Journal of Animal Ecology 2001
70, 1088–1097

Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's auklets

PETER PYLE, WILLIAM J. SYDEMAN and MICHELLE HESTER
PRBO/Marine Science Division, Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, CA 94970, USA

Summary

1. We examined how mate and site fidelity varied with age, experience and sex, and how age, breeding experience, mate experience, site experience and sex affected annual reproductive success and lifetime reproductive output in a declining population of Cassin's auklets (*Ptychoramphus aleuticus*). Our 276 study birds were 2–14 years of age, recruited at age 2–12 years, and had 0–11 years' breeding experience, 0–8 years' experience with the same mate and 0–11 years' experience in the same nest box.

2. Mate fidelity was significantly greater with increasing age in males but not females. There was also a significant negative relationship between mate fidelity and breeding density (as measured by proportion of box occupancy); i.e. the lower the breeding density the higher the incidence of breeding with the same mate.

3. Site fidelity showed significant linear and curvilinear increases with age that were significant in females but not males. There was also a significant negative relationship between site fidelity and breeding density; i.e. the lower the breeding density the higher the incidence of breeding at the same site.

4. Previous breeding experience had no effect on either mate fidelity or site fidelity, and both mate and site fidelity were significantly lower after a breeding season was skipped. In addition, mate fidelity was significantly lower when a site was switched and vice versa.

5. Lifetime reproductive output increased significantly with mate fidelity but showed no relationship with site fidelity. This suggests that fitness is optimized more through mate selection than site selection and that mate fidelity is not a by-product of site fidelity.

6. Annual reproductive success showed a significant linear increase with age in males but not females, and a strong parabolic relationship with breeding experience that was significant in both sexes and significantly greater in males than females.

7. These results suggest that (i) males may be more responsible for mate selection and females for site selection; (ii) improved foraging experience with age and a cost of reproduction may be more important factors in males than females; and (iii) reproductive success may be optimized by behaviour of the male rather than the female.

8. Controlling for the age and experience terms of both parents, experience with a mate had a significant positive linear effect on annual reproductive success. This suggests that mate fidelity is adaptive in Cassin's auklets, and that studies examining the effects of age and experience on reproductive performance should separately consider the duration of the pair bond.

9. Controlling for all other variables, neither experience at a breeding site nor breeding density showed significant correlations with reproductive success.

10. We suggest that reductions in food supply, which correlate with reduced breeding densities, may prevent all but the highest quality breeders (those which have already established a pair bond) from reproducing, and that the increase in quality offsets the reduction in food availability.

Key-words: age, Cassin's auklet, experience, mate fidelity, reproductive success, sex, site fidelity.

Journal of Animal Ecology (2001) **70**, 1088–1097

Correspondence: Peter Pyle, PRBO/Marine Science Division, Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, CA 94970, USA. ppyle@prbo.org

Introduction

A positive effect of age on the breeding performance of long-lived organisms has been well documented (Clutton-Brock 1988; Newton 1989; Saether 1990); this relationship is due, at least in part, to age-related improvements in foraging and reproductive competence (Curio 1983; Nol & Smith 1987; Forslund & Part 1995). Several components can contribute to increased competence with age (Forslund & Part 1995). Success in reproduction can be gained through cumulative foraging experience away from the breeding territory (Burger 1988; Ratcliffe & Furness 1999), breeding experience on the territory (Ainley, LeResche & Sladen 1983; Pyle *et al.* 1991, 1997; Ratcliffe, Furness & Klomp 1998), experience with a mate (Ainley, LeResche & Sladen 1983; Bradley *et al.* 1995; Cezilly & Nager 1996; Ens, Choudhury & Black 1996) and/or experience with other factors, such as predator avoidance and migration, which may allow more energy and/or time to commit to reproduction (Curio 1983; Newton 1989). Thus far, however, no study has investigated all of these possibilities simultaneously (Part & Forslund 1996). For example, it is well known that experience with a mate usually enhances reproductive success (Ens, Choudhury & Black 1996), but it is has not been shown whether increased success results simply from the separate, cumulative breeding experience of each parent, or if length of the pair bond contributes as well (Cezilly & Nager 1996; Part & Forslund 1996).

Between 1981 and 1999 we monitored a population of known-aged Cassin's auklets (*Ptychoramphus aleuticus* [Pallas]) nesting in boxes on Southeast Farallon Island (SEFI) off central California (Ainley & Boekelheide 1990; Pyle 2001). This species is known to exhibit moderate mate fidelity; i.e. birds sometimes divorce (and at times remate after divorce) during consecutive breeding attempts, and there is frequent turnover of mates due to presumed mortality as well as divorce (Emslie, Sydeman & Pyle 1992; Sydeman *et al.* 1996; Pyle 2001). Cassin's auklets on SEFI also display a relatively high degree of breeding dispersal (movement between breeding attempts; Greenwood 1980; cf. Pyle 2001). The population declined by 50% between 1971 and 1989 (Ainley *et al.* 1994) and showed a significant decline within the study population between 1987 and 1999 (Pyle 2001). Several avenues of evidence suggest that the decline has resulted from changes in prey resources with decadal-scale ocean warming (Ainley, Sydeman & Norton 1995; Ainley, Spear & Allen 1996; Pyle 2001), with predation by western gulls (*Larus occidentalis* Audubon) contributing during the early part of the decline (Nelson 1989). Evidence based on age of first breeding and natal dispersal suggests that, as the population has declined, selective equilibrium has resulted in a low-philopatry, low-cost (later breeding and increased survival), strategy becoming increasingly adaptive in this population (Pyle 2001; cf. Spear, Pyle & Nur 1998).

Here we examine how mate and site fidelity have varied with age and experience, and how age, breeding experience, mate experience and site experience have affected annual reproductive success and lifetime reproductive output in this declining population of Cassin's auklets. The objective of these analyses is to simultaneously investigate the proximal factors (e.g. mate fidelity vs. site fidelity, age vs. breeding experience, experience of a mate vs. experience with a mate) affecting reproductive performance in male and female Cassin's auklets at SEFI. We examine how these relationships may have changed during the course of the study, as the population and breeding density within the boxes have declined.

