

Population sex ratio variation in a monogamous long-lived bird, the wandering albatross

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Summary

1. Factors affecting population birth sex ratio and variations of sex ratios within population in very long-lived animals are poorly known, apart for humans that have attracted much attention. We measured the age and sex structure of a population of a monogamous long-lived seabird, the wandering albatross *Diomedea exulans*, where reproductive performance of individuals is known, to examine factors affecting sex ratio variation and survival consequences of producing a particular sex.

2. The overall sex ratio at hatching is significantly biased toward the production of males. Very young and old parents tend to produce an excess of female offsprings, whereas intermediate-aged birds, which represent the bulk of the population, produce an excess of males. Low-quality parents (quality is measured as average breeding success over the cumulated past breeding life, and is not related to condition or age) produce more female chicks compared with high-quality parents that represent the bulk of the population. The combined effect of age and quality of parents produce an extensive sex ratio variation at the level of the population.

3. The survival of male and female parents is influenced differently by their quality and by the sex of offspring. Male parents die in larger numbers when rearing a female chick, whereas low-quality female parents have a lower survival, especially when they rear a male offspring, the sex needing higher parental investment. The differences between males and females parents' survival are probably due their contrasted investment in parental care.

4. After fledging, during the 5–8-year period of immaturity, there is a much higher mortality of males that balances the surplus of males at hatching and fledging and results in a similar number of males and females at the time of recruitment. However, the overall operational sex ratio is male biased due to the slightly higher mortality of adult females that results in an excess of old widowed males: excluding these post-reproductive males leads to an unbiased operational sex ratio.

5. These results show that sex ratio at hatching varies extremely with the age and phenotypic quality of parents, and lead to a complex age and sex structure of the population in this strictly monogamous long-lived species.

Key-words: age effect, individual quality, operational sex ratio, recruitment, survival.

Journal of Animal Ecology (2005) **74**, 285–291

doi: 10.1111/j.1365-2656.2004.00922.x

Introduction

Despite the extensive literature on sex ratio, little is known about structure and sex ratio of natural populations (Orzack 2002). The sex ratio should be close to

equilibrium because of the frequency dependent reproductive advantage of the rare sex (Fisher 1930): selection is expected to favour individuals biasing the offspring sex ratio in response to the ratio of reproductive males and females in the population, i.e. the operational sex ratio (OSR, Emlen & Oring 1977). However, there is little evidence for adaptive sex ratio adjustment in response to OSR (Clutton-Brock & Iason 1986) in

large part due to the difficulties in detecting weak skews in sex ratios, especially primary, unless sample sizes are extensive (Lummaa, Merilä & Kause 1998). Most theories and studies on sex ratio variation have rather focused at the family level and made independently of predictions about population-level patterns because most authors agree that Fisher's equal allocation theory applies (Frank 1990).

Individuals are expected to adjust the sex ratio of their offspring in line with the fitness value of those offspring and the effect of rearing those offspring on their own residual reproductive value (Trivers & Willard 1973; review in Frank 1990). In vertebrates, the most important source of sex ratio data has been polygynous mammals, especially ungulates where sex ratio biases are expected, at least at the family level (Clutton-Brock & Iason 1986; Hewison & Gaillard 1999; Sheldon & West 2004). Much less is known on monogamous species, especially long-lived species where sex ratio variations are likely to occur because of age-related differential reproductive effort or sex-specific differential mortality. For example life history predicts that reproductive effort should increase with age as reproductive value decreases (Stearns 1992), and thus selection may favour adjustment of offspring sex ratio according to the age of parents. These aspects have never been examined in a monogamous long-lived animal with the noticeable exception of humans (review in Lazarus 2002) where studies have focused to a large extent on biases in population, and age-related, birth sex ratio, biases whose origin is still under debate. In birds the advent of molecular techniques for the sexing of young birds has opened important perspectives in this group of vertebrates (Griffiths, Daan & Dijkstra 1996; Fridolfsson & Ellegren 1999). Deviation from parity at the population level appears exceptional (Gowaty 1993) and small in magnitude, especially when considering primary sex ratio, and sex ratio variations within population remain rare (Hardy 2002), although facultative adjustment has been documented in several families (Ellegren, Gustavsson & Sheldon 1996; Komdeur *et al.* 1997).

