POPULATION ECOLOGY - ORIGINAL RESEARCH

Females better face senescence in the wandering albatross

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Abstract Sex differences in lifespan and aging are widespread among animals. Since investment in current reproduction can have consequences on other life-history traits, the sex with the highest cost of breeding is expected to suffer from an earlier and/or stronger senescence. This has been demonstrated in polygynous species that are highly dimorphic. However in monogamous species where parental investment is similar between sexes, sex-specific differences in aging patterns of life-history traits are expected to be attenuated. Here, we examined sex and age influences on demographic traits in a very long-lived and sexually dimorphic monogamous species, the wandering albatross (*Diomedea exulans*). We modelled within the same model framework sex-dependent variations in aging for an array of five life-history traits: adult survival, probability of returning to the breeding colony, probability of breeding and two measures of breeding success (hatching and fledging). We show that life-history traits presented contrasted aging patterns according to sex whereas traits were all similar at young ages. Both sexes exhibited actuarial and reproductive senescence, but, as the decrease in breeding success remained similar for males and females, the survival and breeding probabilities of males were significantly more affected than females. We discuss our results in the light of the costs associated to reproduction, age-related pairing and a biased operational sex-ratio in the population leading to a pool of non-breeders of potentially lower quality and therefore more subject to death or breeding abstention. For a monogamous species with similar parental roles, the patterns observed were surprising and when placed in a gradient of observed age/sex-related variations in life-history traits, wandering albatrosses were intermediate between highly dimorphic polygynous and most monogamous species.

Keywords Breeding success · Breeding probability · Capture–mark–recapture · *Diomedea exulans* · Seabird · Senescence · Sexual dimorphism · Survival

Communicated by Indrikis Krams.

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Introduction

Sex differences in life span and aging are widespread among animals. Understanding the evolutionary causes for sex specific differences in demographic, reproductive and physiological senescence is a contemporary challenge (Bonduriansky et al. 2008). Senescence is defined as an inevitable decrease in physiological function with age, leading to reduced reproduction and survival (for a review, see Monaghan et al. 2008). Since current reproduction can have consequences on other life-history traits such as survival and future reproduction (Williams 1966), differences in aging patterns are expected between sexes if both physiological and fitness costs of reproduction are asymmetric (Stearns 1992; Bell 1980; Reznick 1992). The sex with the highest cost of breeding, defined as the energetic investment relative to the capacities of an individual at a given time and for a given phenotype, is expected to suffer from

an earlier and/or stronger rate of senescence (Vinogradov 1998; Nussey et al. 2009; Preston et al. 2011).

In polygamous breeding systems, as found in many mammal species, males often have to compete for access to reproduction. Sexual selection has led to strong sexual dimorphisms for display or fight that can be associated with different food sources, habitat use, size and metabolic rates between males and females. In ungulates, for instance, males have a lower survival than females linked to the costs of sexually selected traits (Promislow 1992). This can be exacerbated when environmental conditions are harsh because males have lesser fat reserves than females and are thus more prone to starvation (Toïgo and Gaillard 2003). For example, interactions between aging and sex were investigated in five populations of three ungulate species, where, as expected, males had a lower survival than females, and this pattern increased with age (Loison et al. 1999). The increased rate of senescence of males relative to females seemed linked to the particular mating systems and level of male–male aggression.

In monogamous breeding systems, survival is expected to be more similar between sexes. Most monogamous species perform biparental care, although not necessarily the same parental role. In several monogamous species, the presence of a sexual dimorphism is generally associated with different investments in reproduction between sexes according to the advantages/disadvantages of sex-specific phenotypes (Clutton-Brock 1991), which may have consequences on the vital rates of each sex. For example, the high investment of male emperor penguins during the incubation due to a long fasting period is associated with lower adult survival rates in males compared to females (Barbraud and Weimerskirch 2001).

Few studies have investigated sex differences in life histories while taking into account age in monogamous species. We therefore examined sex and age influences on demographic traits in the wandering albatross (*Diomedea exulans*), a very long-lived socially monogamous species standing at an extreme in life-history strategies. They are one of the few Procellariiform species with a marked sexual dimorphism in size (Weimerskirch 1992), males being 10–20 % structurally larger and heavier than females, and with different associated foraging capacities (Weimerskirch et al. 2000; Shaffer et al. 2001; Lecomte et al. 2010). As they lay a single egg clutch, no difference between offspring (e.g. unequal begging) exists within the brood. Males and females share similar parental roles by alternating the same behaviours during both incubation and brooding, although relative investment in chicks is higher in males than in females (Weimerskirch et al. 2000). Sex-specific differences in parental effort during both the incubation and the fledging periods highlighted a higher absolute investment of males during the whole breeding season

linked to their bigger size (Weimerskirch 1995; Weimerskirch et al. 2000). However clues indicated that females needed more time to reconstruct their body condition after the long fasts during incubation (Weimerskirch 1995). Hormonal and foraging senescence have been detected in this species from cross-sectional analyses, particularly for males (Lecomte et al. 2010; Angelier et al. 2006). Old males exhibited much higher costs of foraging than middle-aged males: they foraged further, showed reduced activity and failed to restore baseline corticosterone levels suggesting their level of stress remained high. On the same time, baseline prolactin levels (parental hormone) were found to increase with age only in males (Angelier et al. 2006), suggesting a potential increase in parental investment whereas it remained constant in females.

