Age-related mate choice in the wandering albatross

PIERRE JOUVENTIN*, BENOÎT LEQUETTE* & F. STEPHEN DOBSON†

*Centre d'Études Biologiques de Chizé, Centre National de la Recherche Scientifique, France
†Department of Zoology and Wildlife Science, Auburn University

We studied mate choice in the wandering albatross, *Diomedea exulans*, using data from 32 years of banding returns in the population of the Crozet Islands. We studied mating choices in a single year, when the Crozet Islands population was male biased (8:5, males:females). Thus, we expected that females might show great flexibility of choice of partners. Because age and experience might influence mate choice, we tested the expectation that females would choose the oldest and most experienced males for pair bonding. Pair bonds usually last until one member of the pair dies (0.3% of the birds 'divorce'), so mate choice should be especially important. We found that the ages of males and females in both displaying and bonded (breeding) pairs were significantly correlated. These age-associated pairings were not a passive phenomenon, but appeared to be due to an active process of selection of mates of similar age. First-time breeders sought mates of similar age, but preferred those with the most experience. Remating, experienced birds whose mates had died did not pair with individuals of significantly similar age, but predominantly paired with other widowed birds that, on average, were also relatively old. Mate fidelity in wandering albatrosses may be due to the cost of finding and bonding with a new mate. Pair bonds, and thus breeding, took an average of 3.2 and 2.3 years to establish, for males and females, respectively. Thus, remating exerts a potential average reproductive cost of about 15% of lifetime reproductive success.

© 1999 The Association for the Study of Animal Behaviour

The question of how mates are chosen is an important topic in evolutionary biology, because the qualities of mates can influence the number of offspring that will be left to future generations (Wittenberger 1983). Andersson (1994) identified eight possible benefits of mate choice and reviewed the supporting evidence for each benefit. The possible benefits included identification of the correct species, choosing more fecund partners, gaining food resources, gaining help with parenting, accessing better territories, avoiding hazards, improved genetic or reproductive complementarity of partners, and greater offspring quality. Some of these hypothesized benefits, particularly those relating to genetic quality, may be extremely difficult to test in the field, but others might be examined by comparing the characteristics of mates.

Although experience of mates was not specifically listed, Andersson (1994) suggested that it may sometimes be a beneficial quality. In red-winged blackbirds, *Agelaius phoeniceus*, experienced males acquire better territories and provide more food for nestlings than inexperienced males (Searcy 1979; Yasukawa 1981). Females may be able to identify male experience through its association with age, and because courtship time and song repertoire increase with age (Yasukawa et al. 1980; Searcy & Yasukawa 1981). Female preferences for intense courtship and diversity of song are thus linked to male age and experience, and male experience may result in direct benefits of paternal care and territory quality that increase female fitness (Eckert & Weatherhead 1987; Searcy 1988).

In many species, age and experience of mates may be important influences on mating choices. In several species of bird, for example, breeding performance seems closely related to reproductive experience and age (e.g. passeriforms: Perrins & McCleery 1985; Nol & Smith 1987; coraciiforms: Lessels & Krebs 1989; raptors: Newton et al. 1981; Korpimäki 1988; Newton 1988, 1989; ducks: Afton 1984; Gauthier 1989; seabirds: Coulson 1966; Wooller et al. 1990). When age and experience have such significant effects on reproduction, they should also be criteria for mate choice. In many cases, experience as a mate may be fairly well reflected by an individual's age, and it could be difficult to separate age and experience as criteria for mate choice. Such discrimination might be

Correspondence: F. S. Dobson, Department of Zoology and Wildlife Science, Auburn University, Auburn, AL 36849, U.S.A. (email: fdobson@acesag.auburn.edu). P. Jouventin is now at the Behavioural Ecology Group, CNRS-CEFE, 1919 route de Mende, 34293 Montpellier Cedex 05, France. B. Lequette is now at the Parc National du Mercantour, 23 rue d'Italie, BP 316, 06006 Nice Cédex, France.

possible, however, if individuals of known age and breeding status were studied.

Wandering albatrosses, *Diomedea exulans*, are ideal study animals for an examination of whether age and experience are strong influences on mate choice because of their long-lasting pair bonds and high degree of mate fidelity (Tickell 1968). Mate choice is followed by many years of breeding together, so it should be extremely important for both males and females to make good choices. Skew in the adult sex ratio, however, may facilitate choice by one sex or the other. For the albatross population of the Crozet Islands, for example, males have at times outnumbered females by a ratio of about 8:5, so that females probably have had greater opportunities to choose among several males. Some female albatrosses may spend their entire life cycle mated to a single male, but other females eventually lose their mate and have to find another. Regardless of how many mates a female has, however, mate choices are infrequent events in a reproductive life span that can last more than 40 years (after reproductive maturity at 11–12 years of age; Weimerskirch & Jouventin 1987).