Methods

STUDY POPULATION

The breeding biology of the Cassin's auklet on SEFI was described by Manuwal (1974) and Ainley & Boekelheide (1990), and the study on known-age auklets was described by Pyle (2001). Between 1981 and 1999, 276 'known-age' birds were recorded; for the most part, the analyses presented here were based on 252 birds breeding in 446 boxes during the 1987–99 breeding seasons, when reproductive success of known-age birds was determined. The boxes had been installed in 1977–82; thus, little bias in known-age distributions should occur in our study sample (see Emslie, Sydeman & Pyle 1992). By 1987 there were virtually no burrows among the boxes, so few if any missed breeding attempts occurred due to movement between unchecked burrows and boxes. Beginning in 1978, the ring status of breeding auklets in all boxes was recorded each year. Between 1978 and 1986 unringed breeding adults and chicks were ringed in all boxes, and between 1987 and 1999 unringed mates of known-age birds and chicks were ringed in all boxes. The rings were stainless steel, with ring loss absent, or virtually so (Pyle 2001). Beginning 15 March each year (1987–99) boxes were checked once every 15 days for breeding auklets. When a known-age bird was found the ring status of its mate was determined and the site was monitored on a 5-day schedule to determine hatching status and date, and fledging status, date and weight (see Ainley & Boekelheide 1990; Sydeman *et al.* 1996 for details). Sex of most known-age birds was determined by bill depth (Pyle 2001).

DEFINITION OF DEPENDENT VARIABLES

Age of first breeding (AFB) varied from 2 to 12 years in the study population (Pyle 2001). Due to the incidence of skipped breeding opportunities (see Results), breeding experience was calculated as age minus AFB minus skipped years. As independent variables in logistic regression analyses (see below), we scored mate fidelity and site fidelity (for birds breeding for at least their second time) as 0 (new mate or site) or 1 (same mate or site as the previous attempt). The dependent-variable terms for experience with mate and experience with site were additive, beginning with 0 (indicating no previous experience with the site or mate). These terms were cumulative with respect to remating (after a divorce) or reoccupying a box (after previously moving out).

In order to examine the effect of mate fidelity on reproductive success it is important to separate effects of experience with a mate from effects of age and experience of a mate (see Ens, Choudhury & Black 1996; Part & Forslund 1996; Sydeman *et al.* 1996). As the duration of the pair bond increases so do the age and experience levels of both parents, and this must be accounted for. In our data set the precise age and experience levels of mates were known for only 69 of 683 reproductive attempts. In order to use the entire data set to examine the effects of experience with a mate, we estimated ages and experience levels of mates for the remaining 614 attempts by assuming that they were 3 years old (modal age of first breeding; see Pyle 2001) and that they had no previous experience when first identified (ringed) in the study plot. With each subsequent year of breeding these parameters increased for each individual. We assumed that these estimates were fairly accurate for birds first identified before 1986, when all unringed adults in the study plot were ringed each year. This accuracy probably decreased after 1986, however, when only unringed mates of known-age birds were ringed. We thus performed the following analyses to test the validity of our assumptions and inclusion of mate-age and mate-experience terms in the overall model. First, we ran the model on the data set including the 69 attempts in which mate age and mate experience were precisely known. Secondly, we ran the model on 289 attempts involving mates first identified in the data set in 1986 and before. Thirdly, we examined the results of models on the full data set but assuming that mates first encountered as unringed birds after 1986 were 4, 5, 6 and 7 years old, and had previously bred for 1, 2, 3 and 4 years.

Because annual reproductive success is an incomplete measure of fitness (Ens, Choudhury & Black 1996), we also examined how lifetime reproductive output (chicks produced during all breeding attempts by an individual) was affected by mate and site fidelity, based on data from the entire study period (1981–99, $n = 794$ attempts by 276 birds; see Pyle 2001). Lifetime reproductive output was determined for 120 birds that initiated breeding in 1993 or earlier, and that bred at least twice (such that mate and box fidelity could be assessed), by summing known number of fledged chicks with predicted number of fledged chicks for attempts when fledging status was unknown. Predicted number of chicks was determined from the final logistic regression model (see Results) including year, age and experience terms for both the known-age bird and its mate, and an experience-with-mate term. For these analyses lifetime mate fidelity and box fidelity were scored (for birds with at least 2 years of breeding) as: 1 – (total number of mates (or boxes)/total number of year breeding); thus birds that changed mates or boxes each year received fidelity scores = 0 and those with the same mate or in the same box throughout their lives received scores approaching 1. Although a small proportion of the sample (7·2%) of birds that initiated breeding in 1981–93 was still breeding at the end of the study period (1998 and/or 1999), there is no reason to expect that lifetime reproductive output in these birds was biased with respect to age, experience, mate fidelity or site fidelity. Breeding colony density was scored as the proportion of the 446 study boxes that were active (incubating bird recorded) in a given year (see Pyle 2001).

STATISTICAL ANALYSES

Using Stata (Stata Corporation 1997), we examined factors affecting mate fidelity, site fidelity and reproductive success with multiple logistic regression (Cox & Snell 1989). Because Cassin's auklets can produce up to two chicks per year through double-brooding (Ainley & Boekelheide 1990), we modelled effects on reproductive success (total chicks fledged/year) using ordered logistic regression. Non-linearity (curvilinearity) was tested by examining separately the significance of (1) quadratic (dependent-variable) terms (i.e. x^2); (2) asymptotic terms ($1/[x + c]$, where c is a constant); (3) logarithmic terms ($\log[x - c]$); and (4) exponential terms (e^x) (see Sydeman *et al.* 1991). In all cases where significant curvilinear effects were found the quadratic term resulted in larger r^2 values for the models than other curvilinear terms and thus quadratic terms are reported throughout the paper. No significant effects of higher polynomial terms (e.g. x^3 and x^4) for any variable were found. Linear trends were determined by testing terms without the addition of curvilinear terms for that variable.