Based on these earlier findings, we thus expected higher actuarial senescence in males than in females given their higher costs of foraging at older ages. We modelled simultaneously (in the same model) sex-dependent variations in aging for an array of five life-history traits: adult survival, probability of returning to the breeding colony, probability of breeding and two measures of breeding success (hatching and fledging probabilities). An earlier study found reproductive senescence in both sexes (Weimerskirch 1992), so we also expected reproductive senescence, but we had no a priori sex-specific prediction given the complex relationships between absolute investment which appeared to be higher in males but relative to their size more influential on females. As in previous studies investigating senescence in this species, we used a cross-sectional approach as we were particularly interested in population patterns.

Materials and methods

Study species and field methodology

Wandering albatrosses nest on sub-Antarctic islands throughout the Southern Ocean. The study was conducted at Ile de la Possession in the Crozet Archipelago (46°S, 52°E), Southern Indian Ocean, where 300–400 pairs nest each year. Although the minimal age at first reproduction is 5 years old, 10 years is the mean and modal age of first breeding in this wandering albatross population (Weimerskirch et al. 1997a; Gauthier et al. 2010). Birds return to their breeding grounds in December and females lay a single egg in late December–early January. Both parents incubate alternatively until hatching in March. Chicks are reared for ≈280 days and most young are fledged in November. There is no post-fledging care. This species has a particularly low breeding probability and it was long believed that, given the length of the breeding season, no bird that managed to bring a chick to fledging was entering

reproduction again. However, it was recently demonstrated that up to 6 % of the birds that fledged a chick still breed 2 years in a row, and the species is now considered as a quasi-biennial breeding species (Barbraud and Weimerskirch 2012). Also, approximately 80 % of birds that failed the previous year engage in another breeding attempt the following year.

Monitoring started in 1960, but all chicks have been systematically ringed only since 1966. In December, pre-breeding adults are controlled over the whole island. From mid-January to mid-February, at least three visits are carried out every 10 days at each nest to determine the identity, sex and breeding status (egg laid/egg hatched) of each individual. In mid-April, June and August, all nests are checked to control the survival of chicks. During all visits to the nests, non-breeding individuals are searched for and noted, and, given that ≈80 % egg failures generally occur late during the incubation period, there is a very small chance that these observed non-breeders are indeed early failed breeders or actual breeders. From mid-September to mid-October, all chicks about to fledge are ringed with a stainless steel ring and their survival until fledging controlled.

Multi-state model construction

Capture histories were constituted for all individuals ringed as chicks exclusively so that their age was known with precision. The age at first breeding was selected to be between 5 and 15 years old, as 97.5 % of observations of first time breeders lie in this range. The remaining 2.5 % were ignored as they may correspond to identification errors or birds that had bred before somewhere else (Weimerskirch et al. 1997a). In albatrosses, first breeders can have much lower survival and breeding success than experienced breeders (Nevoux et al. 2007), whatever their age of first breeding (between 5 and 15 years). They were thus considered separately to correct for a potential effect of selective appearance (Van de Pol and Verhulst 2006), but the results are not presented here because, to keep our message as clear as possible, we decided to focus particularly on age and sex effects in experienced adults.

Individuals were sexed in the field based on sexual size and plumage dimorphism, courting and mating behaviours (Weimerskirch et al. 2005). Sex was not known for all individuals, especially the ones that never came back to breed or that bred only a few times, so that the chance of recording their sex was small. Of the 8,929 birds ringed as chicks from 1966 to 2010, 1,672 were females and 1,697 were males. Of the remaining unsexed birds, 97 % were never seen on Possession Island, and most can be considered as dead before recruitment (Inchausti and Weimerskirch 2002). As all individuals needed to be included in

the model in order to avoid overestimating survival, two possibilities were considered. First, we could add uncertain states concerning the sex (Pradel et al. 2008). Second, since a previous study in the same colony estimated a population sex ratio of 0.574 at hatching (Weimerskirch et al. 2005), we could infer the sex of the unsexed birds using a binomial random distribution. As the model was already very complex, we chose to reject the first possibility. Since this sex-inference procedure concerned a large majority of individuals never seen breeding at the colony, it is unlikely that it caused a bias in demographic parameter estimates, except eventually for sex-specific juvenile survival and recruitment. Consequently, we did not test for sex-effects on these two parameters.