The purpose of the present research was to examine choice of mates in wandering albatrosses using a long-term (32-year) study of the breeding biology of the Crozet Islands population. Specifically, we asked whether female albatrosses chose the oldest and most experienced males as mates under two situations: when females were breeding for the first time and when females were remating after losing their mates. Using behavioural data from one breeding season, we evaluated whether mate choice appeared to be a passive selection from available (unmated) males or whether active choice could be demonstrated via the occurrence of significant nonrandom selection of males. Several hundred albatrosses were banded as young every year, so exact ages were known for many adults. Thus, we were able to document rates of mate fidelity and loss, and the reproductive consequences of mate loss. We expected that females mating for the first time and widowed females that chose new mates would select the older and more experienced of the available males.

METHODS

Wandering albatrosses were studied at Possession Island (46°25′S, 51°45′E), in the Crozet archipelago of the Southern Indian Ocean. Banding of this species began in 1959. Since 1966, about 6000 birds (adults and fledglings) were examined for band number each year when birds were on their nests (ring numbers were read for the breeding population of the entire archipelago of about 1637–3250 pairs each year; Weimerskirch et al. 1997a), and new leg bands were given to unbanded birds. Data recorded for each individual included sex, age, plumage characteristics, presence or absence of the single-egg clutch, hatching success, fledging success and the identity of the mate. Between 1985 and the beginning of behavioural observations in 1989 (see below), unmated birds that returned to land to display (Pickering 1989) were also marked with coloured leg bands for individual recognition at a distance during behavioural observations. Thus, displaying males and new couples could be identified without handling or other disturbance to the birds.
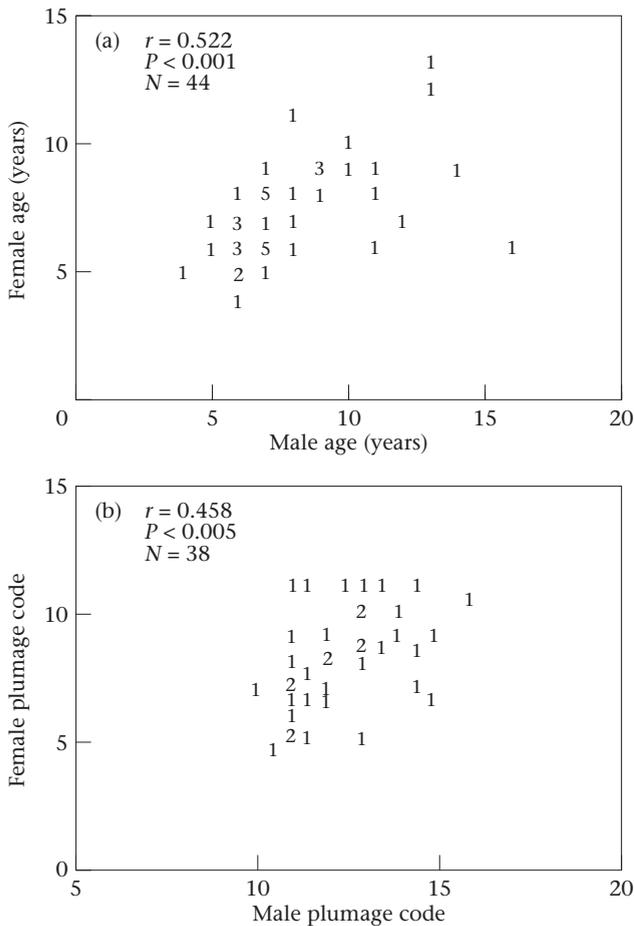
Male and female wandering albatrosses have different patterns of activity on the breeding grounds during their immature period. After 1 or 2 years of visiting the breeding colony, males construct a nest and tend to remain near it, while unmated females move throughout the colony and display with several males (Pickering 1989; Jouventin & Lequette 1990). During this period, displays among several birds are common (Richdale 1950; Pickering 1989; Jouventin & Lequette 1990), and males thus occasionally leave the vicinity of their nests. Both sexes have opportunities during each breeding season to assess the suitability of several potential partners (a mean of 6.6 males displaying to each female; Pickering 1989). For both males and females, it takes several years (range 2–8 years; Pickering 1989) for displaying pairs to become bonded and begin to breed, thus completing mate choice.