We used a backward variable-selection modelling procedure. The final models included only terms with significant effects. Significance levels were estimated using the likelihood ratio test (see Sydeman *et al.* 1991), and likelihood ratio statistics (LRS) are reported. Significance levels of additional (non-significant) effects in the reproductive success model were determined in the same manner by adding the variable to the final model. To control for possible biases related to interannual variation in physical oceanographic conditions, year terms were added to all analyses. For models excluding density, year was included as a categorical variable, that is, terms for each year were included and controlled for in the model. Because density and the categorical year terms were confounded, we examined the effects of density both without the inclusion of year terms, and with the inclusion of year as a continuous linear term (see Pyle 2001). Residuals of all variables used in multiple logistic regressions met assumptions for normality (skewness/kurtosis tests, $P > 0.05$; Stata Corporation 1997). In all analyses, differences between the sexes were tested based on interaction terms between the sex and each variable in the final model; the term 'sex-specific' refers to an effect in which this interaction was significant. Additionally, analyses were performed separately on each sex to look for significant effects of a term on one sex but not the other.

Because our data set includes multiple attempts by the same individual there is the potential for pseudoreplication within our analyses. To examine this possibility we ran our final model on a data set including 428 attempts by birds with at least two years of breeding and included the term 'ring' (for ring number) as a categorical variable (see Spear, Pyle & Nur 1998 for more details). In addition to controlling for an individual main effect, this procedure has the added advantage of providing information on whether or not multiple observations for a single individual showed a correlated response.

Results

KNOWN-AGE BIRDS

Between 1987 and 1999, 252 known-age Cassin's auklets were recorded, 112 females, 134 males and six of undetermined sex. A total of 705 breeding attempts by these known-age birds was recorded for individuals 2–14 years of age and 0–11 years of previous breeding experience. Reproductive success was determined for 688 of these attempts, during which mean annual success (chicks fledged per pair) was 0·658 ± 0·556 (SD); range 0–2. Skipped years, defined as years of absence from the breeding sample between years of breeding, occurred 66 times among 40 birds (19 females and 21 males), and included 47 skipped episodes of 1–4 consecutive years. Thirty of the 66 skipped years (45·5%) occurred during periods of low ocean productivity associated with El Niño events in 1992 and 1998. Lifetime reproductive output was determined for 120 individuals that initiated breeding in 1993 or earlier and that bred at least twice, 56 females, 63 males, and one of undetermined sex. Mean reproductive output in these birds was 3·68 (± 2·68 [SD]; range 0–9·34) chicks fledged.

MATE FIDELITY

Of 475 attempts by 123 Cassin's auklets breeding for at least their second time and for which mate retention status was known, 261 (54·9%) involved the same mates as the previous year and 214 (45·1%) involved new mates. The proportion of mate-faithful attempts was similar for females (0·528, n = 212) and males (0·567, n = 261; LRS = 0·71, P = 0·400). Both with and without control for effects of year, breeding experience and breeding density, mate fidelity was significantly greater with age in males but not females (Table 1, Fig. 1), and

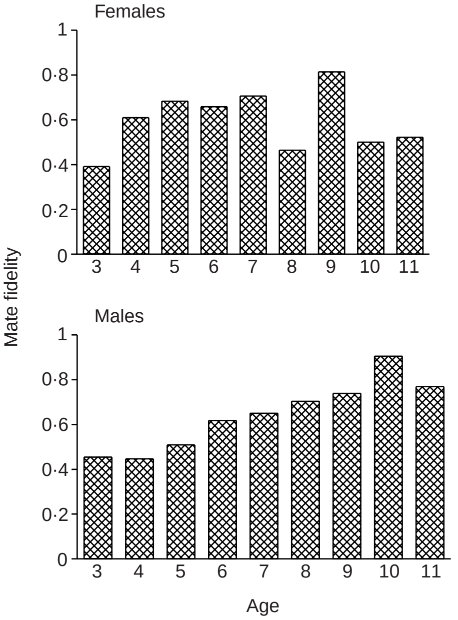

Fig. 1. Effects of age on mate fidelity in female and male Cassin's auklets. See Table 1 for statistical relationships.

Table 1. Relationships between mate fidelity and age, breeding experience and breeding density in Cassin's auklets on Southeast Farallon Island[1]

Variable	Slope	Overall	Females	Males	Sex-specific effect
n (birds/attempts)		123/475	53/212	69/261	122/473
Significant effects					
Age	+0·79	2·45	0·04	5·90*	4·39*
Age^2	–0·05	5·46**	2·24	2·02	1·31
Breeding density	–0·72	5·79**	4·63*	3·74	0·31
Non-significant effects					
Breeding experience	+0·20	0·51	0·03	0·04	0·17
Breeding experience^2	–0·00	1·41	0·09	1·48	0·97

[1] The analyses were limited to birds with at least 2 years' experience; for each observation, mate fidelity (the independent variable) was scored as 0 (different mate) or 1 (same mate) as the previous attempt. For overall (both sexes), females and males, likelihood ratio statistics based on logistic regression are presented. Linear trends were calculated without including quadratic terms for that variable. Slope is presented for the overall analysis only; direction of slope was the same for all three analyses. 'Sex-specific' effects were calculated based on interaction terms. For the overall model, r^2 = 0·117. Significant effects are indicated by asterisks: *P < 0·05, **P < 0·01.