Procellariiform birds, such as albatrosses have several life-history traits that make them interesting model systems for the study of sex-specific parental investment and population sex ratio. They are strictly monogamous, produce at most a single offspring every year, and are long-lived, which results in strongly age-structured populations. Both parents perform similar parental care roles and return year after year to the same colony once they breed, and young birds return to their birth place (Warham 1990). The wandering albatross *Diomedea exulans* (Linnaeus) is one of the few procellariiforms exhibiting a significant sexual dimorphism in size (males are 20% larger than females, Weimerskirch 1992) offering the additional opportunity to test hypotheses concerning parental investment, and the influence of sex ratio biases on population structure. Male chicks require more energy than female chicks, suggesting that they are more costly to rear

(Weimerskirch, Barbraud & Lys 2000) and possibly that rearing a male offspring would decrease longevity, as debated for example in humans (Beise & Volland 2002; Helle, Lummaa & Jokela 2002). In this study we examine the sex ratio at birth, the OSR at the population level, as well the influence of the age and quality of the parents on the sex ratio of offspring and the consequences of rearing male or female chicks for parents in a population of wandering albatrosses where most of the individuals have been monitored since birth.

Methods

FIELD STUDY

We studied the sex ratio at birth in 1999 at Ile de la Possession, Crozet Islands (46°S, 52°E), south-western Indian Ocean. The ongoing mark-recapture programme of the wandering albatross at Ile de la Possession has provided yearly information on the entire population of the island, approximately 400 pairs breeding each year for the last 40 years. Adults were sexed from plumage characteristics, size, and previous capture history. Details of the mark-capture-recapture study can be found in Weimerskirch, Brothers & Jouventin (1997). Banding of chicks prior to fledging has been carried out since 1965. As fledglings return to their birth place (Inchausti & Weimerskirch 2002), the age structure of the population can be determined for birds aged 1–34 years. Banding of breeding birds of unknown age started in 1959. For these individuals we used an estimated age calculated from the year of banding and adding 6 years, the minimum age at first breeding (Weimerskirch *et al.* 1997). Thus in the group of birds aged 34 years or more, age of most birds are probably minimum ages and the numbers of birds older than 40 years is underestimated in Fig. 1. The age of parents was calculated as the age of male + the age of female divided by 2.

In May–June 1999 blood samples were collected from the intertarsal vein of 290 chicks (aged 1–2 months) on all the colonies of Ile de la Possession (Weimerskirch & Jouventin 1987). Two hundred to 300 µL of blood was collected using a 25-gauge needle and a 1 mL syringe. Ninety per cent ethanol was added to the sample, which was stored at ambient temperature and sent back in France for analysis.

MOLECULAR SEXING

Birds were sexed using a molecular method (Fridolfsson & Ellegren 1999). The results were first validated with 15 adult birds of known sex. To perform molecular sexing, DNA was prepared from blood samples using Proteinase K digestion followed by phenol extraction (Fridolfsson & Ellegren 1999). After centrifugation, the pellet was again washed in 1 mL PLB. After removing the supernatant, the pellet was incubated for 1 h at 58 °C.