Mating displays require that both male and female follow complex sequences of specific behaviours (Jouventin & Lequette 1990). Couples do not display after they are bonded. We summarized the development of mating displays into three general stages: (1) preliminary displays, such as the 'sky position', are performed at a distance, (2) advanced displays involve several sequences as birds move closer; and (3) completed displays involve direct contact, grooming and copulation.

For individuals that were not first banded as chicks, we used an alternative method of estimating age. We scored plumage characteristics of unmated birds following the classification of Gibson (1967). The plumage of wandering albatrosses whitens with age (Weimerskirch et al. 1989). The back, head and inner wings do not reach their final stage of whitening until the birds are about 20 years of age (Gibson code ≥ 17), but within the same age class, breeding males are whiter than nonbreeding males (Weimerskirch et al. 1989). For our behavioural study, we considered unmated males with 'dark' plumage (code<16) as immature, and unmated males with 'white' plumage (code ≥ 16) as widowed ('divorce' or abandonment by a living mate was extremely rare, see below). We tested the assumption that whiter males had previously bred by examination of known-aged individuals. A few birds with a high degree of whitening had not previously bred, but these misclassifications could only have lowered the differences between the two maturity classes, and thus any bias was conservative.

Widowed birds experienced a delay of some years in finding a new mate (see below). We estimated this penalty of remating in terms of lifetime chick productivity, calculated by comparing the mean lifetime productivity of birds that remated with that of birds that remained mated. Chick productivity was obtained using the mean age at first breeding, mean adult survival (reflecting the number of years of reproduction) for both males and females, and the mean number of chicks produced per year by mated birds.

Banding for an extended number of years was necessary to produce a large sample of known-aged individuals.
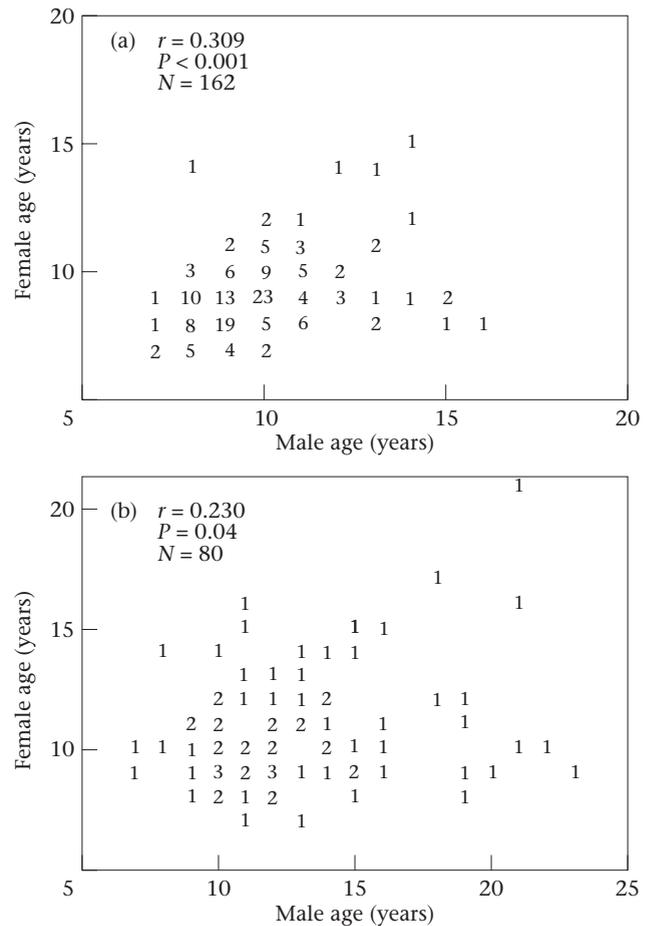
Figure 1. For wandering albatrosses, relationships between (a) the ages of displaying males and females and (b) plumage colour (Gibson code) of displaying males and females. Correlation coefficients (Spearman rank-order correlation coefficient for plumage colour), significance levels and sample sizes are given.

Figure 2. For wandering albatrosses, relationships between ages of paired males and females within (a) new pairs of two first-time breeders and (b) new pairs of one first-time breeder and one widowed bird. Correlation coefficients, significance levels and sample sizes are given.