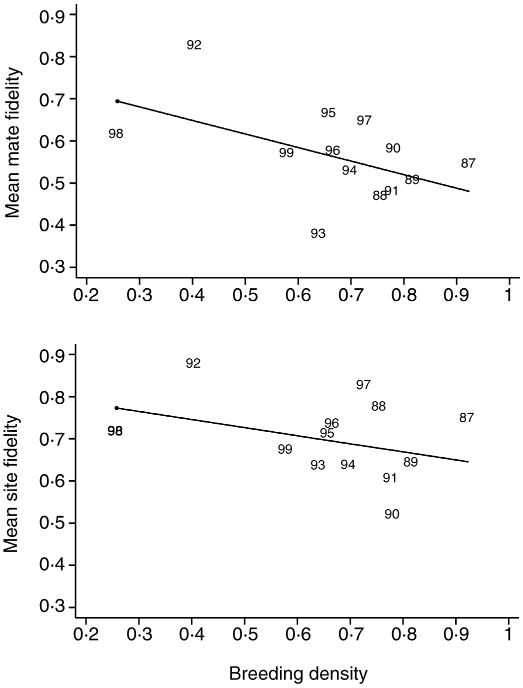

Fig. 2. Effects of breeding density (defined by box occupancy) on mate fidelity and site fidelity in Cassin's auklets. See Tables 1 and 2 for statistical relationships.

this difference was significant (Table 1). When sexes were combined, mate fidelity showed a significant negative curvilinear (but not linear) relationship with age (Table 1), resulting from the positive linear effect in males combined with the non-linear effect in females (see Fig. 1). Both with and without control for effects of year, age and breeding density, there were no significant linear, curvilinear or sex-specific correlations between mate fidelity and breeding experience (Table 1). Both with and without control for year (linear, continuous-variable term), age and breeding experience, there was a significant negative linear relationship between mate fidelity and breeding density; i.e. the lower the breeding density the higher the incidence of breeding with the same mate (Fig. 2). This effect was even stronger when the continuous year term was removed from the model (LRS = 7·79, $P = 0·005$). Although significant in females but not males, the difference in this relationship between the sexes was not significant (Table 1).

Mate fidelity was significantly lower after a breeding season was skipped (0·085, $n = 47$) than in a second consecutive breeding season in which the interim season was not skipped (0·421, $n = 259$; LRS = 19·25, $P < 0·0005$). Similarly, mate fidelity was significantly lower when a site was switched (0·236, $n = 148$) than when breeding occurred at the same site (0·691, $n = 327$; LRS = 80·73, $P < 0·0005$). These relationships were similar in males and females.

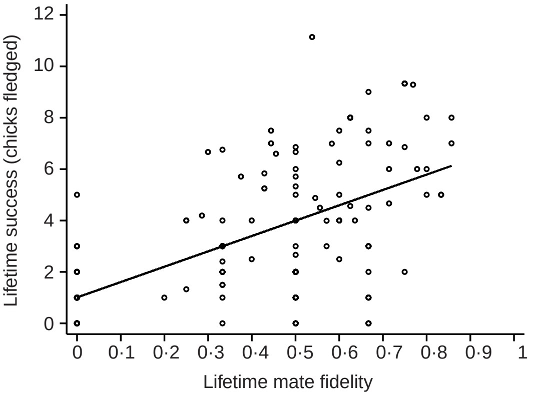

Fig. 3. Positive linear relationship (see text) between estimated lifetime success and lifetime mate fidelity in Cassin's auklets.

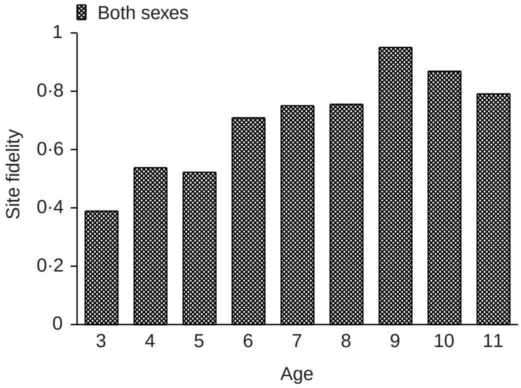

Fig. 4. Effects of age on site fidelity in Cassin's auklets. See Table 2 for statistical relationships.

Both with and without control for year of first breeding, age of first breeding, number of years breeding and lifetime site fidelity, lifetime reproductive output showed a significant increase with lifetime mate fidelity (birds with at least two attempts that had initiated breeding in 1993 or earlier; multiple regression; $n = 120$, $t = 2·14$, $P = 0·037$; Fig. 3). This relationship was linear (quadratic term, $t = 1·82$, $P = 0·071$) and showed no difference between the sexes (ANCOVA, $F_{7,111} = 0·02$, $P = 0·884$).

SITE FIDELITY

Of 480 attempts by 124 Cassin's auklets breeding for at least their second time and for which site fidelity was known, 328 (68·3%) were in the same sites as the previous year and 152 (31·7%) were in new sites. The proportion of site-faithful attempts was similar for females (0·692, $n = 214$) and males (0·678, $n = 264$; LRS = 0·10, $P = 0·751$). Both with and without control for effects of year, breeding experience and breeding density, site fidelity showed a significant linear increase and curvilinear decrease with age (Table 2, Fig. 4). Although this relationship was significant in females but not males, the difference between the sexes was not significant (Table 2). Both with and without control for effects of year, age and breeding density, there were no significant linear, curvilinear or sex-specific correlations between site fidelity and breeding

Table 2. Relationships between site fidelity and age, breeding experience and breeding density in Cassin's auklets on Southeast Farallon Island[1]

Variable	Slope	Overall	Females	Males	Sex-specific effect
n (birds/attempts)		124/480	53/214	70/264	123/478
Significant effects					
Age	+1·34	7·43**	6·05*	2·88	1·65
Age^2	–0·07	7·14**	5·33*	2·25	1·58
Breeding density	–0·31	4·18*	2·22	2·90	2·69
Non-significant effects					
Breeding experience	+0·13	2·16	0·03	3·26	2·67
Breeding experience^2	–0·02	0·14	0·96	0·34	1·76

[1] See Table 1 for further information on statistical procedures and presentation. For the overall model, $r^2 = 0{\cdot}242$. Significant effects are indicated by asterisks: *$P < 0{\cdot}05$, **$P < 0{\cdot}01$.

