



RECRUITMENT OF CASSIN'S AUKLET (*PTYCHORAMPHUS ALEUTICUS*): INDIVIDUAL AGE AND PARENTAL AGE EFFECTS

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ABSTRACT.—Recruitment is an important aspect of life history that is difficult to estimate without long-term data. We used 28 years of data to create multistate capture–mark–recapture models with maturity status as state to provide estimates of age-dependent probabilistic recruitment (transition from juvenile to breeder state) of Cassin's Auklets (*Ptychoramphus aleuticus*) breeding at Southeast Farallon Island, California. We found strong evidence for age effects in recruitment and survival, but not in breeding propensity. We also examined parental-age effects on return rate of offspring. Although an average of 70% of a cohort begins breeding by age 4, fledglings from 2- to 4-year-old mothers were less likely to become breeders than fledglings produced by older mothers. This may be attributable to age-related differences in egg production and maternal offspring-rearing abilities that could contribute to differences in fledgling recruitment rates. Eggs of younger mothers had lower volume and their fledglings had lower mass than those of older mothers. We suggest that researchers, managers, and population modelers consider the possibility that young breeding birds that successfully fledge young do not always produce viable offspring that will become breeders. Received 23 March 2011, accepted 16 December 2011.

Key words: age of first breeding, *Alcidae*, Cassin's Auklet, demography, juvenile survival, mark–recapture, multistrata, parent quality, *Ptychoramphus aleuticus*.

Contratación de pygmaea de Cassin (*Ptychoramphus Aleuticus*): efectos de cada edad y edad Parental

RESUMEN.—Reclutamiento es un aspecto importante de la historia de la vida que es difícil estimar sin datos a largo plazo. 28 Años de datos se utilizan para crear modelos multistate capture–mark–recapture con el estado de madurez como Estado proporcionar estimaciones dependiente de la edad probabilística contratar (transición del juvenil al Estado de criador) crestada de Cassin (*Ptychoramphus aleuticus*) cría en isla Farallón de sureste, California. Encontramos pruebas sólidas para efectos de la edad en la contratación y la supervivencia, pero no en la propensión de cría. También examinamos parental edad efectos sobre la tasa de retorno de descendencia. Aunque un promedio del 70% de una cohorte comienza cría por 4 años, polluelos de 2 a 4 años de edad las madres eran menos propensos a convertirse en criadores de polluelos producción por las madres mayores. Esto puede atribuirse a diferencias relacionadas con la edad en la producción de huevos y maternas habilidades de crianza de los hijos que podrían contribuir a las diferencias en las tasas de reclutamiento incipiente. Huevos de las madres más jóvenes tenían menor volumen y sus polluelos tenían menor masa que las de las madres mayores. Sugerimos que los investigadores, administradores y modeladores de población consideren la posibilidad que cría joven que vuelan con éxito jóvenes no siempre producen descendencia viable que se convertirá en criadores. Sugerimos que los investigadores, administradores y modeladores de población consideren la posibilidad que cría joven que vuelan con éxito jóvenes no siempre producen descendencia viable que se convertirá en criadores.

JUVENILE SURVIVAL AND the age at which an organism begins to reproduce (called primiparity, age of first breeding, or recruitment age) are important life history traits that influence population dynamics (Croxall and Rothery 1991, Hatchwell and Birkhead 1991, Charnov 1997, Morris and Doak 2002). According to life history theory, individuals should begin reproducing at the age that maximizes lifetime reproductive success (Stearns 1992). Age of first breeding can have a profound influence on an individual's fitness (Cole 1954, Stearns 1992, Krüger 2005), and variation among individuals in this parameter can strongly influence population

growth (Porter and Coulson 1987, Caswell 2001). Furthermore, reproductive success and survival commonly increase with age (Sæther 1990, Forslund and Pärt 1995, Ezard et al. 2007), and the strength of this increase will affect whether or not early recruitment is favored by selection.