In addition, not all wandering albatrosses from the population visit Possession Island in any given year, because many pairs breed every other year. Thus, our analyses were conducted primarily on data collected during the 1989 Austral summer, to avoid problems of including individuals in analyses more than once. Behavioural observations of displaying unmated birds were conducted on 28 January and 19 February 1989. We compared means and standard errors using Student's t tests. We used Bartlett's tests to examine homogeneity of variances prior to t tests, and we performed the approximate t test (Sokal & Rohlf 1981) in cases of inequality of variances. We used a nonparametric Spearman rank-order correlation coefficient to examine associations of plumage scores within pairs.

RESULTS

Age-assortative Mating in First-time Breeders

We observed a significant correlation between the ages of unmated birds that were displaying to each other (Fig. 1a). On average ($\pm$ SE), the ages of displaying pairs differed by only 0.64 ± 0.34 years (males: 8.05 ± 0.39 years, range 4–16; females: 7.41 ± 0.28 years, range 4–13; $N=44$ pairs). Plumage scores within displaying pairs were also significantly correlated (Fig. 1b).

Of the 329 pairs that included at least one first-time breeding bird, almost half (49.2%, $N=162$) were composed of two first-time breeders, 37.7% ($N=124$) were composed of a first-time breeder and an experienced breeder, and 13.1% ($N=43$) were composed of a first-time breeder and a bird of unknown age and experience. Within bonded pairs for which both partners were first-time breeders, ages of mates were significantly correlated (Fig. 2a) and on average differed by 0.82 ± 0.15 years (males: 9.90 ± 0.14 years, range 7–16; females: 9.08 ± 0.11 years, range 7–15; $N=162$ pairs). The proportion of first-time breeders that paired with experienced birds was slightly greater than expected from random pairings among unmated birds (37.7% of paired birds compared with 29.6% of 203 unmated birds that were widows; approaches significance, $\chi^2_1 = 3.67$, $P=0.055$). For 80 first-time breeders paired with experienced birds, the ages of mates were significantly correlated (Fig. 2b), and on average differed by 2.23 ± 0.44 years (males: 13.13 ± 0.41

Table 1. Status of the mate chosen by male and female wandering albatrosses when re-pairing (sample size in parentheses)

Status	Male	Female	Total
Widowed	69.1% (96)	74.0% (97)	71.5% (193)
First breeders	22.3% (31)	18.3% (24)	20.4% (55)
Status unknown	8.6% (12)	7.6% (10)	8.1% (22)
Total sample	139	131	270

Table 2. Duration of remating period and estimated reduction of the average lifetime reproductive success due to remating for male and female wandering albatrosses

	Duration of remating (years)		Decline in lifetime reproduction (%)*	
Age	Male $\bar{X}\pm$SD (N)	Female $\bar{X}\pm$SD (N)	Male	Female
$\geq$20 years	3.88±2.41 (41)	2.53±1.70 (32)	17.32	16.98
<20 years	2.14±1.61 (14)	1.35±1.00 (17)	9.55	9.06
Average†	3.20±2.03 (111)	2.27±1.43 (119)	14.29	15.23

*The cost of remating was estimated as the percentage reduction in mean lifetime reproductive output.
†Birds of unknown age included.

years, range 7–23; females: 10.90 ± 0.27 years, range 7–21; N=80 pairs).

Extreme Mate Fidelity

From the final 19 years of study, 772 rebreeding histories between 421 pairs of mates were available for examination. On average, 77.6% of birds reunited for breeding with their previous mate, 20.9% became widowed and subsequently paired with a new mate, and 0.3% divorced. The partners of the remaining 1.3% were absent from the colony for at least 2 years, but later returned.

Quicker Remating by Younger Birds

For birds that remated after being widowed, males and females differed in age by 3.19 ± 2.97 years, but the ages of mates were not correlated (rank r=0.047, N=20, P=0.84). The proportion of widowed birds that remated with another widow was significantly higher than expected from random selection of mating partners among unmated birds (respectively, 71.5 and 29.6%, N=270 and 203; χ^2_1=106.2, P<0.001; Table 1). There were no significant differences between males and females in the proportions of mates that were chosen from widowed birds, first-time breeders and birds of unknown status (χ^2_2=0.60, P>0.44).