Table 3. Relationships between reproductive success and age, breeding experience, estimated age and breeding experience of mate, mate experience, site experience and breeding density in Cassin's auklets on Southeast Farallon Island[1]

Variable	Slope	Overall	Females	Males	Sex-specific effect
n (birds/attempts)		218/683	96/304	117/372	213/676
Final model (significant effects)					
Age	+0·15	5·11*	1·85	7·45**	5·09*
Age of mate	+0·24	3·99*	3·93*	0·19	2·89
Breeding experience^2	–0·06	17·50***	5·21*	17·49***	4·30*
Experience of mate^2	–0·07	8·64**	4·02*	1·04	3·17
Experience with mate	+0·22	4·81*	1·85	2·71	0·84
Non-significant effects					
Age^2	–0·01	0·81	0·54	0·02	1·90
Breeding experience	+0·56	1·29	0·95	1·98	1·30
Experience of mate	+0·36	1·20	1·34	0·96	1·65
Experience with mate^2	–0·06	2·62	0·72	2·46	0·18
Experience at site	+0·14	2·79	1·43	0·86	0·13
Experience at site^2	–0·16	0·58	0·05	1·47	0·03
Breeding density	+1·36	2·80	0·68	2·52	0·14

[1] Likelihood ratio statistics based on ordered logistic regression on the term total chicks fledged are presented; see text for methods of determination. See Table 1 for further information on statistical procedures and presentation. An LRS value could not be obtained for the term Age of mate^2 due to colinearity. For the overall model, $r^2 = 0{\cdot}189$. Significant effects are indicated by asterisks:*$P < 0{\cdot}05$, **$P < 0{\cdot}01$, ***$P < 0{\cdot}001$.

experience (Table 2). Both with and without control for year (linear, continuous-variable term), age and breeding experience, there was a significant negative linear relationship between site fidelity and breeding density; i.e. the lower the breeding density the higher the incidence of breeding at the same site (Fig. 2). This effect was even greater when the year term was removed from the model (LRS = 6·53, $P = 0{\cdot}011$). The difference in this relationship between the sexes was not significant (Table 2).

Site fidelity was significantly lower after a breeding season was skipped (0·298, $n = 47$) than in a second consecutive breeding season in which the interim year was not skipped (0·595, $n = 262$; LRS = 14·26, $P < 0{\cdot}0005$). Similarly, site fidelity was significantly lower when the mate switched (0·472, $n = 214$) than when breeding occurred with the same mate (0·866, $n = 261$; LRS = 85·07, $P < 0{\cdot}0005$). These relationships were similar in males and females.

Controlling for year of first breeding, age of first breeding, number of years breeding and lifetime mate fidelity, lifetime reproductive output did not show a significant relationship with lifetime site fidelity (birds with at least two attempts and which initiated breeding before 1994; multiple regression; $n = 120$, $t = 1{\cdot}15$, $P = 0{\cdot}251$). In addition, this relationship showed no sex-specific effect (ANCOVA, $F_{7,111} = 0{\cdot}64$, $P = 0{\cdot}429$).

EFFECTS OF AGE AND EXPERIENCE ON ANNUAL REPRODUCTIVE SUCCESS

Controlling for all other significant variables, reproductive success showed a significant linear increase with age that was significantly greater in males than in females (Table 3; Fig. 5). This linear effect was also found for age of mate (when unringed mates after 1986 were assumed to be 3 years of age; $P = 0{\cdot}046$), being significant for male mates but not for female mates.

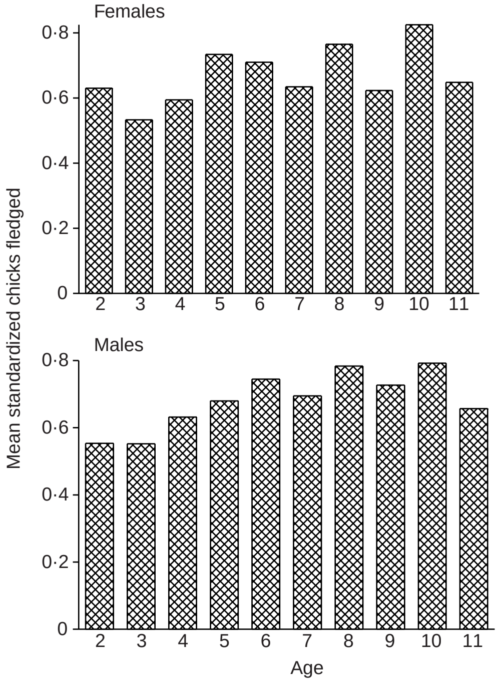

Fig. 5. Effects of age on reproductive success in female and male Cassin's auklets. 'Standardized chicks fledged' represents reproductive success after controlling for the other significant variables in Table 3, based on residuals from multiple regression analysis. For figure representation, age groups of 11–14 years, breeding-experience groups of 9–11 years and mate-experience groups of 5–8 years have been pooled.

Significance levels were smaller when unringed mates after 1986 (n = 105 involved in 167 breeding attempts) were assumed to be age 4, 5, 6 and 7 years when first observed (LRS = 3·86–3·63, P = 0·049–0·057).

Controlling for other significant effects, breeding experience showed significant negative curvilinear but not linear (parabolic) relationships with annual reproductive success for both the known-age bird (Table 3, Fig. 6) and its mate (Table 3), assuming unringed mates after 1986 had no previous breeding experience. As with age, this breeding-experience effect was significantly greater in males than in females (Table 3, Fig. 6). The quadratic experience-of-mate effects became progressively weaker when unringed mates after 1986 were assumed to have 1, 2, 3 and 4 (LRS = 4·91–1·32, P = 0·027–0·251) years of previous breeding experience when first observed.