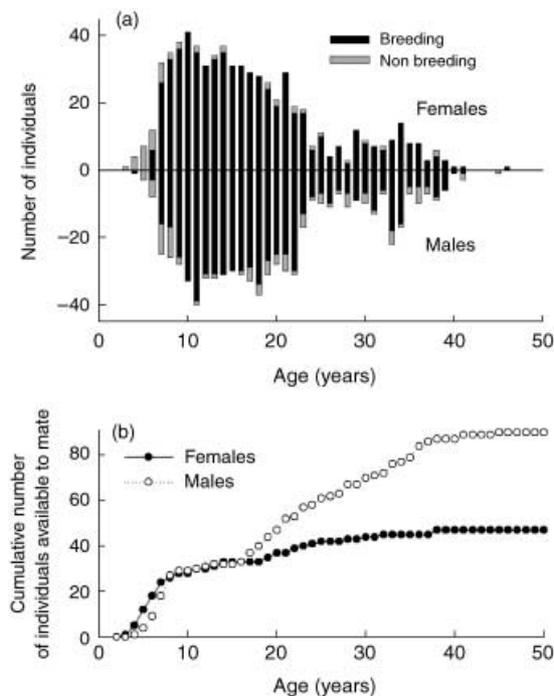


Fig. 1. Changes in relation to age in (a) the number of breeding and nonbreeding males and females alive in 1999 in the wandering albatross population of Ile de la Possession, and (b) in the cumulative number of nonbreeding males and females available to mate according to age. When testing the significance of the sex ratio for each age class, the bias became significant only from 23 years ($\chi^2_1 = 4.2$, $P = 0.041$) and older ages.

We were able to extract DNA from 256 samples of the 290 samples collected in the field because of problems with the conservation of samples and the inability to extract DNA. Polymerase chain reaction reactions were performed in 20 μL volumes on a Perkin Elmer 9600 Thermal Cycler using 0.5 U AmpliTaq polymerase, 200 μM deoxyribonucleoside triphosphate, 10 mM Tris-HCl pH 8.3, 50 mM KCl, 2 mM MgCl_2 , and 2 pmol of primers 2550F (5'-GTTACTGATTCGTC TACGAGA-3') and 2718R (5'-ATTGAAATGATC CAGTGCTT-3'). The thermal profile comprised an initial denaturing step of 94 $^\circ\text{C}$ for 4 min. We then ran 25–35 additional cycles consisting of a denaturation step at 94 $^\circ\text{C}$ for 30 s, an annealing step at 50 $^\circ\text{C}$ for 30 s, and an extension step at 72 $^\circ\text{C}$ for 40 s. There was a final extension step of 5 min after the last cycle. Polymerase chain reaction products were separated in 1% agarose gels, run in standard TBE buffer for 1 h, and visualized by ethidium bromide staining.

OPERATIONAL SEX RATIO, SURVIVAL OF IMMATURES AND ADULTS

Wandering albatrosses have a biennial breeding cycle, birds rearing a chick take a sabbatical year the following season (Tickell 1968) when they remain continuously at sea (Weimerskirch & Wilson 2000) so that only approximately half of the breeding population is present on land during a particular season. The population

structure in 1999 was calculated as the number of birds breeding in 1999, plus the birds in sabbatical year that had fledged a chick in 1998 and were alive in 2000, plus the nonbreeding population present on land in 1999. The OSR (following Clutton-Brock & Parker 1992) was calculated as the proportion of males in the nonbreeding population present on land in 1999 and available to mate. The proportion of male and female fledglings surviving to breeding was calculated for 10 cohorts of chicks fledged between 1980 and 1990 on Ile de la Possession and recaptured subsequently on the island until 2002. The quality of adult parents rearing chicks in 1999 was estimated from their past reproductive performances measured as the average breeding success over years prior to 1999, i.e. over 33 years, for birds with at least three seasons of known breeding success. Thus for young individuals, because of their short reproductive history, no estimate of quality is available.

The survival of adults rearing chicks of known sex in 1999 was estimated from their recapture histories between 2000 and 2003. To study the relationship between age of the parent and sex of offspring we also used the sample of 87 chicks sexed at fledging that was studied by Lequette & Weimerskirch (1990) and Weimerskirch *et al.* (2000). The mass of adult breeding birds was measured in 2000 and 2001 at the start of incubation shifts (see Weimerskirch 1992).

All statistical tests were performed using SYSTAT 10, and curve fitting with Sigma-Plot 2000.

Results

POPULATION STRUCTURE AND OPERATIONAL SEX RATIO

In 1999 the population (1371 individuals) was composed of 1235 breeders and of 136 nonbreeders available to mate (Fig. 1a). Among these nonbreeders the OSR was strongly male biased (65.5% of males, $\chi^2_1 = 12.8$, $P < 0.01$). This bias was due to an excess of males among older birds: this bias becomes significant when including birds older than 23 years (Fig. 1b).