It took time for widowed birds to find new mates and begin breeding again. Males spent significantly more time as widowed nonbreeders than did females (t_{228}=3.99, P<0.001; Table 2). The amount of time before success at pairing with a new mate depended on age and sex (two-way ANOVA: $F_{1,226}$=12.28, P<0.001; and $F_{1,226}$=8.74, P<0.01; respectively). The interaction of age and sex

was not significant ($F_{1,226}$=0.87, P>0.05). Older males ($\geq$20 years) spent a significantly longer time as nonbreeders than young ones (<20 years, t_{53}=2.51, P<0.01), and a similar pattern was observed in females (t_{44}=3.06, P<0.001). Older males also remained nonbreeders significantly longer than older females (t_{71}=2.8, P<0.01), but there was no significant difference between young males and young females (t_{27}=1.67, P=0.11).

Males sometimes courted females that were already incubating eggs, although pairings did not result from these courtships (Jouventin & Lequette 1990). Compared with their proportion in the population of nonbreeding birds, older widowed males ($\geq$20 years) courted significantly more of the incubating females than immature males (binomial test: P<0.01; Table 3).

Unbalanced Sex Ratio in Widowed Birds

Human-induced mortality due to fishing practices caused a significant male bias in the adult sex ratio of wandering albatrosses on the Crozet Islands (Weimerskirch & Jouventin 1987). The adult sex ratio (118 males:88 females) differed significantly from one (χ^2_1=4.37, P<0.05; Table 4). Of 56 older birds ($\geq$20 years), males were significantly more numerous than females (44 males:12 females, χ^2_1=18.29, P<0.001), but the sex ratio of 150 younger birds did not differ significantly from one (74 males:76 females, all immatures <20 years of age, χ^2_1=0.027, P=0.88). The proportion of males thus differed significantly between younger and older birds (χ^2_1=14.25, P<0.001).

Among widowed birds, there were significantly more males than females (47:13, compared with 118 males:88 females in the nonbreeding population; χ^2_1=15.33,

Table 3. Number of widowed and immature males during behavioural observations (28 January and 19 February 1989) and their participation in different behaviours

Behaviour	Immatures (N=53)	Widowers (N=46)	χ^2*	P
'Sky position' display	10	15	1.86	>0.17
Courtship	88	8	54.6	<0.001
Flight initiation	11	16	1.72	>0.18
Win fight	23	29	1.78	>0.18
Court incubating female	4	17	†	<0.01

*Comparison (χ^2 one-sample test) of observed ratio against ratio of males present.
†Binomial test due to small sample.

Table 4. Structure of the nonbreeding population during the breeding season of 1989

	Males	Females	Total
<20 years			
Immatures	67	73	140
Widowed	4	3	7
≥20 years			
Immatures	1	2	3
Widowed	43	10	53
Total	115	88	203

Table 5. Percentages of response by individual young females (<20 years) to display behaviours (number of displays in parentheses) performed by immature and widowed males

Female	Immatures*	Widowers
1	100% (10)	0% (3)
2	100% (16)	0% (3)
3	90% (10)	25% (4)
4	80% (10)	20% (5)
5	83% (6)	0% (3)
6		0% (20)

*Differed significantly from widowed, Mann–Whitney U test, two-tailed, P<0.01.

P<0.001; rare cases of divorces were included as widowed; Table 4). Widowed birds accounted for 29.1% of the nonbreeding population. Most older males ($\geq$20 years of age) were widowers, a significantly higher proportion than among younger males (respectively, 97.7% of 44 and 5.4% of 74; χ^2_1=98.13, P<0.001). The same difference was observed between older ($\geq$20 years of age) and younger females (83.3% of 12 older and 4.0% of 76 younger females were widows, χ^2_1=51.88, P<0.001).

Behaviour and Attractiveness of Nonbreeding Males

During behavioural observations in 1989, immature ('dark') and widowed ('white') males were equally numerous, and the proportion of immatures was similar to that in the nonbreeding population (53.5 and 59.1%, Tables 3 and 4, respectively, χ^2_1=0.47, P=0.49). Widowed and immature males performed attractive postures ('sky position' from Jouventin & Lequette 1990) with about equal frequency (Table 3). However, compared with immature males, widowed males performed significantly fewer courtship displays than expected from their observed proportion. When displaying, widowed males were more frequently observed to occupy a nest than immature males (75.0% of 20 displays, and 25.0% of 28, respectively, χ^2_1=9.82, P<0.01). Widowers were also more frequently seen alone at the nest than immatures (91.1% of 56 observations, and 25.8% of 31; χ^2_1=36.01, P<0.001). Both categories of males initiated conflicts about equally, and conflicts were won (one of the two males walked away) about equally.

Young females (<20 years) behaved positively to the displays of males by performing a corresponding display sequence of their own. These females responded positively much more frequently to the displays of immature males than to those of widowed males (Table 5). When two males and one female were involved in a display, young females remained significantly more frequently with the immature than with the widowed male (41 cases with immatures, and three cases with widowers, χ^2_1=32.82, P<0.001).