Controlling for the age and experience terms of both the known-age bird and its mate, experience with a mate had a significant linear relationship with annual reproductive success of the known-age bird (Table 3, Fig. 7). This relationship showed no sex-specific effect (Table 3). The experience-with-mate term was also significant when the data were restricted to attempts with mates first identified before 1987 (n = 289, LRS = 2·13, P = 0·033) and nearly significant when the analysis was restricted to pairs in which the age and experience of both parents were known (n = 69, LRS = 1·92, P = 0·055).

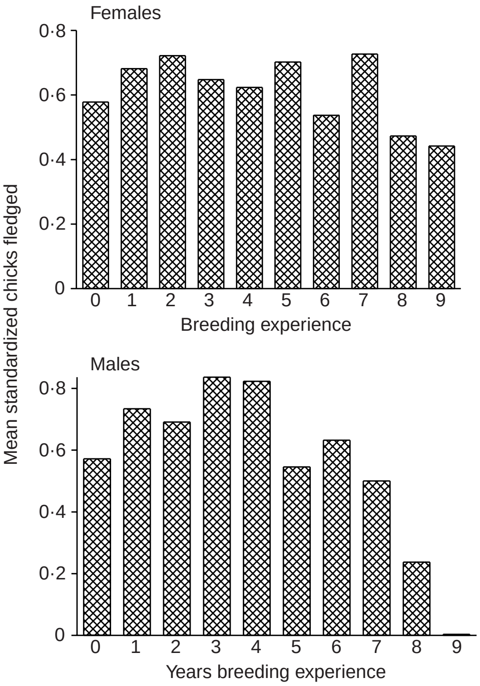

Fig. 6. Effects of breeding experience on reproductive success in female and male Cassin's auklets. See Fig. 5 for definition of 'Standardized chicks fledged' and for information on pooled data.

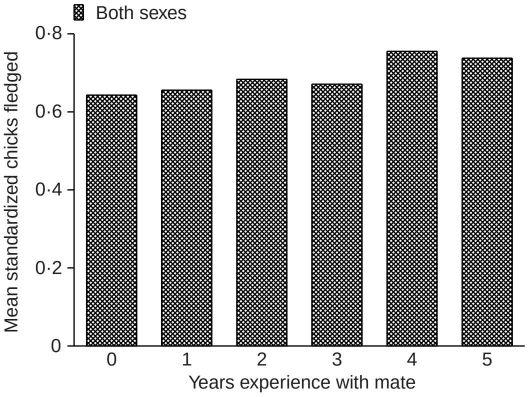

Fig. 7. Effects of mate experience on reproductive success in Cassin's auklets. See Fig. 5 for definition of 'Standardized chicks fledged' and for information on pooled data.

Controlling for the significant effects of the terms in the final model, both experience at a breeding site and breeding density showed no significant correlations with reproductive success (Table 3). The breeding density term remained non-significant (LRS = 2·76, P = 0·097) when year terms were removed from the model, and reproductive success also showed no relationship with year when density was removed (LRS = 1·21, P = 0·261). There were also no significant interactions between any of the significant effects in the final model and breeding density (LRS < 0·82, P > 0·365).

Finally, when the model was re-examined using 428 attempts by birds that had bred at least twice and including the term 'ring' (for ring number), only one change was observed in significance levels for terms in the final model (Table 3), including both sexes. The age-of-mate term for females was no longer significant (LRS = 1·83, $P = 0{\cdot}068$). Otherwise, significance levels were the same for all other terms shown in Table 3. The categorical term ‘ring’ was not significant (multiple regression, $P = 0{\cdot}097$).

Discussion

MATE FIDELITY AND SITE FIDELITY

Among Cassin’s auklets on SEFI, both mate and site fidelity increased with age but not previous breeding experience. Although relationships between mate fidelity and both age and experience have been documented in long-lived birds (Ens, Choudhury & Black 1996) few previous studies have examined both simultaneously, and most studies have speculated that mate fidelity increased with increased breeding experience rather than age. The correlations with age but not experience in Cassin’s auklets suggest that other factors may affect mate and site fidelity besides fitness advantages related to experience with a mate (Black 1996); e.g. as birds age they may commit less energy to acquiring new mates or sites. In addition, a quality effect may be occurring; i.e. older birds may be of higher quality and better able to retain the mates and sites of their choice.

The relationship between age and mate fidelity was significantly stronger in males, whereas that between age and site fidelity was significant in females but not males. This suggests sex-specific roles during the courtship period: males may be more responsible for mate selection and females for site selection (see Greenwood 1980). Our results also suggest that improved foraging experience with age and a cost of reproduction may be more important factors in males than females. It is possible that older males, because of their higher reproductive potential, are better able to retain or select high-quality mates than younger males, further improving their reproductive output (since experience with mates also results in increased reproductive success). Older males that lose mates may seek other high-quality females at other sites. Older females, on the other hand, appear more apt to remain at their sites when switching mates, despite the fact that site experience appears to have little if any relationship with reproductive success. Therefore, these data suggest that reproductive success is optimized by behaviour of male rather than female Cassin’s auklets; that is, the life-history traits of the male have greater bearing on reproductive success than those of the female.

Mate fidelity increased significantly with decreased breeding density despite the fact that, theoretically, fewer returning birds should result in more mate turnover (Rowley 1983; Ens, Safriel & Harris 1993; Ens, Choudhury & Black 1996). This result suggests that a quality effect may be acting in combination with a cost to acquiring a new mate. We suggest that only the highest quality birds breed during years of low food availability (e.g. 1992 and 1998) and that these birds are more likely to have already established a long-term pair bond. Additionally, the high rate of skipping during such years and the significant increase in mate switching after skipped years suggest that birds are unable to acquire new mates after mortality; i.e. mate acquisition may be too costly (in terms of energy and lost time) to overcome during high-stress years (see Switzer 1993; Schjorring, Gregersen & Bregnballe 2000). The increase in site fidelity with decreasing breeding density may also indicate that only higher-quality individuals are breeding in low-density years (see also below).