SEX RATIO OF CHICKS

In 1999 the sex ratio of 256 chicks 1 month after birth was strongly biased toward males (57.4% of males, Pearson $\chi^2_1 = 5.64$, $P = 0.018$). The mortality between hatching and the age of 1 month when the chicks were sexed was negligible (two of 292 chicks surveyed) indicating that we are measuring the primary sex ratio (if we assume that there is no bias in mortality in the egg). The mortality between the age of 1 month and fledging (at the age of 8–9 months) was very low (1.9%, two males and three females chicks died) and produced no changes in sex ratio at fledging.

The sex ratio shows significant changes with the age of parents (Fig. 2a), with a trend for very young birds and old birds to produce more females, and chicks

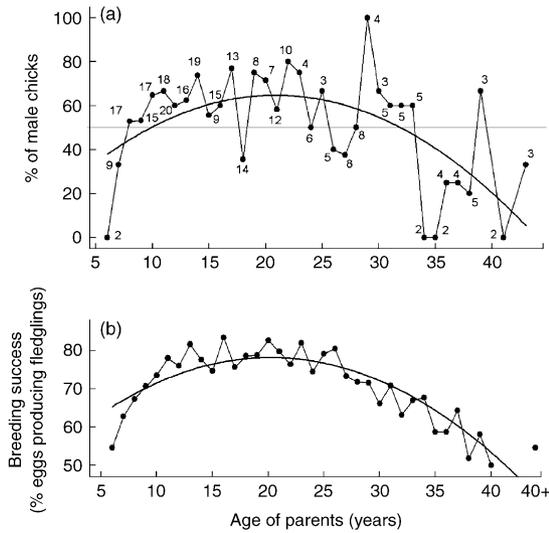


Fig. 2. (a) Change in relation to the average age of parents in the proportion of male chicks (figures indicate sample size; quadratic function $y = 11.7 + 5.1x - 0.12x^2$, $R^2 = 0.351$, $P = 0.0008$). We used average age of parents because wandering albatrosses mate with partners of similar ages, trends are similar when using father age or mother age, and (b) change in the breeding success in relation to the age of parent (quadratic function $y = 52.2 + 2.6x - 0.063x^2$, $R^2 = 0.774$, $P < 0.0001$).

from prime age parents having a sex ratio biased toward males [Generalized Linear Model (GLM) for sex ratio with age, and its square, treated as a continuous variable, age term $F_{1,301} = 5.48$, $P = 0.020$, age squared term $F_{1,301} = 7.77$, $P = 0.005$].

QUALITY OF PARENTS

Wandering albatrosses have on average a high breeding success (average 0.766 chick per breeding attempt, $n = 10\ 280$ breeding attempts), which moreover varies according to the age of the parents (Fig. 2b). We used the past reproductive performances as a measure of individual phenotypic quality. The sex ratio of offsprings was influenced by the past reproductive performance of their parents, birds with lower overall breeding success tending to produce more females (GLM for sex ratio with breeding success as continuous variable; male parents: $F_{1,186} = 4.7$, $P = 0.031$; female parents: $F_{1,174} = 2.9$, $P = 0.094$). There is no significant relationship between age and our measure of quality (females: $r_{163} = -0.105$, $P = 0.179$; males: $r_{154} = -0.03$, $P = 0.712$). The combined effect of age and quality of parents results in an extensive sex ratio variation at the level of the population (Fig. 3).

Within the population the individuals with low previous breeding success represent only a small proportion (Fig. 4). Because the frequency distribution of the breeding success over measured lifetime is clearly bimodal, we separate individuals into poor-quality and high-quality individuals (Fig. 4). Poor-quality parents produced an excess of females, and high-quality parents an excess of males (GLM; male parents: $F_{1,186} = 8.0$, $P = 0.004$; female parents: $F_{1,174} = 5.1$, $P = 0.023$).