To encompass the complex potential interactions between life-history traits in quasi-biennial breeding species, a four-state model with two observable states corresponding to successful (SB) and failed breeders (FB) and two unobservable states standing for the post-successful (PSB) and post-failed breeders (PFB) should be used (Converse et al. 2009; Hunter and Caswell 2009; Barbraud and Weimerskirch 2012). As, in this study, the focus is put on age effects, a chick state (C, coded as 1 in capture histories) was added in the model. This allowed the determining and tracking of the age of each individual in the model, and the estimating of additional demographic parameters such as juvenile survival and recruitment probability. As we wanted to develop breeding success into hatching and fledging success probabilities, the FB state was divided into FBE (failed breeders at the egg stage, coded as 2 in capture histories) and FBC (failed breeders at the chick stage, coded as 3 in capture histories). The SB state was coded as 4 in capture histories. Because a substantial number of birds were observed as non-breeders at the colony, probably looking for mates, an additional observable state for non-breeders that came back to the colony (ONB, coded as 5 in capture histories) with its corresponding non-observable state (PONB) were added to the model (Appendix A, ESM). This additional information could be particularly helpful in (1) improving detection probability estimates on which the performance of all transition estimators depends, in particular survival and breeding probabilities, and (2) calculating another demographic parameter: return probability (Pardo et al. 2013). Therefore, our input data for the multi-state model consisted of individual recapture histories in the form of "1000002304045", for instance, where recruitment and breeding status at each age can be tracked. Zeros before recruitment correspond to the immature period where birds remain unobservable at sea. The few observations of immature birds on breeding grounds were ignored in this study. Zeros in the adult life can correspond to five events: PFBE, PFBC, PSB, PONB or dead. These underlying states and the transition probabilities based on the life

cycle in Appendix A, ESM allowed us to give demographic estimations of several life-history traits at the same time.

Multi-state models were parameterised in terms of five demographic traits including four successive reproductive traits: the survival probability (φ), return probability given survival (r), breeding probability given return (β), hatching probability given breeding (ω) and fledging probability given hatching (γ; see possible transitions in Appendix A, ESM; see matrices in Appendix B, ESM). Such an approach helps a better understanding of the architecture of senescence (Bouwhuis et al. 2009) as well as the potential differences between sexes that may arise at the population level. We deliberately chose to use multi-state modelling instead of generalised mixed modelling since this allowed us to intrinsically take into account the previous breeding state of individuals, which are particularly important in obtaining unbiased estimates of survival and reproduction in quasi-biennial breeding species. Capture–recapture models also allow the taking into account of the probability of detecting individuals (P) given their return to the colony. The difference between return probability and detection probability may be hard to get. The former informs on the probability that an individual came back to the colony, and, if it did, on the probability that it was detected or not. By considering these two parameters, we can thus estimate the proportion of individuals that came back to the colony without breeding which can represent essential information for population dynamics (Jenouvrier et al. 2005) and parameter estimation performance (Pardo et al. 2013). States were considered to be random variables, and successive states were assumed to obey a Markov chain. Transition probabilities between states were thus modelled with a five-step procedure, where survival, return, breeding, hatching and fledging are considered as five successive steps in transition matrices. Goodness-of-fit tests were performed for multi-state models (Pradel et al. 2008) using the software U-Care v.2.3.2 (Choquet et al. 2009). We ran the test on the Jolly–Move (JMV) umbrella model with only observable states (SB, FBE, FBC,ONB), excluding the first marking of fledglings (C state) at the nest because this state was never re-observed, and thus contributed no information to the test (Crespin et al. 2006).

Model selection procedure

In models with unobservable states not all parameters are identifiable (Hunter and Caswell 2009). Our aim was to test for age and sex-specific differences in demographic traits. Therefore models were constrained so that demographic traits were not state dependent, while still taking into account the bienniality of the species in the model structure. In addition for age (a) dependent models, parameters were constrained to be equal at $a = 1$, $a = 2$ and $a = 3$, and

$a = K - 3$, $a = K - 2$ and $a = K - 1$ (where K is the maximum potential age reached in our dataset given that the first chicks were ringed in 1966; Hunter and Caswell 2009).

Models were run with program E-Surge v.1.7.1 (Choquet et al. 2008). We started from a general model including an interactive effect of sex (g) and age (a) on each trait [φ(g.a) r(g.a) β(g.a) ω(g.a) γ(g.a) P(g.a)]. Model selection was firstly performed on detection probability then on fledging, hatching, breeding, survival and return probabilities. We had some difficulties properly estimating return probabilities, so we first selected the best model structure on survival while using the simplest age and sex structure on return probability which had the least parameters [model g + a (lin), see below for model notation], and selected the best model structure on return probability afterwards. The selected model structure on the trait previously modelled was kept to model the following trait of concern while keeping the general model structure for the other traits (Table 1). On each trait, we tested for age and/or sex effects. When age effects were selected, age-dependent linear (lin) and quadratic (quad) trends were applied either with an additive effect (g + a, where both sexes have different intercepts but a common slope) or an interaction effect (g.a, where both sexes have separate intercepts and slopes; Table 1).

As aging theories predict that life-history traits should start to senesce after the age of primiparity (Hamilton 1966), we started studying age effects from that point. We chose this average as our focus here was not to look at individual differences in aging but the differences between sexes at the population level. Between age 5 (the minimal age at first breeding) and age 10, parameters were set age-dependent and are not presented here for simplicity. Model selection was based on the Quasi-Akaike Information Criterion corrected for low sample sizes (QAICc). When ΔQAICc was less than 2 between two models, the parsimony principle was applied and the model with the least number of parameters was selected.