The completeness of development of displays was observed for unmated birds, and displays were classified as preliminary, advanced, or complete (see Methods). We examined the ages of displaying partners at each stage. In preliminary displays, partners differed in age by 3.80 ± 1.36 years (N=5 pairs). For advanced displays, partners differed in age by 2.06 ± 0.51 years (N=36 pairs), but this reduction of difference in age of partners compared to that in preliminary displays was not statistically significant. Finally, the ages of partners with completed displays, resulting in pair bonding, differed by only 1.00 ± 0.61 years (N=25) on average, a significant reduction in difference in age from the advanced displays (t_{36} test, P=0.002).

Reproductive Cost of Remating

Wandering albatrosses have a mean age at first breeding of 10.4 years for males and 9.6 years for females, a mean life expectancy of 32.83 and 24.50 years, respectively (Weimerskirch & Jouventin 1987), and a mean productivity of 0.33 chicks a year (Jouventin &

Weimerskirch 1988). The average number of young produced during 22.4 or 14.9 years of reproduction is thus 7.39 for males and 4.91 for females. An average bird needed 3.20 years (male) and 2.27 years (female) to remate. This results in an average reduction in mean lifetime chick production of 14.29% for males and 15.23% for females (Table 2). The potential loss of chick production was greater for older individuals, because it took them longer to begin rebreeding.

DISCUSSION

Age-assortative Mating: Passive or Active?

Wandering albatrosses showed significant age-assortative pairing. Ages of mating partners are often correlated in populations of breeding birds (Pugesek & Diem 1981; Marzluff & Balda 1988; Reid 1988; Amat 1990; Bradley et al. 1995). This correlation is generally attributed to the contemporary recruitment of birds of the same cohort to the breeding population; followed by long-term pair bonding (Reid 1988). Age-assortative mate choice, however, could be an active process (Black & Owen 1995). We tested for active age-assortative mate choice in wandering albatrosses.

Immature wandering albatrosses, both males and females, arrived at the colonies later in the breeding season than more experienced birds. This could promote passive mating that is assortative with respect to age, but there are five factors that suggest that observed age correlations are not merely the result of a passive process. First, there is marked variation in the age at which birds return to the colony for their first breeding season, so that potential mates show a considerable range of age. Second, there is considerable variation in the length of the immature period, during which it can take 2–8 years of display activity before a pair begins to breed (Pickering 1989). Third, there is a considerable overlap between the periods when birds of different degrees of nonbreeding experience are present (Pickering 1989). Fourth, our results indicated that females paired according to the male's age, and that pairing differed significantly from the expectation of randomly selecting among available males. Finally, as the pairing process became more complete, as reflected by more highly developed display sequences, ages of males and females became more similar through changes in partners.

In wandering albatrosses, the weight of evidence suggests that selection of potential partners on the basis of age is an active, rather than a passive assortative-mating process. In the Crozet Islands population, old males spent several years searching for and attracting a mate. This was not likely to be due to older widowed males being less active, as they more frequently possessed a nest than young immature males. They also performed displays at a slightly higher rate and were slightly more successful at winning fights than young immature males, although these differences were not statistically significant.

While we do not know whether old widowed males actively sought young partners, they were clearly unsuccessful at pairing with young females that were breeding for the first time. Older widowed males were seen alone at the nest more frequently than immature males, and they were less involved in courtships than would be expected according to their number. This delay in remating is likely to be due more to the difficulty of finding a partner of similar age, itself a result of the lack of old females, and probably reflects active discrimination of males by females. When initiating displays, young females were more inclined to respond to younger males than to older males, and when they were in the presence of two potential displaying partners, females (mainly immatures) remained with the younger male. However, we do not have any information concerning any active discrimination of females by males.

Age and Experience

How can we assess the relative importance of age and experience in the mate choices of wandering albatrosses? We found significant correlations between the ages of displaying pairs in first-time breeders, despite the wide variation in ages of potential mates. Even if immature wandering albatrosses choose a similar-aged partner, however, experience may have been a secondary factor influencing mate choice. When breeding for the first time, immatures tended to choose an experienced partner, as evidenced by the relatively high proportion of experienced birds that paired, compared with the frequency of experienced birds in the population. Even then, however, the age of the partner was still a predominant factor, as significant age-correlations were present within breeding pairs composed of one immature and one experienced bird. Thus, our original expectation of preference for older and more experienced mates, based on previous studies of mate choice (e.g. Andersson 1994), was not apparent for young females. Young female wandering albatrosses appeared to prefer mates of the same age, and experience was only a secondary factor.