Here, using 28 years of data, we estimate age-specific demographic traits (recruitment, survival, and breeding propensity) of the planktivorous Cassin's Auklet (*Ptychoramphus aleuticus* Pallas) in the eastern North Pacific Ocean. We studied Cassin's Auklets on Southeast Farallon Island, California, in the central

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portion of the California Current System. We used a particular case of multistate capture–mark–recapture modeling with two states (juvenile and breeding adult), one of which (juvenile) was unobservable except at fledging, to examine recruitment as a probabilistic event (Pradel and Lebreton 1999, Kendall and Nichols 2002, Crespin et al. 2006, Lebreton et al. 2009). Our models explicitly model the transition from juvenile to breeder while controlling for variation in survival and recapture probabilities. This updates Pyle's (2001) estimates of Cassin's Auklet age of first breeding from the same colony.

We also estimated age-specific survival and recapture probability and used model selection to identify the most parsimonious age curve for the three demographic traits. Determining age curves for vital rates under the model selection process provides insight into the nature of how age affects demographic processes and describes a species' life history. The recapture probability of species with high breeding-site tenacity, such as seabirds, is biologically interesting to the extent that it incorporates the conditional probability that an individual will breed in a particular year, given that it has survived to that year (Lebreton et al. 1992). Thus, recapture probability is an estimate of minimum breeding propensity and is equivalent to $1 - \text{probability of skipping breeding}$.

Previous multistate studies on marine birds have documented recruitment (transition from juvenile to breeder state) as categorically age-specific (Crespin et al. 2006), increasing linearly with age (Jenouvrier et al. 2008), and increasing to a plateau through an inverse age function (Lee et al. 2008). Age-specific survival has been described as a constant (Nur and Sydeman 1999; Lee et al. 2007, 2008), a negative linear function (Dunnet and Ollason 1978, Spear et al. 1987), a constant that exhibits senescent decline in oldest ages (Buckland et al. 1983, Bradley et al. 1989, Aebischer and Coulson 1990, Croxall et al. 1990), or a quadratic curve in which survival increases with age to a midlife optimum and then declines as the oldest birds senesce (Rattiste and Lilleleht 1987, Frederiksen and Bregnballe 2000). Age-specific breeding propensity has been described infrequently for seabirds, but varying patterns have been observed: a constant (Lee et al. 2008), a linear increase with age (Ollason and Dunnet 1988, Thomas and Coulson 1988), a steady increase to an asymptote, then constant (Wooler et al. 1989), or a linear decrease with age (Mills 1989).

Although recruitment age is typically defined as the age at which an organism starts to reproduce, this definition does not consider the differential fate of independent offspring from parents of different ages and experience levels. Just as reproductive success and survival can increase with age (Forslund and Pärt 1995, Ezard et al. 2007), the probability that independent offspring will themselves survive to become breeders might also increase with parental age (Meathrel and Carey 2007). Intrinsic factors such as parental age, egg size, and fledging mass can influence postfledging survival and recruitment (Ludwigs and Becker 2006, Becker and Bradley 2007, Morrison et al. 2009). Probability of recruitment may be related to parental quality traits that increase with the parent's age, such as body mass (Meathrel et al. 1993, Morrison et al. 2009), egg size (Boersma 1982), or offspring provisioning (Pugesek 1995). Thus, offspring of young parents may have a lower probability of surviving and becoming breeders themselves than offspring of more mature parents. Models of population dynamics that assume that all independent offspring have equal probability of recruitment, regardless of parental age, may

be inaccurate. We examined effects of parental age on offspring recruitment by estimating return rate of fledglings as a function of parental age. In order to clarify potential reasons for differential return rates, we compared younger versus older parents to test for differences in adult mass, egg volume, and fledgling weight.

The objectives of our study were to (1) use capture–mark–recapture data to estimate age-specific variation in recruitment probability, survival, and breeding propensity; (2) select a parsimonious model of age functions for demographic traits using six competing age curves; and (3) examine the relationship between the age of a parent and the probability that its offspring would return to breed. Temporal variation in parameter estimates is known to exist in this population (Lee et al. 2007) but will be the focus of a separate paper (N. Nur et al. unpubl. data). Because of our interest in examining age-specific patterns in demographic traits, we controlled for temporal variation but did not explore temporal models explicitly.