Results

The age-specific distribution of individuals observed at the colony was not even between sexes ($\chi^2 = 99.823$; $df = 41$, $P < 0.001$; Fig. 1a). The proportion of females recaptured on the colonies was higher than males before the mean observed recruitment age at 10 ($\chi^2 = 34.022$; $df = 9$; $P < 0.001$) and males were more abundant than females in middle-aged individuals before 22 ($\chi^2 = 51.809$; $df = 13$; $P < 0.001$), suggesting that there may not be enough middle-aged females to breed with. After 22 years old, no significant differences in sex ratio were detected ($\chi^2 = 14.778$; $df = 21$; $P = 0.833$; Fig. 1a). The oldest male in the dataset

Table 1 Model selection procedure applied on each trait consecutively to select the best age and sex structures on life-history traits of wandering albatrosses (*Diomedea exulans*) at Crozet Islands from 1966 to 2010: detection, fledging, hatching, breeding, survival and return probabilities

	Detection (P)	Fledging (γ)	Hatching (ω)	Breeding (β)	Survival (φ)	Return (r)	QAICc	np
General model	g.a	g.a	g.a	g.a	g.a	g.a	72,011.00	437
Selection on P	g + a	g.a	g.a	g.a	g.a	g.a	72,230.78	403
	a	–	–	–	–	–	71,994.31	404
	g + a (lin)	–	–	–	–	–	75,101.58	375
	g.a (lin)	–	–	–	–	–	72,005.96	377
	g + a (quad)	–	–	–	–	–	76,459.16	376
	g.a (quad)	–	–	–	–	–	72,013.64	378
	a (lin)	–	–	–	–	–	72,014.07	370
	a (quad)	–	–	–	–	–	**71,988.90**	**371**
Selection on γ	**a (quad)**	g + a	g.a	g.a	g.a	g.a	71,987.49	337
	–	a	–	–	–	–	72,029.40	336
	–	g + a (lin)	–	–	–	–	71,981.92	307
	–	g.a (lin)	–	–	–	–	71,973.40	311
	–	**g + a (quad)**	–	–	–	–	**71,968.24**	**308**
	–	g.a (quad)	–	–	–	–	71,968.57	313
	–	a (lin)	–	–	–	–	71,973.85	305
	–	a (quad)	–	–	–	–	71,972.12	306
Selection on ω	**a (quad)**	**g + a (quad)**	g + a	g.a	g.a	g.a	71,945.89	266
	–	–	a	–	–	–	72,272.06	264
	–	–	g + a (lin)	–	–	–	71,914.65	236
	–	–	g.a (lin)	–	–	–	71,920.02	240
	–	–	**g + a (quad)**	–	–	–	**71,911.93**	**237**
	–	–	g.a (quad)	–	–	–	71,919.66	242
	–	–	a (lin)	–	–	–	71,946.48	233
	–	–	a (quad)	–	–	–	71,936.39	234
Selection on β	**a (quad)**	**g + a (quad)**	**g + a (quad)**	g + a	g.a	g.a	71,908.94	203
	–	–	–	a	–	–	72,045.91	201
	–	–	–	g + a (lin)	–	–	71,841.89	173
	–	–	–	**g.a (lin)**	–	–	**71,825.46**	**177**
	–	–	–	g + a (quad)	–	–	71,861.32	174
	–	–	–	g.a (quad)	–	–	71,824.57	179
	–	–	–	a (lin)	–	–	72,010.29	171
	–	–	–	a (quad)	–	–	72,026.54	172

Table 1 continued

	Detection (P)	Fledging (γ)	Hatching (ω)	Breeding (β)	Survival (ϕ)	Return (r)	QAICc	np
Selection on ϕ	**a (quad)**	**g + a (quad)**	**g + a (quad)**	**g.a (lin)**	g + a	g + a (lin)	71,712.31	78
	–	–	–	–	a	–	71,726.93	76
	–	–	–	–	g + a (lin)	–	71,696.75	47
	–	–	–	–	g.a (lin)	–	71,700.49	52
	–	–	–	–	g + a (quad)	–	71,695.82	48
	–	–	–	–	**g.a (quad)**	–	**71,693.67**	54
	–	–	–	–	a (lin)	–	71,737.46	45
	–	–	–	–	a (quad)	–	71,737.47	46
Selection on r	**a (quad)**	**g + a (quad)**	**g + a (quad)**	**g.a (lin)**	**g.a (quad)**	g + a	71,764.00	85
	–	–	–	–	–	a	71,888.64	83
	–	–	–	–	–	g + a (lin)	71,759.91	54
	–	–	–	–	–	g.a (lin)	71,689.35	59
	–	–	–	–	–	g + a (quad)	71,721.98	55
	–	–	–	–	–	g.a (quad)	71,712.87	60
	–	–	–	–	–	**a (lin)**	**71,681.71**	**52**
	–	–	–	–	–	a (quad)	71,693.86	53

On each trait, sex (g), age (a) or constant (.) effects were tested. For detection probability, time (t) effects were also investigated. To model age effects, we used either age-dependent estimations (a alone) or age-dependent linear (*lin*) or quadratic (*quad*) trends. To model the combined effects of age and sex, we used either additive (different intercepts but same slope) or interaction (different intercepts and slopes) effects between sexes. In bold, is the model that had the lowest QAICc for the trait of concern while keeping the general model structure ($g.a$) on all other traits not yet selected and the best model structure on traits that were previously selected. All age trends were applied from age 10 onwards

np is the number of structural parameters, there is no rank deficiency in the final model that has 52 parameters