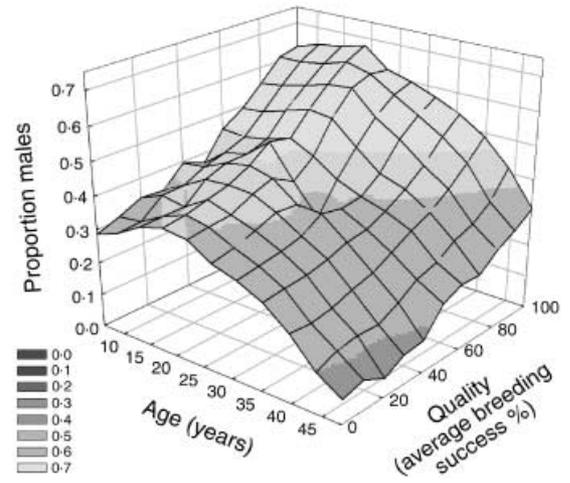


Fig. 3. Model showing the relation between sex ratio, age, and previous lifetime reproductive success.

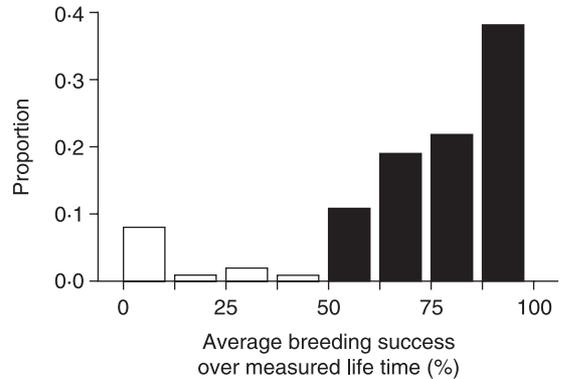


Fig. 4. Frequency distribution of the average reproductive success over lifetime of wandering albatrosses with the separation between poor-quality (white bars) and high-quality (black bars) individuals at 50%.

SURVIVAL OF ADULTS AND IMMATURE BIRDS

For male parents, to the contrary of what could be expected, the mortality of males rearing female chicks was higher than that of parents rearing male chicks (Table 1; 88.8% of the parents rearing male chicks returned to the colony 2 or 3 years later as compared with 76.8% of those rearing females). For female parents, the sex of the offspring had no direct influence on their survival. Poor-quality female had a lower survival, and there was a significant interaction between female quality and the sex of the offspring indicating that when rearing a female chick good- and low-quality birds survive similarly, whereas when rearing a male, high-quality females survive better than low-quality birds (Table 1). Older parents survived less than parents of intermediate age (Table 1).

Of the 2026 offspring fledged between 1980 and 1990, 940 (46.4%) have been recaptured on the island at some time up to 2002. Among these 940 individuals, 457 were males (48.6%, Pearson $\chi^2_1 = 0.72$, $P = 0.396$). Assuming that the sex ratio at fledging between 1980

Table 1. Generalized Linear Model (GLM) testing the effects on adult survival of males and female parents of the sex of offspring, age of parent, and quality of parent. Statistics are given for the full model before the variable is removed through a backward stepwise selection if $P > 0.1$, all interactions terms were tested, but not reported unless significant

Effect	d.f.	<i>F</i>	<i>P</i>
Male			
Sex of offspring	1	4.6	0.033
Age of parent	1	3.4	0.066
Quality of parent	1	0.1	0.753
Error	185		
Female			
Sex of offspring	1	0.4	0.522
Age of parent	1	6.4	0.012
Quality of parent	1	5.4	0.021
Quality × Sex of offspring	1	6.8	0.009
Error	173		

and 1990 was as biased as that observed in 1999 (see Discussion for justification), the proportion of males surviving from fledging to the first return on land was lower than that of females (0.393 vs. 0.559, respectively, $\chi^2_1 = 54.7$, $P < 0.0001$). This implies that the mortality rate was 29.6% higher for males than for females during the period of immaturity.

Discussion

BIRTH AND OPERATIONAL SEX RATIOS

In this study we have been able to measure sex ratio just after hatching by using molecular sexing: this is rarely done and important because sex-specific mortality of chicks is likely to occur, especially in sex dimorphic species. In wandering albatrosses the sex ratio shortly after hatching is biased toward males (57.4% of males). Similar biases (not significant because of small sample size) were observed during other seasons, in 1986 and 1994 (54%, Weimerskirch *et al.* 2000) and in 2002 (56.1%, $n = 41$, unpublished) indicating that the bias is probably consistent over years. The male bias remains until fledging 6 months later, i.e. until the end of parental investment mainly due to the mortality of chicks during the period of parental that is consistently low over years (Weimerskirch *et al.* 1997).