METHODS

Data collection.—Data were collected from 1981 to 2009 on Southeast Farallon Island, Farallon Island National Wildlife Refuge, California (37°42'N, 123°00'W), site of one of the largest Cassin's Auklet breeding populations in the United States, outside of Alaska. Biologists from PRBO Conservation Science (hereafter PRBO) have been monitoring the population size, reproductive success, and diet of Cassin's Auklets on Southeast Farallon Island since 1971. Cassin's Auklets on Southeast Farallon Island nest in rock crevices and in burrows excavated in soil. Between 1978 and 1983, PRBO and collaborators installed 446 nest boxes to facilitate data collection from individually marked auklets. Nest boxes were unevenly distributed among 10 areas in accessible portions of the island (Pyle 2001). Boxes were located in soil and rock scree; no boxes were placed in cliff habitats, although auklets breed there.

In 1978, we began to mark adults and fledglings with individually number-coded stainless-steel leg bands. Band loss was estimated as <0.1% per year (Pyle 2001), so this factor was considered negligible to our estimates. From 1981 to 2009, we captured and resighted breeding birds annually in all nest boxes. Beginning on 2 March each year, we checked all nest boxes every 5–15 days for breeding auklets. When a known-age bird was found, we monitored the site every 5 days to determine breeding success (Abraham and Sydeman 2004). Each individual known-age auklet was assigned an annual breeding-status record. Annual records of resightings and breeding status were compiled as individual encounter histories through time. We pooled the sexes for analyses because we expected no sex differences in a socially monogamous species such as Cassin's Auklet in which incubation and offspring-provisioning responsibilities are apparently fully shared (Manuwal 1974a, b); previous analyses indicated no significant sex-related differences in demographic parameters (Lee et al. 2007). For this analysis, we selected only known-age birds banded as chicks at Southeast Farallon Island.

Statistical analyses.—Cassin's Auklets return to the breeding colony only as breeders. Thus, we used a particular case of multistate capture–mark–recapture modeling with two states, juvenile pre-breeders (J) and adult breeders (B) of which one (J) was unobservable except when banded and released just prior to fledging (Kendall and Nichols 2002, Reed et al. 2003, Crespin et al.

2006). For multistate models, codes are used in the longitudinal individual encounter histories to distinguish between sampling occasions (years). Annual observations for each individual were classified according to breeding state. Fledglings were classified as juvenile pre-breeders, coded as J in encounter histories. If a bird returned to breed and was captured in a nest box, it was classified as a breeder and was coded as B in the encounter history.

Three kinds of parameters can be estimated with these models: apparent survival probability (S_a^B), conditional transition probability (ψ_a^{JB}), and capture probability (p_a^B) (Kendall and Nichols 2002, Reed et al. 2003). S_a^B is the probability that an individual in state B at age a survives until age $a + 1$ (an apparent survival probability because we cannot differentiate between mortality and permanent emigration from the study area). ψ_a^{JB} is the probability that an individual in state J at age a is in state B at age $a + 1$, given that it survived from age a to $a + 1$; and p_a^B is the probability that an individual is recaptured at age a in state B, given that it is alive and present in the study area at age a . In addition to age intervals such as a to $a + 1$, time-specific intervals such as year t to $t + 1$ are easily modeled.

Following Pradel and Lebreton (1999), Reed et al. (2003), and Crespin et al. (2006), some constraints were needed in the recapture, survival, and transition probabilities to make parameters estimable. First, auklets in state J are never available for recapture between fledging and primiparity (J is an unobservable state after fledging); thus, recapture probability is fixed to zero for birds of all ages in state J. Second, because auklets can be recaptured only as breeders (state B) and no Cassin's Auklet in our data set ever began breeding before age 2, recapture probability for 1-year-olds in state B is also fixed to zero. Recapture probability of breeders estimated in this analysis indicates minimum breeding propensity, where breeding propensity is the probability that an adult will attempt to breed in a given year. Breeding propensity = $1 -$ skipping probability, where skipping probability is the probability that an adult will not breed in a given year. Third, juvenile survival (survival from fledging to the minimum age at first breeding) is estimated over the age interval from 0 to 2, so survival from age 0 to 1 was fixed to 1 and survival from age 1 to 2 equals the compound juvenile survival from ages 0 to 2. Fourth, survival after the minimum age of first breeding (age 2) is set as equal for the two states. This assumes no cost of reproduction and estimates survival as the mean of breeders and pre-breeders for ages 2 to 15. Finally, transition probabilities in recruitment analyses are unidirectional (i.e., once an individual starts breeding, it remains a breeder for the rest of its life). Thus, the parameter ψ_a^{BJ} , the probability of transitioning from breeder to pre-breeder, is fixed at zero.