– Means the model is the same as upper. *np* is the number of structural parameters, there is no rank deficiency in the final model that has 52 parameters
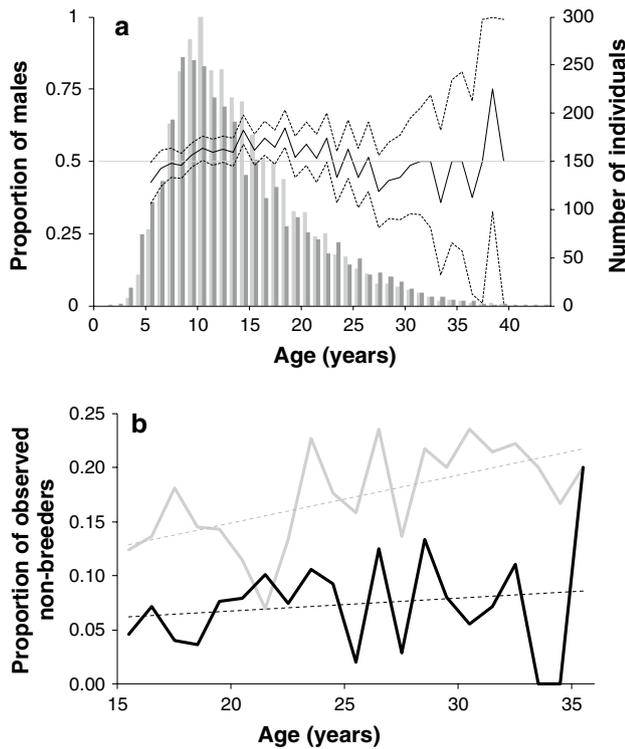
Fig. 1 a Proportion of males (*black line*) in the data and age pyramid showing the number of individual wandering albatrosses (*Diomedea exulans*) (breeders and non-breeders) at each age for both females (*dark grey*) and males (*light grey*) from the start of the monitoring in 1966 to 2010. *Dotted lines* are the 95 % confidence intervals of the proportion of males and the *grey line* represents the equal proportion of males and females. Birds that had not yet recruited were taken into account whereas they were absent from the analyses. **b** Proportion of observed non-breeders on the total number of observations for females (*black*) and males (*grey*) wandering albatrosses as a function of age. These numbers were drawn from 15 years old, as before that age observations could correspond to immature birds coming back on land before recruiting; they stop at 35 because after that age, sample size was lower than 5. *Dotted lines* represent linear regressions for each sex, only the slope for males was significant
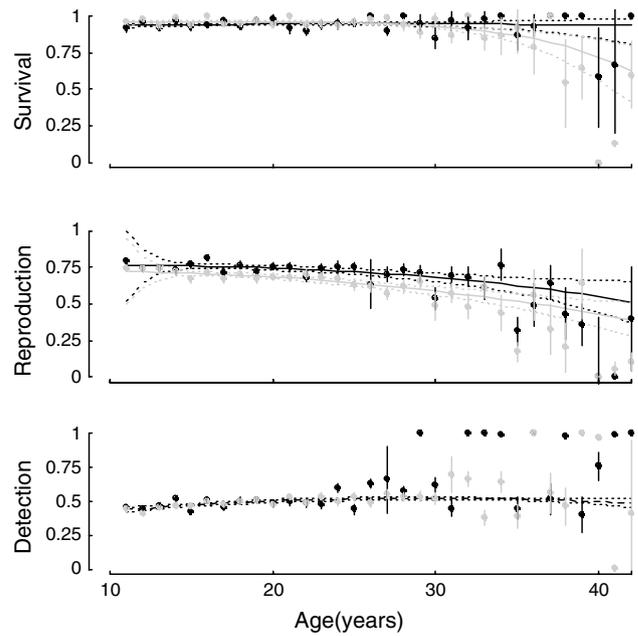
Fig. 2 Age-dependent responses of females (*black*) and males (*grey*) for survival, global reproduction (product of return, breeding, hatching and fledging probabilities) and detection probabilities. The detailed patterns of different age-dependent reproduction are given in Fig. 3. *Dashed line* represents the average response between sexes for a trait where sex effects were not selected (Table 1). 95 % confidence intervals are represented by *dotted lines*. *Dots* represent raw data with their standard errors. Sample sizes in each age-class and each sex can be found in Fig. 1

was 39 years old and the oldest female 43. The averaged proportion of observed non-breeders across ages from 15 to 35 was more than twice (2.34) as high in males (0.17 ± 0.042) than in females (0.07 ± 0.043; Fig. 1b). Furthermore, whereas the proportion of female observed non-breeders did not vary with age (Pearson $r = 0.156$, $df = 19$, $P = 0.499$), in males, it increased significantly (Pearson $r = 0.601$, $df = 19$, $P = 0.004$; Fig. 1b).

Goodness of fit tests ($\chi^2 = 570.936$; $df = 576$; $P = 0.552$ for females and $\chi^2 = 646.339$; $df = 698$; $P = 0.919$ for males) indicated that the general JMV model fitted the data correctly.