At the level of the wandering albatross population, the overall OSR, the ratio of males to females available to mate in a population at a given moment (Emlen & Oring 1977), is biased toward males. OSR is often difficult to measure, yet it is essential for understanding the variation in sex role and intensity of mating competition that may influence the evolution of biased sex ratios (Kvarnemo & Ahnesjö 2002). A bias in OSR might lead to lowered mean fecundity among individuals of the more abundant sex. In the wandering albatross the differential between the number of males and females results only from the larger number of old males (Fig. 1b), probably due to the slightly higher sur-

vival of adult males compared with females (0.951 vs. 0.942, Weimerskirch *et al.* 1997; unpublished). In the 1970s and earlier 1980s, the survival of wandering albatrosses was lower than today due to the impact of long line fisheries, which were affecting females to a larger extent than males (Weimerskirch & Jouventin 1987; Weimerskirch *et al.* 1997). This higher mortality that occurred 15–30 years before 1999 could be an additional reason for the larger number of old males compared with old females. The surplus of old males is made of post-reproductive individuals that have bred previously but do not breed anymore because they are unable to find a mate as a result of the tendency of wandering albatrosses to mate with partners of similar ages (Jouventin, Lequette & Dobson 1999). If we consider the young birds ready to be recruited into the population (aged 7–15 years mainly, Weimerskirch *et al.* 1997), there is no sex bias toward either sex (Fig. 1b).

The return to unbiased OSR in recruiting birds from a strongly male-biased sex ratio at hatching is the result of the higher mortality (30%) of males during their first years at sea. In other species of birds and mammals juvenile mortality among males is also generally higher and assumed to be due to the larger size and thus higher energy requirements as a result of food stress (Clutton-Brock, Albon & Guinness 1985). In humans the sex ratio at birth is also above parity (proportion of males = 0.512–0.514, Lazarus 2002) and similarly explained in terms of a greater male mortality during the period of parental care or just after (Fisher 1930). We are confident that in wandering albatross the higher mortality of males is not due to sex-biased dispersal because (i) of the strong philopatry of juveniles to the natal island (99.3% of birds return to their natal island, sex pooled; Inchausti & Weimerskirch 2002), and because (ii) females tend to disperse more than males (89.1% of males returned to their birth colony, whereas only 77.1% of females did so, the remaining dispersing to other colonies within the natal island; Weimerskirch unpublished). Fisher's (1930) theory predicts not conception or hatching sex ratios, but the total investment in offspring until the end of parental investment. Therefore, over the population as a whole we expect to find equal expenditure or investment in the two sexes, not necessarily equal numbers. Thus at the population level the overall sex ratio is that expected by Fisher's theory (1930), but importantly not as a result of equal investment but as a result of differential mortality during the first years at sea of immatures, possibly through an adjustment to equalize overall investment in the sexes.

AGE, PHENOTYPIC QUALITY, AND SEX RATIO

As the costs of raising the more expensive sex should vary between parents, differences may favour sex ratio variation (Clutton-Brock 1991). The tendency we observed for a female-biased sex ratio to be produced by very young and especially old individuals could be the result of such selection. However, the tendency to

produce more females at older ages does not support the prediction that reproductive effort should increase as reproductive value decreases (Stearns 1992) with a larger proportion of males produced at old ages (e.g. Côté & Festa-Bianchet 2001). The result for albatrosses producing more females at older ages rather suggests a decreased efficiency at older ages (Curio 1983), as suggested also by a decline in breeding success with age (Fig. 2). The only comparable data available on very long-lived animals concerns humans where the sex ratio drops in a similar direction to that of albatrosses for fathers aged more than 39 years (Jacobsen, Møller & Mouritsen 1999). In shorter-lived mammals such as ungulates, there is no clear trend in age-related variation in progeny sex ratio (reviewed in Hewison *et al.* 2002), although in some species the trends in the sex ratio of progeny according to mother's age was similar to that of albatrosses, i.e. with a dome shape (Saltz 2001).

