms are essential features to assess local population conditions, model population trajectories, understand possible influences of environmental external factors, and to evaluate the effectiveness of management actions in cases of population decline (Schaub & Abadi 2011). Information on these traits is needed to target which parts of the life cycle may be more important in limiting population recovery (Henaux et al. 2007, van Rees et al. 2018). When studying life cycles, basic population models should include the age at first reproduction (AFR), longevity, and the number of offspring produced.

Life-history theory predicts that early AFR is favoured by natural selection if reproducing early increases the likelihood of achieving reproduction and, in turn, increases fitness compared with a later start (Brommer et al. 2002). Reduction of fitness with delayed AFR has been reported in several species with very different life-history strategies (McGraw & Caswell 1996, Charmantier et al. 2006). However, early AFR may be counter-selected if by delaying maturity it enables an individual to gain experience, and as a result improve its survival and lengthen its reproductive lifespan (Brommer 2000, Barbraud & Weimerskirch 2005). Therefore, delaying reproduction can be a good choice in bad environmental conditions, particularly when there is shortage of food or a high population density in territorial birds (Kruger 2005). In cooperative birds, individual conditions may influence the decision to breed at an early age or to delay breeding and switching to be a helper (Covas et al. 2004, Mumme et al. 2015; Cucco & Bowman 2018).

In a few species, stabilising selection on AFR has also been reported. In particular, Tettamanti et al. (2012) found evidence for stabilising selection acting on both AFR and age at last reproduction (ALR) in the Alpine Swift *Tachymarptis melba*, suggesting that "individuals should refrain from reproducing in their first 2 years of life, i.e. when inexperienced, and that reproducing after 7 years of age had little effect on lifetime fitness, probably due to senescence".

Despite the fundamental importance of these life history traits in shaping fitness, they are often poorly investigated in many birds with delayed maturation. For example, AFR is unknown in most species of swifts around the world and even among the well-studied Western Palaearctic species (not recorded for *Apus affinis*, *A. alexandri, A. caffer, A. pallidus, A. unicolor*, Cramp 1985). To date, detailed data have been reported only for the Common Swift *A. apus* and the Alpine Swift. In the Common Swift, the AFR was discussed by Perrins (1971) when reporting data collected in the Oxford tower (Lack 1956). In this site, only eight out of 621 swifts ringed as nestling returned to the tower when they were two years old (one), three years old (four), and four years old (one). Observing that two individuals did not lay eggs, three did not hatch the laid eggs, and only the bird first caught at the age of four years laid at about the normal time, he concluded that successful breeding seems unlikely to occur before the age of four. Apparently based on this evidence, Cramp (1985) stated the Common Swift probably attain maturity at 4 years. In southern Scotland Thomson et al. (1996) controlled 12 birds which returned to breed in the natal colony, finding an average first breeding age of 2.8 year (5 birds were first recorded breeding at age 1 year, 1 at 2, 2 at 3, 1 at 4, 1 at 5, and 2 at 6). Other observations came from Switzerland, where Weitnauer (1947) found that nine birds ringed as young returned in the following summer, i.e. when 12 months old, and occupied nest-holes as non-breeders. Other six individuals bred in the following year at two years old. In Sweden, Magnusson and Svärdson (1948) also reported three birds occupying nest-holes as non-breeders at one year old. More recent work based on colour ringed juveniles at a Swiss colony found a higher percentage of juveniles visiting the birth colony in the second calendar year of life (age 1 year), and variable percentages (from 13 to 30%) over the next year, declining to 3-7% at age 3 (4^{th} cy) when some birds are new adult breeders (Genton & Jacquat 2014).

The other Palaearctic species, Alpine Swift, reaches AFR normally at 2-3 years and rarely at 1 year (Lack & Arn, 1947, Arn 1960, Cramp 1985). Tettamanti et al. (2012) showed that AFR in this species varies between 2 and 5 years. They suggested also that on average female Alpine Swifts were reproducing for the first time and ending their reproduction at significantly earlier ages compared to male, but that there were no differences between the sexes in reproductive lifespan.