Model selection clearly indicated different patterns in survival with age between males and females (Table 1). Before age 27, survival probability was significantly higher in males on average at 0.960 ± 0.004 than in females 0.944 ± 0.003. Subsequently, female survival remained

stable reaching 0.939 ± 0.039 at the oldest, but male survival dropped to 0.625 ± 0.104 at age more than 42, suggesting a strong actuarial senescence (Fig. 2).

A global measure of age-dependent reproduction was calculated as the product of return, breeding, hatching and fledging probabilities (Fig. 2). It showed a clear senescence with a significant difference between sexes. Males started from a lower value compared to females at age 11 (respectively, 0.719 ± 0.114 and 0.759 ± 0.120), and suffered from a higher rate of global reproductive senescence as they reach values of 0.392 ± 0.060 and 0.513 ± 0.073, respectively, at age 42.

Return probability was not different between sexes (Table 1). This trait did not present any variation with age and stayed at 0.999 ± 0.000, suggesting that all birds had the same probability of returning to breeding colonies whatever their age and sex (Fig. 3).

The probability of detecting an individual given it was alive was identical in males and females (Table 1). Although the selected model suggested a quadratic trend with age of detection probabilities, the variation was small and the average detection probability was 0.502 ± 0.006 (Fig. 2).

As for survival, the breeding probability varied differently between sexes according to age. Females had a
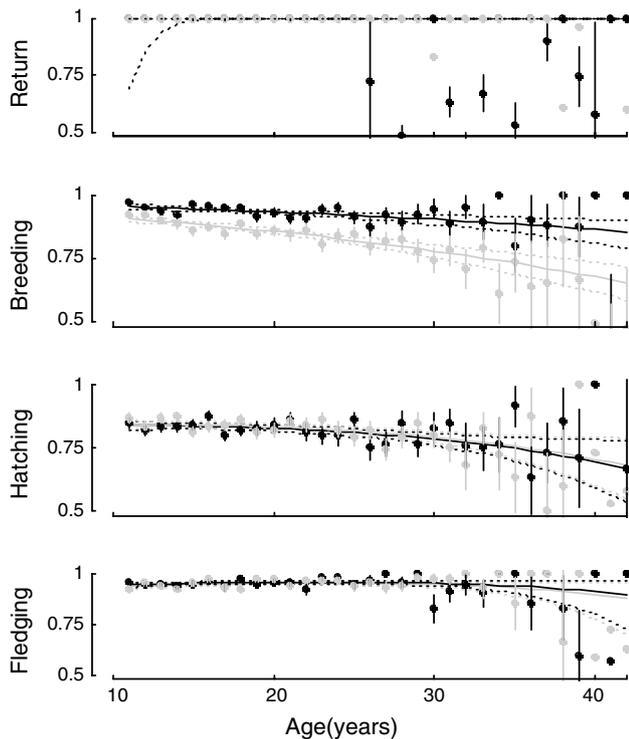
Fig. 3 Age-dependent responses of females (*black*) and males (*grey*) for all reproductive traits. *Dashed line* represents the average response between sexes for a trait where sex effects were not selected (Table 1). 95 % confidence intervals are represented by *dotted lines*. *Dots* represent raw data with their standard errors. Sample sizes in each age-class and each sex can be found in Fig. 1

significantly higher breeding probability (0.955 ± 0.004) than males (0.906 ± 0.006) at age 11 (Fig. 3). Both probabilities decreased substantially with age, but at a faster rate in males down to 0.654 ± 0.034 at age 42–44 (27.8 % decrease) than in females (0.854 ± 0.027; 10.6 % decrease).

Model selection indicated sex and age effects on hatching and fledging probabilities (Table 1). Both decreased with age at a similar rate in males and females, although the differences between sexes were very small (Fig. 3) and the 95 % confidence of the estimates largely overlapped. Age-effects were stronger on hatching than on fledging probability. Hatching probability decreased from 0.843 ± 0.009 at age 11 down to 0.677 ± 0.063 at age 42 and older (19.7 % decrease), and fledging probability decreased from 0.942 ± 0.007 at age 11 down to 0.888 ± 0.059 at age 42 and older (5.7 % decrease; Fig. 3).

Discussion

This work demonstrated the existence of considerable sex-related differences in ageing in a monogamous and dimorphic species, the wandering albatross. By using a multi-trait

approach, we studied variations in survival, return, breeding, hatching and fledging probabilities, and demonstrated that females better face senescence in this species. Indeed, males and females presented both actuarial and reproductive senescence, but the rate of senescence was higher in males in particular in survival. Although hatching and fledging probabilities decreased with age, they remained similar for males and females. By contrast, breeding probabilities decreased at a faster rate in males than in females. These results are discussed in the light of differential physiological and fitness costs of reproduction but also of population processes that may affect ageing in some specific demographic traits.