In fact, familiarity with the mate may be an especially important aspect of 'experience' in wandering albatross. Black (1996) suggested that strong mate fidelity might improve cooperation between mates, facilitate prolonged biparental investment, and reduce potential costs of remating (e.g. finding a new mate). All of these factors appeared critical to the life history of the wandering albatross. Cooperation between adults was essential for raising the single chick. One parent must remain with the egg or young chick, while the other forages at a distance of a few 100 to several 1000 km away (Weimerskirch et al. 1997b). Food must then be returned to the chick. Both partners must feed, so foraging turns must be taken during the prolonged period of biparental care, a period of about 11.5 months (Jouventin & Mougin 1981). Reproductive costs of remating appeared substantial for this species (see below). Furthermore, in some species of birds, reproductive success increases as pairs stay together (e.g. Ens et al. 1996). In the wandering albatross, however, reproductive success is remarkably uniform for pairs that stay together (Weimerskirch 1992), so that fidelity is probably influenced more by the cost of changing mates than by a direct advantage of the length of the pair bond.

The Cost of Remating

Remating appears to be highly costly for wandering albatross, as a single divorce diminishes the mean lifetime potential reproduction of individuals by about 10–20%. Black (1996) suggested that for species such as the wandering albatross, individuals should suffer a fitness cost if they change mates, a hypothesis that is supported by the reproductive cost of remating. This cost appeared to be more important for old birds than for young ones. Paradoxically, pairing with a younger bird might thus improve lifetime reproductive success, even if a younger mate were initially inexperienced. The benefit of younger mates is a long potential reproductive life span, a benefit that was not listed in Andersson's (1994) review of benefits of mate choice. This new benefit may be particular to long-lived species like the wandering albatross, but it points out the general principle that there may be many benefits to mate choice, some of which have yet to be discovered.

Acknowledgments

References

Afton, A. D. 1984. Influence of age and time on reproductive performance of female lesser scaup. *Auk*, **101**, 255–265.

Amat, J. A. 1990. Age-related pair bonding by Eurasian wigeons in relation to courtship activity. *Auk*, **107**, 197–198.

Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

Black, J. M. 1996. Introduction: pair bonds and partnerships. In: *Partnerships in Birds* (Ed. by J. M. Black), pp. 3–19. Oxford: Oxford University Press.

Black, J. M. & Owen, M. 1995. Reproductive performance and assortative pairing in relation to age in barnacle geese. *Journal of Animal Ecology*, **64**, 234–244.

Bradley, J. S., Wooller, R. D. & Skira, I. J. 1995. The relationship of pair-bond formation and duration to reproductive success in short-tailed shearwaters *Puffinus tenuirostris*. *Journal of Animal Ecology*, **64**, 31–38.

Coulson, J. C. 1966. The influence of the pair-bond and age on the breeding biology of the kittiwake gull *Rissa tridactyla*. *Journal of Animal Ecology*, **35**, 269–279.

Eckert, C. G. & Weatherhead, P. J. 1987. Ideal dominance distributions: a test using red-winged blackbirds (*Agelaius phoeniceus*). *Behavioral Ecology and Sociobiology*, **20**, 43–52.

Ens, B. J., Choudhury, S. & Black, J. M. 1996. Mate fidelity and divorce in monogamous birds. In: *Partnerships in Birds* (Ed. by J. M. Black), pp. 345–401. Oxford: Oxford University Press.

Gauthier, G. 1989. The effect of experience and timing on reproductive performance in buffle-heads. *Auk*, **106**, 568–576.

Gibson, J. D. 1967. The wandering albatross *Diomedia exulans*: results of banding and observations in New South Wales coastal waters and the Tasman Sea. *Notornis*, **14**, 47–57.

Jouventin, P. & Lequette, B. 1990. The dance of the wandering albatross *Diomedea exulans*. *Emu*, **90**, 122–131.

Jouventin, P. & Mougin, J. L. 1981. Les strategies adaptatives des oiseaux de mer. *Terre et Vie*, **35**, 217–272.

Jouventin, P. & Weimerskirch, H. 1988. Demographic strategies of southern albatrosses. *Proceedings of the XIXth International Ornithological Congress*, **2**, 865–871.

Korpimäki, E. 1988. Effects of age on breeding performance of Tengmalm's owl *Aegolius funereus* in Western Finland. *Ornis Scandinavica*, **19**, 21–26.