In an evolutionary framework, it is conceivable that birds which delay their first reproduction can enjoy an increased longevity (but see Brommer et al. 2002). Senescence and reduced extrinsic mortality should select for mechanisms that postpone physical deterioration, resulting in longer life spans and extended breeding opportunities (Wasser & Sherman 2010).

In this study, we present the first data about AFR and age of the longest-lived individuals in Pallid Swift, and compared the finding with those of Common Swift, a species showing a high morphological similarity but striking differences in breeding biology (Pellegrino et al. 2017).

MATERIALS AND METHODS

The study area is located in NW Italy (Boano et al. 2015, Boano et al. 2020), with breeding colonies in Carmagnola (followed from 1976 to 2021) and Torino (from 1987 to 1992). The Carmagnola colony (lat. 44.84°, long. 7.72° E, 239 m asl) is localized in two facing buildings (Capello private house and Lomellini Palace) where the birds nest in wall's holes. Up to 2015, our main ringing activity was done in a subset of the colony with nests accessible from inside (Capello house), ringing all nestlings, a portion of the breeding adults, and some explorative individuals of unknown status, mainly in July and September. From 2016, due to change in property and destination of the building, we shifted to the other building (Lomellini Palace) catching adult birds from outside the nesting holes with butterfly-type nets (Pichorim & Monteiro-Filho 2010). During the study period the colony rose from 30 to more than 100 pairs. In the Torino (lat. 45.07° long. 7.67°, 260 m asl) colony 30-50 pairs of Pallid Swift nested in the cavity of blind boxes of a school building, and here we ringed almost all nestlings and many adults. In the first study years, several breeding adults were sexed by control of the individual laying eggs (Malacarne et al. 1993), then, more recently, by genetic sexing methods (Fridolfsson et al. 1999, Ilahiane et al. 2022). All the necessary research and ringing permits were granted and renewed over time to the authors by the ISPRA and Città Metropolitana di Torino.

For the purpose of comparisons and as a useful life parameter that allows evaluating the potential length of reproductive life (Charnov & Berrigan 1990, Tettamanti et al. 2012) we considered the adult mean lifespan (MLS) of Pallid Swift to be 3.64 years (c.i. 2.1-5.1 years), from the formula: MLS =1/-$\log_e$(*Phi*) where (*Phi*) was the value of annual survival provided by Boano et al. (1993, 2020), and the approximate confidence intervals calculated according to Brownie et al. (1985).

When discussing bird age, it is important to pay attention to the definition used, especially when we compare papers from different authors. Sometimes age is defined directly, or as "calendar year", or with the Euring code. In this paper we clearly state when we speak of year of age or calendar years, however Tab. 1 may be useful to avoid confusion.

RESULTS

From the beginning of our research 1181 chicks and 423 adults were ringed at the nest in their nest cavity in Carmagnola (n = 612 nestlings, 330 adults) and in Torino (n = 569 nestlings, 93 adults), obtaining also a high number of recapture events (416 in Carmagnola, 33 in Torino).

Due to the very low philopatry of young Pallid Swift, and to the low access to the building to catch adults in Torino, only 10 chicks were later recaptured in successive years (Tab. 2). Two individuals were found at age 2 years, but one was just inspecting the cavities and the other was found dead in the area with no evidence of breeding. The first certain reproductive evidences were found for 5 individuals at age 3 (plus one found dead in the nest cavity), and two individuals at age 4, with a mean of 3.3 years. All these data are reported in Tab. 2 with the nesting and recovery sites, the sex (when known), the breeding status recorded, and the age expressed also as calendar years for clarity.

Table 1. Comparative table of ageing terminology for a hypothetical bird born in June of the year "N". According to their reproductive status, birds in 2^{nd}/3^{rd} calendar years could also be named immatures/subadults.