Male reproductive strategies are generally associated with elevated mortality rates and are considered to follow a 'live fast, die young' strategy (Bonduriansky et al. 2008). Based on anisogamy, females cannot increase their breeding success as much as males as they are constrained by time and resource investment in their offspring. However, males can keep increasing their fitness by maximising the number of females they mate with, leading to a high wear-and-tear strategy, particularly in highly dimorphic polygynous species. This can lead to a lower survival rate of males and an earlier onset of ageing (Loison et al. 1999; Clutton-Brock and Isvaran 2007; Preston et al. 2011). It is still unclear if these patterns can apply to birds that are mostly monogamous, but comparative studies appear as a good tool to identify the determinants of sex-differences in life-histories. In 1994, Owens and Bennett (1994) used 37 bird species to investigate if the sex-bias in mortality could be linked to sexual dimorphism and sex-bias in parental care at different moments of the breeding cycle. They found that only the latter had a significant effect and that the sex that presented a bias in parental care (in particular, during the chick rearing period) suffered from a sex-biased mortality. In all the bird species they considered, females tended to be the sex that cared the most and thus presented the highest mortality. However, the seabirds dataset used by Owens and Bennett, a taxa that is known to present shared parental roles in the vast majority of species, sexes presented similar mortality rates. Clutton-Brock and Isvaran (2007) went a step further by examining ageing in a comparative analysis on species with contrasted sexual and social strategies. They showed that sex differences in adult life expectancy (the numbers of years that an individual expects to live on average after reaching adulthood) were stronger and more frequent in polygamous than in monogamous species. The authors recognised the inevitable bias that most polygamous species they studied were mammals and most monogamous species were birds, but it is still intriguing to note that the relative adult life expectancy (male/female adult life expectancy) estimated for the wandering albatross from our survival estimates was ≈0.93. This value is

above the range of average values found by Clutton-Brock and Isvaran (2007) for polygamous species (0.68–0.76), but below the range found for monogamous species in their study (0.99–1.12). This suggests that the breeding system alone is not responsible for sex-specific differences in aging patterns. In species such as the wandering albatross, in which parental roles are identical and shared, we believe sexual dimorphism may be partly responsible for sex-specific differences in aging pattern, although Owens and Bennett (1994) found its effect of life-history traits insignificant in their study.

According to Carey (2003), male–female survival crossovers (here males present higher survival values than females during early breeding life whereas females present higher values than males in late breeding life) could be an artefact of compositional change in the male and female subpopulations due to demographic heterogeneity (Vaupel and Yashin 1985). Difference in demographic heterogeneity in males and females may be due to greater variance in males frailty that in females frailty (Vaupel et al. 1979). Such a phenomenon is likely to play a role since variance in heterogeneity in survival is ≈28 greater in male wanderers than in females (Barbraud et al. 2013). Male–female differences in survival could be due to biological differences between males and females at the individual level manifested as differences in age-specific mortality (Carey 2003). These differences can be grouped in three interrelated categories.

1. *Constitutional endowment.* This includes all structural, physiological, endocrinological and immunological factors that may affect the ability of each sex to resist both external (disease, stress, physical challenge) and internal sources (deterioration) of mortality. Lecomte et al.'s 2010) study tested for nine baseline physiology markers as proximate causes of senescence, no significant change with age was detected in wandering albatrosses. However, they noticed changes in behaviour with age that coincide with the sex differences we found, this is discussed below.

2. *Physiological costs of reproduction.* Each sex has specific costs of reproduction including hormones, gonad development and production of eggs or offspring. Thus, differences in sex/age-specific life-history traits might be expected. Contrary to our expectations, hatching or fledging probabilities changed with age in a similar way in both sexes in the wandering albatross. This is despite the fact that, during incubation, females restore their body condition with more difficulty than males, have to increase their foraging duration, have a reduced foraging efficiency, and forage in different and less productive zones than males (Weimerskirch 1995). By contrast, during the chick-rearing period, males invest more by delivering larger and more energetic meals relative to their mass and more often than females (Weimerskirch et al. 2000). Additionally, females stopped feeding the chick earlier than males (Weimerskirch et al. 1997b). One might thus hypothesise that these differences in terms of costs of reproduction might compensate between the sexes, which would explain why we did not detect a sex effect on reproductive senescence. However, previous studies have demonstrated that, whereas females kept a constant foraging effort with age, males exhibited a decrease in their foraging capacities. Old males (>30 years) foraged in different waters than prime-aged males, making longer trips at sea and gaining less mass per trip (measured directly as in Lecomte et al. 2010 or indirectly via corticosterone levels as in Angelier et al. 2006). The exact same trends were detected in a closely related species, the grey-headed albatross (*Thalassarche chrysostoma*) (Catry et al. 2006). Still, both sexes presented quite an abrupt senescence on their global reproduction as previously found (Weimerskirch 1992; Weimerskirch et al. 2005; Lecomte et al. 2010). It is therefore possible that the decrease in foraging capacities in old males is not sufficient to alter hatching and fledging probabilities differentially from females. This could be particularly the case in old individuals, since old females might spare their reproductive costs by producing more female chicks (Weimerskirch et al. 2005), which are less energetically costly to raise than male chicks due to their differences in size and growth. The proximate causes of the decrease in old males foraging abilities compared to females' remains mysterious (Lecomte et al. 2010). Finally, the lower survival of females compared to males at younger ages may result from higher costs of first reproduction for females as found in a sexually dimorphic monogamous species with similar life-history traits, the greater flamingo (*Phoenicopterus roseus*) (Tavecchia et al. 2001).