There is much interest in the subject of whether mate fidelity is dictated by site fidelity or vice versa (Morse & Kress 1984; Desrochers & Magrath 1996; Ens, Choudhury & Black 1996). We do not yet have enough data on true mate fidelity vs. divorce in Cassin’s auklets to answer this question with the present data (see also Sydeman *et al.* 1996). However, our results suggest that fitness is optimized more through mate selection than site selection in Cassin’s auklets and thus we predict that mate fidelity is not a by-product of site fidelity, as inferred for species which forage for food resources within their territories (Desrochers & Magrath 1996; Newton & Wyllie 1996; Payne & Payne 1996). There appears to be little variation in site quality for Cassin’s auklets on SEFI, all boxes (and presumably natural burrows) being roughly the same in terms of reproductive fitness (Pyle 2001). It might be expected, therefore, that burrow-nesting species such as the Cassin’s auklet will optimize mate selection over site selection (but see Morse & Kress 1984), whereas the reverse may be true in species foraging within their territories and colonial, surface-nesting species more subject to predation.

BENEFITS AND COSTS OF AGE, EXPERIENCE AND MATE FIDELITY

Reproductive success showed a significant linear increase with age of males, a highly significant parabolic relationship with previous breeding experience of both sexes and a significant linear increase with experience with a mate. Few other studies have been able to examine effects on success of these three parameters simultaneously (Forslund & Part 1995; Black 1996; Part & Forslund 1996). Western gulls breeding on SEFI showed similar linear increases in success with age of males and parabolic relationships with breeding experience (Pyle *et al.* 1991). In that species it was suggested that foraging experience increased with age (cf. Burger 1988; Ratcliffe & Furness 1999), especially of males, whereas reproductive success increased with breeding experience during the first few attempts (especially in females) but thereafter was affected by a cost of reproduction (Pyle *et al.* 1991, 1997). The same patterns appear to be occurring in Cassin’s auklets, with the exception that the experience effect is stronger in males than females. This suggests that male Cassin’s auklets, in addition to equal sharing in incubation (which does not occur in western gulls; Pierotti 1981), may serve additional roles in reproduction which are more costly than those of females.

Few previous studies have documented an increase in reproductive success with duration of the pair bond while controlling for age and breeding experience of both members of the pair (cf. Black 1996), although coordination of breeding activities between a pair has often been suggested in support of monogamy (Bradley *et al*. 1995; Ens, Choudhury & Black 1996). Here we found a pair-bond effect after controlling for age and experience terms of both parents, supporting the suggestions of Emslie, Sydeman & Pyle (1992) and Sydeman *et al*. (1996) that mate fidelity is adaptive in Cassin's auklets and those of Cezilly & Nager (1996) that studies examining the effects of age and experience on reproductive performance also consider the duration of the pair bond.

Alternatively, it is possible that a quality effect is influencing this relationship. We suggested above that higher quality males may be retaining the mates of their choice; thus, increased reproductive success with duration of the pair bond may be a result (at least partially) of this increased-quality effect. In this respect, however, it is interesting that addition of the categorical term 'ring' had no effect on the significance level of the positive pair-bond effect (or on other effects in the model) and that the term itself was not significant ($P = 0{\cdot}097$). This suggests that the pair-bond effect is genuine, and that biases due to variation in quality of individual auklets on this effect may be minimal.

Finally, the lack of significant density-dependent effects on reproduction in Cassin's auklets is surprising. Ainley & Boekelheide (1990) also found that interannual variation in incubation and chick rearing was not as marked in Cassin's auklets as in other breeding seabirds on SEFI. We suggest that, during short-term reductions in food supply, lower quality but not higher quality breeders are prevented from reproducing, and that the increase in quality offsets the reduction in food availability. Our observations on density-dependence in mate and site fidelity, combined with the fact that both natal dispersal distance and age of first breeding increase with decreased breeding density (Pyle 2001), supports this premise.

Acknowledgements

We thank the US Fish and Wildlife Service/San Francisco Bay National Wildlife Refuge, managers of the Farallon Island National Wildlife Refuge, for facilitating and supporting our research on the island. We are also grateful to the numerous interns that collected the known-age Cassin's auklet data, under the supervision of Farallon Biologists David Ainley, Bob Boekelheide, Jay and Teya Penniman, Harry Carter, Steven D. Emslie, Joan Walsh, Elizabeth McLaren, Kelly Hastings and Kyra Mills. Tom Roudybush and Jerry Nusbaum constructed most of the boxes used in our studies. We thank David Ainley, Nadav Nur and two anonymous referees for providing critical reviews of the manuscript. This is contribution 928 of the Point Reyes Bird Observatory.

References

Ainley, D.G. & Boekelheide, R.J. (1990) *Seabirds of the Farallon Islands. Ecology, dynamics, and structure of an upwelling-system community*. Stanford University Press, Stanford, California.

Ainley, D.G., LeResche, R.E. & Sladen, W.J. (1983) *Breeding Biology of the Adelie Penguin*. University of California Press, Berkeley, California.

Ainley, D.G., Spear, L.B. & Allen, S.G. (1996) Variation in the diet of Cassin's auklet reveals spatial, seasonal, and decadal occurrence patterns of euphausiids off California, U.S.A. *Marine Ecology Progress Series*, **137**, 1–10.

Ainley, D.G., Sydeman, W.J., Hatch, S.A. & Wilson, U.L. (1994) Seabird population trends along the west coast of North America: causes and the extent of regional concordance. *Studies in Avian Biology*, **15**, 119–133.

Ainley, D.G., Sydeman, W.J. & Norton, J. (1995) Upper trophic level predators indicate interannual negative and positive anomalies in the. California Current food web. *Marine Ecology Progress Series*, **118**, 69–79.