Years	**N**		**N+1**		**N+2**		**N+3**	
Months	**June**	**Jul-Dec**	**Jan-Jun**	**Jul-Dec**	**Jan-Jun**	**Jul-Dec**	**Jan-Jun**	**Jul-Dec**
Descriptive terms	pullus	juvenile	adult	adult	adult	adult	adult	adult
Euring Code (known age)	1	3	5	5	7	7	9	9
Month / Years of age	0 mth	1-6 mths	7-12 mths	1 mths	1 year	2 years	2 years	3 years
Calendar year	1^{st} cy	1^{st} cy	2^{nd} cy	2^{nd} cy	3^{rd} cy	3^{rd} cy	4^{th} cy	4^{th} cy

Table 2. Pallid Swifts ringed as nestlings and found in subsequent years. Ringing and recovery places: CC = Carmagnola, Capello house subcolony; CL = Carmagnola, Lomellini subcolony; CO = Carmagnola, near other colony; TS = Turin, School; TR = Trana town.

Ringing data			**Recovery data**					
Ring N	**Date**	**Place**	**Years**	**Place**	**Breeding or other status**	**Sex**	**Age (years)**	**Calendar year**
L968685	04/07/1979	CC	1983	CC	Breeding, rearing 2 nestlings (in the same cavity of birth!)	0	4	5th cy
R03157	14/07/2014	CC	2018, 2019	CL	Probably breeding (attending the same nest-hole in 2018 and 2019)	0	4	5th cy
W6876	28/07/1988	CC	1991, 1992	CC	Breeding, rearing 2 nestlings in 1991 and 2 in 1992	F	3	4th cy
W24020	28/07/1991	CC	1994	CO	Found dead in the nest cavity after some rainy days, May 25 (skin MCCI-617)	F	3	4th cy
W53099	23/07/2004	CC	2007	CC	Breeding, rearing 3 nestlings	0	3	4th cy
W53164	15/07/2006	CC	2009, 2010	CC	Breeding, rearing 2 nestlings in 2009, then paired in the nest in 2010	0	3	4th cy
W53167	15/07/2006	CC	2009	CC	Breeding, rearing 2 nestlings	0	3	4th cy
Z14850	15/09/1988	TS	1991, 1992	CC	Breeding, rearing 3 nestlings both in 1991 and 1992	M	3	4th cy
R03141	1/10/2013	CC	2015	CL	Roosting in nest-hole, July 14	0	2	3rd cy
W14451	21/06/1988	TS	1990	TR	Found dead, May 27 (A. Peano)	0	2	3rd cy

Table 3. Breeding adults recaptured more than 4 calendar years after ringing in Carmagnola (TO).

Ring N	**Sex**	**Ringing date**	**Controlled in years**	**Last Control**	**Year, months, days from ringing**	**Cy from ringing**
W6865	M	28/07/1988	1989-1992, 1994, 1998, 2002, 2007	19/07/2007	18y, 11m, 21d	19
W53176	0	17/07/2006	2007, 2010-2011, 2014-2015	14/07/2015	8y, 11m, 27d	9
W2701	M	16/07/1984	1990-1991	28/07/1991	7y, 0m, 12d	7
R02001	0	11/09/2012	2013, 2016, 2018-2019	22/09/2019	7y, 0m, 10d	7
W53026	0	15/07/2000	2001, 2007	19/07/2007	7y, 0m, 4d	7
W53025	0	15/07/2000	2006-2007	19/07/2007	7y, 0m, 4d	7
W53187	0	19/07/2007	2014	09/07/2014	6y, 11m, 20d	7
W2778	M	30/07/1985	1986, 1988-1989, 1991-1992	17/07/1992	6y, 11m, 17d	7
R03190	0	13/07/2015	2017-2021	24/09/2021	6y, 2m, 11d	6
R03143	0	09/07/2014	2015, 2020	27/07/2020	6y, 0m, 18d	6
R03189	F	13/07/2015	2016, 2018-2021	14/07/2021	6y, 0m, 1d	6
W2747	F	31/07/1984	1988, 1990	10/07/1990	5y, 11m, 10d	6
R03153	0	14/07/2014	2017-2019	22/09/2019	5y, 2m, 7d	5
W24087	0	19/07/2007	2012	11/09/2012	5y, 1m, 23d	5
W2706	0	16/07/1984	1989	24/07/1989	5y, 0m, 8d	5
W53024	0	15/07/2000	2005	18/07/2005	5y, 0m, 3d	5
W24091	0	19/07/2007	2012	19/07/2012	5y, 0m, 0d	5
W53193	F	19/07/2007	2012	23/04/2012	4y, 9m, 4d	5

DISCUSSION

In this study of the Pallid Swift we show that some individuals can return from Africa to the European breeding sites when 2 years old, but we found no proof of reproduction at this age. The first documented breeding attempts were attested when individuals were 3 years old.