3. *Behavioural predispositions.* This category includes all behavioural traits evolved to locate, compete for and defend territories and mates. Since both sexes exhibited the same variations in breeding success, it is relatively unlikely that the male-biased mortality at older ages was linked to an elevated relative intrinsic fitness cost of reproduction compared to females. Indeed, unlike polygamous species, wandering albatrosses are not fighting for mates, do not have to guard females nor develop costly secondary sexual characters. However, we saw that their patterns of sex-differential ageing were intermediate between those observed in strict monogamous and strict polygynous species (Clutton-Brock and Isvaran 2007). Wanderers display before starting to mate even with their usual partner and

even more if they need to find a new mate (Jouventin and Lequette 1990). Divorce rate is low in this species (≈10 %), but inevitably increases with age due to increased chances of losing the current partner through its death. Therefore, the costs of displaying might be more elevated in older than in younger males. Also, male wanderers stay ashore longer than females before laying to build and guard the nest (average males 16 days, females 5 days). Consequently, they have to bear a fasting period three times longer than that of females. As their foraging ability is strongly reduced at older ages, it is possible that they have more difficulties reconstructing their condition compared to old females, resulting in higher mortality.

In the Crozet wandering albatross population, there is a highly skewed sex ratio due to female-biased mortality in fisheries (Weimerskirch and Jouventin 1987; Weimerskirch et al. 2005). This mortality was very high in the late 1980s and is now lower, but is highly suspected to still be relatively important in subtropical zones north of Crozet where females forage and encounter trawlers targeting tuna. We suspect that the sex ratio imbalance due to fisheries bycatch may represent a cause of decrease in males breeding probability if not enough females are available for widowed males (already demonstrated in Weimerskirch et al. 2005). Additionally, one interesting thing that may arise and should be tested more deeply in the future is the potential link between the skewed population sex ratio and the aging patterns we found. Indeed, in the age pyramid of this population, we saw an excess of middle-aged males. In wandering albatrosses, we know from a companion study that the decrease in male breeding probability results in an increasing numbers of males that are present at breeding colonies without breeding (Pardo et al. 2013). Although Jouventin et al. (1999) showed that wanderers tend to pair with a partner of approximately the same age, this was only shown for individuals up to 20 years old. Therefore, we suspect that, given the skewed sex ratio, females older than 30 may tend to pair with available middle-aged males instead of males of the same age that appeared senescent and exhibited reduced survival probability. Such a phenomenon of male out competition from breeding by younger individuals was demonstrated in fallow deer (*Dama dama*; McElligott et al. 2002). Also, non-breeders may represent lower quality individuals independently of their age as demonstrated in Black-legged Kittiwakes (*Rissa tridactyla*; Cam et al. 1998), thus explaining why the difference in breeding probabilities of males and females wandering albatrosses presents such an increase with aging.

Finally, part of the decrease in male survival might be an artefact if old males stayed permanently at sea. Although temporary emigration linked to the biennial habits of this species was corrected in our model with the use of unobservable states, permanent emigration was not. Previous studies have demonstrated that permanent emigration can create an underestimation of survival probability (Pollock 1982). In our case, emigration by males is unlikely, since most breeding sites of the species were surveyed, and previous studies never documented emigration of old breeding individuals (Inchausti and Weimerskirch 2002) or even of younger breeders. However, we can not exclude the possibility that old males unable to mate stayed permanently at sea or came back punctually to breeding sites and were not recaptured.

As the length of individually-marked datasets increases, the number of studies demonstrating senescence is rising. Bouwhuis et al. (2012) developed a tool to compare the fitness cost of senescence between species, which can also be applied to investigate differences between sexes. Using this tool for the wandering albatross data allowed us to estimate that the fitness cost of senescence was 2.3 times larger in males than in females (1.487 vs. 0.667, respectively). We also worked these numbers in the relationship found for birds between peak survival rate and fitness cost of senescence in Bouwhuis et al. (2012) (Appendix C, ESM). The wandering albatross data allowed the filling of a gap that the authors noted in their study: a lack of long-lived birds. Wandering albatrosses positioned well in the relationship for birds, with relatively very low fitness cost of senescence compared to mammals of equivalent survival. This could be explained by the fact that the number of individuals concerned by the lowest rates of senescence after 30 years old is relatively small compared with prime-aged birds.

Conclusions and perspectives

Wandering albatross sex differences in aging revealed complex and unexpected patterns: both sexes presented the same senescence patterns on breeding success although differences in relative physiological costs of breeding are known. Males exhibited a substantial reduction in breeding probability that may be explained by the fitness costs of reproduction associated with the wear-and-tear strategy common in males across taxa, in particular in polygamous species but perhaps also in dimorphic monogamous species. The drop in male breeding probability also seemed to be influenced by a population level phenomenon: female biased bycatch rates that led to a middle-aged population sex ratio skewed towards males.

Males also showed stronger rate of and earlier onset of senescence on survival probability, highlighting that, although being more often killed in fisheries, females better face senescence. Such age- and sex-related studies bring exciting information on the links between the evolution of

sex differences and the evolution of aging in a species that stands at an extreme in life-history traits. Our study thus prepares for new inter-specific comparative studies on age- and sex-dependent patterns in the polygamous/monogamous gradient.

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