Black, J.M. (1996) Introduction: pair bonds and partnerships. *Partnerships in Birds* (ed. J.M. Black), pp. 3–20. Oxford University Press, Oxford.

Bradley, J.S., Wooller, R.D., Skira, I.J. & Serventy, D.L. (1995) The influence of mate retention and divorce upon reproductive success in short-tailed shearwaters *Puffinus tenuirostris*. *Journal of Animal Ecology*, **59**. 487–496.

Burger, J. (1988) Effects of age on foraging in birds. *Proceedings of the 19th International Congress* (ed. H. Ouellet), pp. 1127–1140. University of Ottawa Press, Ottawa.

Cezilly, F. & Nager, R.G. (1996) Age and breeding performance in monogamous birds: the influence of pair stability. *Trends in Ecology and Evolution*, **11**, 27.

Clutton-Brock, T.H. (1988) *Reproductive Success. Studies of individual variation in contrasting breeding systems*. University of Chicago Press, Chicago.

Cox, D.R. & Snell, E.J. (1989) *Analysis of Binary Data*. Chapman & Hall, London.

Curio, E. (1983) Why do young birds reproduce less well? *Ibis*, **125**, 400–404.

Desrochers, A. & Magrath, R.D. (1996) Divorce in the European blackbird: seeking greener pastures? *Partnerships in Birds* (ed. J.M. Black), pp. 177–191. Oxford University Press, Oxford.

Emslie, S.D., Sydeman, W.J. & Pyle, P. (1992) The importance of mate retention and experience on breeding success in Cassin's auklet (*Ptychoramphus aleuticus*). *Behavioral Ecology*, **3**, 189–195.

Ens, B.J., Choudhury, S. & Black, J.M. (1996) Mate fidelity and divorce in monogamous birds. *Partnerships in Birds* (ed. J.M. Black), pp. 344–401. Oxford University Press, Oxford.

Ens, B.J., Safriel, U.N. & Harris, M.P. (1993) Divorce in the long-lived and monogamous oystercatcher *Haematopus ostralegus*: incompatibility or choosing a better option? *Animal Behaviour*, **45**, 1199–1217.

Forslund, P. & Part, T. (1995) Age and reproduction in birds – hypotheses and tests. *Trends in Ecology and Evolution*, **10**, 374–378.

Greenwood, P.J. (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140–1162.

Manuwal, D.A. (1974) The natural history of Cassin's auklet *Ptychoramphus aleuticus*. *Condor*, **76**, 421–431.

Morse, D.H. & Kress, S.W. (1984) The effect of burrow loss on mate choice in the Leach's storm petrel. *Auk*, **101**, 158–160.

Nelson, D.A. (1989) Gull predation on Cassin's auklet varies with lunar cycle. *Auk*, **106**, 495–497.

Newton, I. (1989) *Lifetime Reproduction in Birds*. Academic Press, New York.

Newton, I. & Wyllie, I. (1996) Monogamy in the sparrowhawk. *Partnerships in Birds* (ed. J.M. Black), pp. 249–267. Oxford University Press, Oxford.

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.

Part, T. & Forslund, P. (1996) Age and breeding performance in monogamous birds: the influence of mate experience. *Trends in Ecology and Evolution*, **11**, 220.

Payne, R.B. & Payne, L.L. (1996) Dispersal, demography, and the persistence of partnerships in Indigo Buntings. *Partnerships in Birds* (ed. J.M. Black), pp. 305–320. Oxford University Press, Oxford.

Pierotti, R. (1981) Male and female parental roles in the western gull under different environmental conditions. *Auk*, **98**, 532–549.

Pyle, P. (2001) Age of first breeding and natal dispersal distance in a declining population of Cassin's auklets. *Auk*, **118**, in press.

Pyle, P., Nur, N., Sydeman, W.J. & Emslie, S.E. (1997) Costs of reproduction and the evolution of deferred breeding in the western gull. *Behavioral Ecology*, **8**, 140–147.

Pyle, P., Spear, L.B., Sydeman, W.J. & Ainley, D.G. (1991) The effects of experience and age on the breeding performance of western gulls. *Auk*, **108**, 25–33.

Ratcliffe, N. & Furness, R.W. (1999) The effect of parental age and experimentally manipulated brood size on the foraging effort and breeding performance of great skuas (*Catharacta skua*). *Journal of the Zoological Society of London*, **249**, 195–201.

Ratcliffe, N., Furness, R.W. & Klomp, N.I. (1998) Influences of breeding experience on the reproductive performance of great skuas. *Journal of Avian Biology*, **29**, 293–298.

Rowley, I. (1983) Re-mating in birds. *Mate Choice* (ed. P. Bateson), pp. 331–360. Cambridge University Press, Cambridge.

Saether, B. (1990) Age-specific variation in reproductive performance in birds. *Current Ornithology*, **7**, 251–283.

Schjorring, S., Gregersen, J. & Bregnballe, T. (2000) Sex difference in criteria determining fidelity towards breeding sites in the great cormorant. *Journal of Animal Ecology*, **69**, 214–223.

Spear, L.B., Pyle, P. & Nur, N. (1998) Natal dispersal in the western gull: proximal factors and fitness consequences. *Journal of Animal Ecology*, **67**, 165–179.

Stata Corporation (1997) *STATA Statistical Software: release 5·0*. Stata Corporation, College Station, Texas.

Switzer, P.V. (1993) Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology*, **7**, 533–555.

Sydeman, W.J., Huber, H.R., Emslie, S.D., Ribic, C.A. & Nur, N. (1991) Age-specific reproductive success of northern elephant seals in relation to previous breeding experience. *Ecology*, **72**, 2204–2217.

Sydeman, W.J., Pyle, P., Emslie, S.D. & McLaren, E.B. (1996) Causes and consequences of long-term partnerships in Cassin's auklets. *Partnerships in Birds* (ed. J.M. Black), pp. 211–222. Oxford University Press, Oxford, UK.

Received 9 November 2000; revision received 1 August 2001