Recruitment is a probabilistic event conditional on three different, potentially independent probabilities (Clobert et al. 1993): (1) survival from fledging to age $a - 1$; (2) fidelity to the natal area; and (3) transition from the "juvenile" state at age $a - 1$ to the "breeder" state at age a . Hereafter, "recruitment probability" refers to this transition probability (ψ^{JB}) from pre-breeder to first-time breeder (Pradel and Lebreton 1999). As emphasized by Clobert et al. (1993), unless relevant data from colonies within the plausible range of natal dispersal are available, the first two components cannot be separated and their product is "apparent survival" (S). Because there are no banding and resighting data from nearby colonies, which number very few, we deal only with apparent survival and local recruitment in this analysis.

With previous studies in mind, our *a priori* model set for age functions included S , p , and ψ parameters modeled as (1) constant; (2) linear (increase or decrease) with age (linear age); (3) quadratic with age ($\text{age} + \text{age}^2$; age^2); (4) cubic with age ($\text{age} + \text{age}^2 + \text{age}^3$; age^3); (5) decelerating increase with age [$\ln(\text{age})$]; (6) a plateau with age ($1/\text{age}$); and (7) age-specific. We ranked these models in Program MARK (White and Burnham 1999) for each parameter to determine the most parsimonious age curve. We used model averaging to create an age curve that included model-selection uncertainty when making inferences (Burnham and Anderson 2002).

To estimate age-specific survival, recapture, and transition probability, we used multistate capture–mark–recapture models in MARK. We used a fully age-specific model with 15 age classes in survival and recapture and 10 age classes in recruitment to obtain age-specific estimates. No formal goodness-of-fit test is available for multistate models with an unobservable state. Following Lebreton et al. (2009), we initially suppressed the first capture event to focus on adults with a global single-state model with only year-specific variation in survival and recapture probabilities [$S(\text{time}) p(\text{time})$]. We assessed goodness-of-fit for the Cormack-Jolly-Seber model with the program U-CARE (Choquet et al. 2005). Subsequent model selection incorporating various age and state structures was based on $qAIC_c$ (Akaike's information criterion corrected for small sample sizes, based on quasi-likelihood; Burnham and Anderson 2002), with MARK integrating the correction from the overdispersion factor. All age-specific estimates and age-curve model-selection presented here were done while controlling for temporal variation by modeling year as a categorical effect in all estimated parameters (recapture, survival, and recruitment). For clarity, we did not include the temporal effect in our model notation, but it is present in all parameters.

We performed age-curve model selection on each parameter sequentially in the order p^B , S^B , and ψ^{JB} (Doherty et al. 2010). In each sequential step, we kept previously modeled parameters in their most parsimonious form (Lebreton et al. 1992). We confirmed earlier sequential model rankings by repeating model selection on each parameter with the other two parameters in their most parsimonious form. We selected models for each parameter individually. We used the logit link function throughout, and a second-part variance estimation procedure. We used $qAIC_c$ weights (w_i) as a measure of the strength of evidence for a given model, but considered models with $qAIC_c$ differences ($\Delta qAIC_c$) < 2 to be equivalent (Lebreton et al. 1992).

We examined the effect of parent age on return rate (a proxy for recruitment) for fledglings from years 1981–2004 whose paternal or maternal age was known. Small sample sizes of fledglings with known-age parents prohibited us from including this covariate in the capture–mark–recapture analysis. A small proportion of fledglings from the last years of the study may not have started breeding in 2009, but we think that this bias was small because of the large sample of birds released from 1981 to 2002. We restricted the analysis of parental age effects on return rate to fledglings with parents ages 2–10 to ensure sample sizes > 10 in each age class. We estimated return rate according to parental age using a multilevel mixed-effects logistic regression with the sexes analyzed separately. Response variable for each fledgling was binomial (1 = returned to breed, 0 = never recaptured after fledging). Parental age was a categorical fixed effect. We included a random effect of parental identity to control for pseudoreplication because some