As in mammals, in birds maternal condition is likely to be an important factor that underlie the sex ratio reported in correlative studies (Nager *et al.* 1999). In young wandering albatrosses adult body condition increases with age until first breeding in both males and females, and in old females condition declines after the age of 25–30 years (Weimerskirch 1992). These changes in body condition parallel the changes in sex ratio reported in this study (Fig. 2), suggesting that condition could be a critical factor determining the age-related sex ratio variation we observed. Thus individuals in poor condition might be expected to produce the sex that is less likely to be affected by poor parental state, and the least demanding to rear.

However, our study underlines the existence of another factor that has not been considered previously because of the difficulty to obtain individual long-term data on reproductive success, phenotypic quality. Phenotypic quality in albatrosses is not related to body condition as generally considered in other species (females $r_{127} = 0.063$, $P = 0.482$; males $r_{131} = -0.08$, $P = 0.354$), nor to size or age, but appears to be an inherent characteristic of individuals that will have to be clarified in the future. This factor may explain the paradox that parent males die in larger numbers when they rear a female. In wandering albatrosses, male chicks are more costly to produce than female chicks, because they require more food during the 8-month period of growth (Weimerskirch *et al.* 2000). Where one sex is more expensive to rear, the costs of raising the more expensive sex may vary between parents and these differences may favour sex ratio variation (Fisher 1930), but may also result in differential mortality. One would expect that the survival of parents rearing male chicks would be decreased as compared with that of those rearing females, as found in other species and possibly in humans (Helle *et al.* 2002). This is the case for low-quality females, but surprisingly the consequences in terms of survival are the opposite for males. The reasons for this paradox are not clear, but one

might expect the consequences of rearing a chick to be different for the two parents because investment and costs are quite different in male and female wandering albatrosses: males invest more in chick provisioning, but costs may be higher for females (Weimerskirch *et al.* 2000). The most likely reason for this paradox is that pairs of low phenotypic quality produce more female chicks, and die in larger numbers, not because of the sex of their offspring, but because of their poor quality. Wandering albatrosses do not divorce even if they face successive failures (unpublished) as might be expected for a long-lived animal (MacNamara & Forslund 1996) that take several years to select a partner, and breed with partner of similar age (Jouventin *et al.* 1999). Possible consequences of this particular mating strategy are that the quality of individual mates and of the pair are not dissociable, and thus it is difficult to separate their effects clearly, leading to the complex pattern observed in our study for the survival of males and females.

Conclusions

The results of this study show the complexity of the factors that lead to the age and sex structure of a population of long-lived animals. They show that the proportion of male at hatching may vary extensively, ranging from nearly 0.1 in poor-quality old individuals to nearly 0.8 in good-quality 25-year-old individuals (Fig. 3). They also show similar trends in population structure, sex ratio at birth, male bias mortality during immaturity, sex ratio at equilibrium for the mature part of the population, female bias for offspring produced by old parents, to that observed in humans. The only difference between humans and albatrosses is the slightly higher mortality of adult males in humans, which results in an excess of females at very old age, whereas in albatrosses there is an excess of old males because of the slightly higher mortality of females. However, this difference might not be of high significance in evolutionary terms as in both species these old adults are generally no longer reproductive. It is obvious that the mechanisms that were selected for the implementation of such similar patterns were different in humans and in albatrosses. However, they have probably evolved in a similar direction because the two species share similar life-history traits such as longevity, sexual dimorphism, and perhaps monogamy, of paramount importance for the evolution of sex ratios.

Acknowledgements

The long-term study was supported by Institut Paul Emile Victor (IPEV Program n°109). We thank D. Besson for her assistance in processing the database information, D. Bouret and G. Luneau from INRA for their help with the molecular sexing and J.M. Gaillard, S. Orzack, P. Blanchard, A. Millon, and two anonymous referees for helpful comments.

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Received 31 March 2004; accepted 30 July 2004