The AFR is a key demographic parameter that is probably under high selective pressure (Fay et al. 2016). A delayed onset of reproduction beyond maturity can be an optimal strategy explained by a long life span and costs of early reproduction (Mourocq et al. 2016). For example, individuals that attain sexual maturity earlier can have a significantly shorter lifespan than those that delayed reproduction (Oli et al. 2002; Ancona et al. 2015). In other cases, life-span is not affected by early AFR, but the optimal age at first reproduction can be higher because of lower reproduction at early ages (Kruger 2005). The costs of reproduction for first-time breeders can be particularly high during harsh environmental conditions (Barbraud & Weimerskirch 2005, Covas et al. 2004). An intriguing difference concerns the two very similar European species, the Pallid and the Common Swift (Pellegrino et al. 2017). Our data show that both AFR and lifespan of the Pallid are not noticeably different from those of the Common Swift. This could constitute an evolutionary advantage, given that the Pallid Swift can lay two clutches per year, while the Common lays only a single clutch. However, the lower annual production of chicks of the Common Swifts could be counterbalanced by a higher survival of juveniles. Unfortunately, no data on juveniles survival are available due to logistical difficulties related to the low philopatry (pers. obs.).

Data available for our study species (this study) and other Palaearctic swifts (Perrins 1971, Tettamanti et al. 2012) showed that there were individual differences in AFR, with some individuals breeding successfully from the age of three, and others not breeding until their fourth year. These results can be interpreted through differences in the quality of breeding individuals. First reproduction may act as a filter, selecting individuals of higher quality (Barbraud & Weimerskirch 2005; Aubry et al. 2011).

In a few species, stabilising selection on AFR has also been reported. In particular, Tettamanti et al. (2012) found evidence for stabilising selection in Alpine Swift acting on both AFR and age at last reproduction, suggesting that individuals should not breed in their first two years of life and that breeding after 7 years of age had little effect on lifetime fitness.

In our study species, we cannot calculate with complete accuracy the age at last reproduction, because we do not know the true age of the oldest individuals, as all were first captured as adult breeders (age unknown). However, from our evidence that Pallid Swift does not engage in breeding activity before the age of three, we can calculate that the individual recaptured after 19 years was at least 22 years old. Moreover, several individuals recaptured after 7-9 years, were at least 10-12 years old, and likely testifies to the presence in the colony of several high-quality individuals. These values are significantly higher with respect to the mean value of about 6.64 years, obtained adding three years to the mean life span as an adult of 3.64 years (c.i. 2.1-5.1) estimated from survival statistics (Boano et al. 1993, 2020).

Future studies could examine the breeding success of these long-living individuals, in order to test whether they follow a common pattern of evolutionary theories of senescence, which predict that morphological and behavioural attributes that reduce mortality should select for mechanisms that postpone physical deterioration (resulting in longer life spans and extended breeding opportunities: Wasser & Sherman 2010), or whether reproducing at older ages has little effect on lifetime breeding success (Thomson et al. 1996, Tettamanti et al. 2012).

In conclusion, precise values for AFR and life-span in most species are unknown but of potential significance because failure to incorporate accurate estimates of these parameters in population models may lead to flawed population projections (Cooper et al. 2009). Accurate estimates could be utilized to build demographic models to study population recovery, i.e. the case happened to Pallid Swift in Corse after rat eradication (Martin & Thibault 2022), or to envisage a swift's colony recovery after destruction due to building restructuring (Schaub et al. 2016, Swift Conservation 2022).

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