parents were present in the data in >1 year. We used AIC_c to rank 4 competing models of return rate (Burnham and Anderson 2002). Our only *a priori* models were (1) an age-specific model and (2) a constant-age model. Post hoc models suggested by patterns in the age-specific model were (3) ages 2–4 different from ages 5–10, and (4) age 2 different from ages 3–10. Return rate is uncorrected for recapture probability, but because capture–mark–recapture analysis revealed only a very weak effect of age on recapture probability, we expected little bias from imperfect recapture probability. Return rate according to parental age was the number of recruits divided by the number of fledglings by age of parent. To determine effects of parental age on egg production or offspring provisioning, we examined differences between young parents (mothers: ages 2–4, fathers: age 2) and older parents (mothers: ages 5–10, fathers: ages 3–10) in adult mass, egg volume, and fledgling mass. We used *t*-tests to determine whether significant differences existed in adult mass, egg volume, or fledgling mass between age groups.

RESULTS

From 1981 to 2009, we marked and released 6,031 Cassin's Auklet young (age 0); only offspring that successfully fledged were considered "released." Of these offspring, 470 (7.8% of marked fledglings) were eventually recruited to the study population.

Goodness-of-fit tests of the single-state capture–mark–recapture model indicated some lack of fit between our data and

the CJS model [$S(\text{time}) \times p(\text{time})$] due to a transient effect (test 3.SR: $\chi^2 = 36.77$, $df = 26$, $P = 0.078$) and trap-happiness effect (test 2.CT: $\chi^2 = 59.74$, $df = 23$, $P < 0.0001$). We expected that the age structures we subsequently investigated would account for this lack of fit in the time-dependent CJS model. We estimated an overdispersion parameter (\hat{c}) based on our state- and age-dependent general model [$S(\text{state} \times \text{age}15) p(\text{state} \times \text{age}15) \psi(\text{state} \times \text{age}10)$]. The value of \hat{c} was 1.41, indicating minimal overdispersion of our state- and age-dependent general model (Cooch and White 2012).

Model selection results for capture–mark–recapture data indicated strong evidence for age effects in recruitment, but less so in survival and recapture (Table 1). The recapture probability was best modeled as an inverse function of age, but support for this model was similar to that for the constant model (Table 1). The model-averaged curve of recapture shows little variation with age (Fig. 1, top). Recruitment probability was best modeled as a cubic age curve or an inverse function of age: $qAIC_c$ weights indicate that both models had similar support (Table 1). The best model for apparent local survival was the positive quadratic curvilinear function (Table 1), but $qAIC_c$ weights indicate that this model had similar support as the constant model of survival. The model-averaged curve for survival indicates that the youngest and oldest birds had lower survival probabilities than middle-aged (ages 5–10) birds (Fig. 1, bottom). The model-averaged curve for recruitment indicates a rapid increase in recruitment probability for birds ages 2–4, then a slow decline in age-specific recruitment for ages >4 (Fig. 1,

TABLE 1. Table of model-selection results for age effects on recapture (p^B), recruitment (ψ^B), and survival (S^B) probabilities of breeding Cassin's Auklets on Southeast Farallon Island, California, 1981–2009 ($\hat{c} = 1.41$). Age structures within each parameter were ranked while holding the other two parameters in their most parsimonious form. Temporal variation was controlled by modeling year as a categorical variable in each parameter. We used quasi AIC corrected for small sample size to rank models ($qAIC_c$) and $qAIC_c$ weights (w_i) as a measure of the strength of evidence for a given model, but considered models with $qAIC_c$ differences ($\Delta qAIC_c$) <2 as equivalent; k = number of parameters.