Lessels, C. M. & Krebs, J. R. 1989. Age and breeding performance of European bee-eaters. *Auk*, **106**, 375–382.

Marzluff, J. M. & Balda, R. P. 1988. Pairing patterns and fitness in a free-ranging population of pinyon jays: what do they reveal about mate choice? *Condor*, **90**, 201–213.

Newton, I. 1988. Age and reproduction in the sparrowhawk. In: *Reproductive Success* (Ed. by T. H. Clutton-Brock), pp. 201–219. Chicago: University of Chicago Press.

Newton, I. 1989. *Lifetime Reproduction in Birds*. London: Academic Press.

Newton, I., Marquiss, M. & Moss, D. 1981. Age and breeding in sparrow hawks. *Journal of Animal Ecology*, **50**, 839–853.

Nol, E. & Smith, J. N. M. 1987. Effects of age and breeding experience on seasonal reproductive success in the song sparrow. *Journal of Animal Ecology*, **56**, 301–313.

Perrins, C. M. & McCleery, R. H. 1985. The effect of age and pair bond on the breeding success of great tits *Parus major*. *Ibis*, **127**, 306–315.

Pickering, S. P. C. 1989. Attendance patterns and behaviour in relation to experience and pair-bond formation in the wandering albatross *Diomedea exulans* at South Georgia. *Ibis*, **131**, 183–195.

Pugesek, B. H. & Diem, K. L. 1981. Ages of mated pairs of California gulls. *Wilson Bulletin*, **98**, 610–612.

Reid, W. V. 1988. Age correlation within pairs of breeding birds. *Auk*, **105**, 278–285.

Richdale, L. E. 1950. The pre-egg stage in the albatross family. *Biological Monographs*, **3**, 1–92.

Searcy, W. A. 1979. Female choice of mates: a general model for birds and its application to red-winged blackbirds (*Agelaius phoeniceus*). *American Naturalist*, **114**, 77–100.

Searcy, W. A. 1988. Dual intersexual and intrasexual functions of song in red-winged blackbirds. *Proceedings of the XIXth International Ornithological Congress*, **2**, 1373–1381.

Searcy, W. A. & Yasukawa, K. 1981. Does the 'sexy son' hypothesis apply to mate choice in red-winged blackbird? *American Naturalist*, **117**, 343–348.

Sokal, R. R. & Rohlf, F. J. 1981. *Biometry*. 2nd edn. London: W. H. Freeman.

Tickell, W. L. N. 1968. The biology of great albatrosses *Diomedea exulans* and *Diomedea epomophora*. *Antarctic Research Series*, **12**, 1–55.

Weimerskirch, H. 1992. Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in the wandering albatross. *Oĩkos*, **64**, 464–473.

Weimerskirch, H. & Jouventin, P. 1987. Population dynamics of the wandering albatross, *Diomedea exulans* of the Crozet islands: causes and consequences of the population decline. *Oĩkos*, **49**, 315–322.

Weimerskirch, H., Lequette, B. & Jouventin, P. 1989. Development and maturation of plumage in the wandering albatross *Diomedea exulans*. *Journal of Zoology*, **219**, 411–422.

Weimerskirch, H., Brothers, N. & Jouventin, P. 1997a. Population dynamics of wandering albatross *Diomedea exulans* and Amsterdam albatross *D. amsterdamensis* in the Indian Ocean and their relationships with long-line fisheries: conservation implications. *Biological Conservation*, **79**, 257–270.

Weimerskirch, H., Cherrel, Y., Cuenot-Chaillet, F. & Ridoux, V. 1997b. Alternative foraging strategies and resource allocation by male and female wandering albatrosses. *Ecology*, **78**, 2051–2063.

Wittenberger, J. F. 1983. Tactics of mate choice. In: *Mate Choice* (Ed. by P. Bateson), pp. 435–447. Cambridge: Cambridge University Press.

Wooller, R. D., Bradley, J. S., Skira, I. J. & Serventy, D. L. 1990. Reproductive success of short-tailed shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. *Journal of Animal Ecology*, **59**, 161–170.

Yasukawa, K. 1981. Male quality and female choice of mate in the red-winged blackbird (*Agelaius phoeniceus*). *Ecology*, **62**, 922–929.

Yasukawa, K., Blank, J. L. & Patterson, C. B. 1980. Song repertoires and sexual selection in the red-winged blackbird. *Behavioral Ecology and Sociobiology*, **7**, 233–238.