Parameter	Model	$qAIC_c$	$\Delta qAIC_c$	w_i	k	qDeviance
Recapture p^B	1/age	5,263.75	0	0.25	100	1,447.08
	ln(age)	5,263.92	0.17	0.23	100	1,447.25
	Constant	5,264.17	0.42	0.20	99	1,449.51
	Linear age	5,264.27	0.51	0.19	100	1,447.60
	Age ²	5,266.00	2.25	0.08	101	1,447.32
	Age ³	5,267.61	3.85	0.04	102	1,446.92
	Age categorical	5,279.57	15.81	0.00	114	1,438.78
Recruitment ψ^B	Age ³	5,083.61	0.00	0.45	101	1,210.55
	1/age	5,083.94	0.32	0.38	99	1,214.91
	Age ²	5,086.17	2.56	0.13	100	1,215.12
	ln(age)	5,089.20	5.58	0.03	99	1,220.17
	Age categorical	5,091.56	7.95	0.01	107	1,208.38
	Linear age	5,095.07	11.46	0.00	99	1,226.04
	Constant	5,104.99	21.38	0.00	98	1,237.99
Survival S^B	Age ²	5,091.56	0	0.35	107	1,208.38
	Constant	5,092.43	0.87	0.23	106	1,213.29
	Age ³	5,093.34	1.78	0.14	108	1,208.13
	ln(age)	5,093.88	2.32	0.11	107	1,212.72
	Linear age	5,094.43	2.87	0.08	107	1,213.27
	1/age	5,094.47	2.90	0.08	107	1,213.30
	Age categorical	5,100.77	9.21	0.00	116	1,197.31

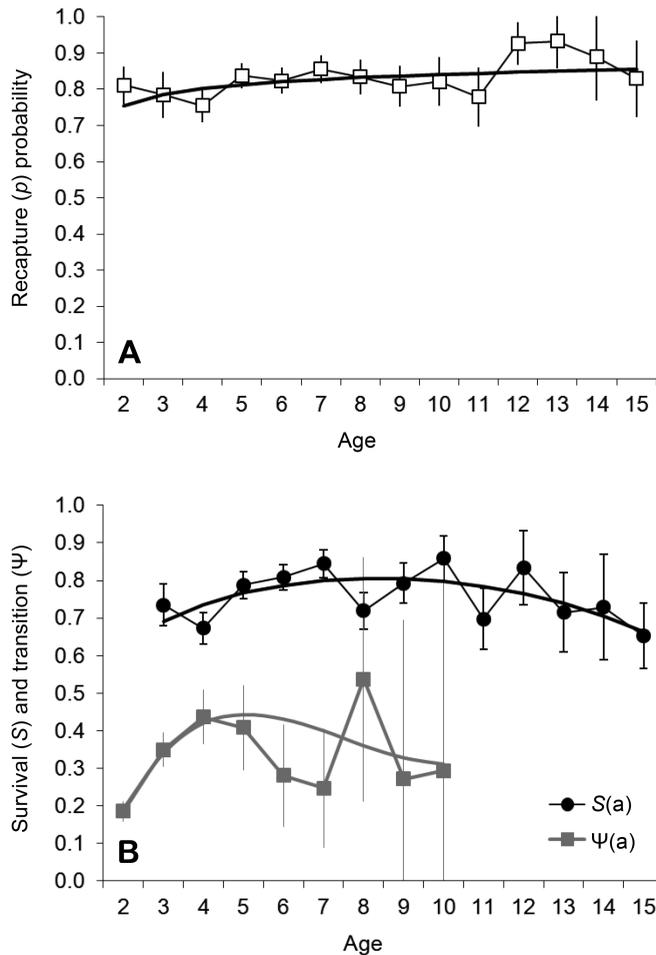


FIG. 1. (A) Age-specific estimates of recapture probability (\pm SE) in age a for Cassin's Auklets fledged at Southeast Farallon Island, California, 1981–2009. (B) Age-specific estimates (\pm SE) of local survival (circles) to age a from age $a - 1$ and recruitment (squares) in age a for Cassin's Auklets fledged at Southeast Farallon Island, California, 1981–2009. Curves are model-averaged estimates from all models with non-zero $qAIC_c$ weights. Temporal variation was controlled for by modeling year as a categorical variable in each parameter.

bottom). The age-specific estimates for recruitment indicate there may be a bimodal distribution with most birds recruiting between ages 2 and 7, and a second wave of recruits aged >7 .

Calculations from model-averaged parameter estimates show most individuals in a cohort recruit at age 3 (27%), and by 8 years postfledging $>95\%$ of a given cohort has been recruited (Fig. 2). Mean age of recruitment (\pm SD) for years 2000–2009 was 3.6 (\pm 1.54) years, compared with Pyle's (2001) estimate for years 1981–1999 of 3.3 (\pm 1.32). Mean (\pm SD) estimates from model-averaged age-specific estimates for breeding-age Cassin's Auklets (age ≥ 2) were as follows: recapture probability (minimum breeding propensity) = 0.826 ± 0.029 ; apparent local survival = 0.757 ± 0.047 ; recruitment = 0.358 ± 0.078 . Juvenile survival (ages 0 to 2) was 0.145 (95% confidence interval [CI]:

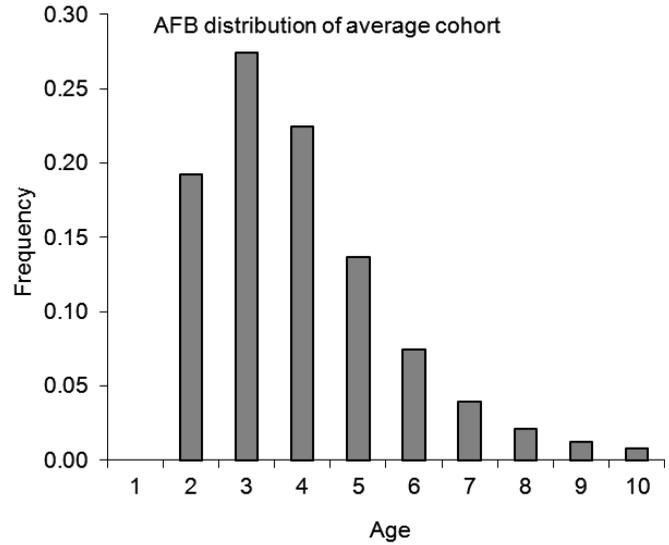


FIG. 2. Frequency distribution for ages at first breeding (AFB) for a typical cohort of Cassin's Auklets fledged at Southeast Farallon Island, California, 1981–2009. The AFB frequencies were computed from the model-averaged recruitment curve in Figure 1.

0.118–0.178). Assuming equal survival in both years, the square root of juvenile survival (0.381) is an approximation of annual survival for ages 0–1 and 1–2.

In the analysis of parental age effects on offspring return rate, we observed 57 recruits (9.3%) out of the 612 fledglings whose parents' age was known. The age-specific model of return rate was not superior to the constant model for males, although females ages 2–4 had no fledglings return (Fig. 3). Model rankings (Table 2) revealed that the best model for female parents was as follows: 2- to 4-year-olds had lower fledgling return rates than 5- to 10-year-olds ($\beta = -2.38$, 95% CI: -4.43 to -0.34). The best model for male parents was that 2-year-olds had higher fledgling return rates than 3- to 10-year-olds ($\beta = 1.04$, 95% CI: 0.06 – 2.03).

Mean maternal weights at the beginning of the breeding season (\pm SE) did not differ between younger (ages 2–4: 177.3 ± 1.2 g) and older (ages >4 : 177.8 ± 0.8 g) mothers ($t = 0.40$, $P = 0.69$, $n = 72$ and 141), but egg volume of younger mothers ($32,009 \pm 337$ μ L) was significantly lower than that of older mothers ($33,122 \pm 300$ μ L; $t = 3.30$, $P = 0.001$, $n = 73$ and 137). Fledgling weight at 35 days was also significantly lower for younger (140.6 ± 2.9 g) than for older mothers (155.8 ± 1.6 g; $t = 5.18$, $P < 0.0001$, $n = 56$ and 125). Paternal weights were significantly lower in younger fathers (age 2: 176.1 ± 1.0 g) than in older fathers (ages 3–10: 185.9 ± 0.7 g; $t = 9.49$, $P < 0.001$, $n = 25$ and 354), but fledgling weights at 35 days were the same for 2-year-old fathers (151.9 ± 2.9 g) and older fathers (151.2 ± 2.0 g; $t = -0.34$, $P = 0.59$, $n = 24$ and 317).

DISCUSSION

We found strong evidence for age effects in recruitment and survival, but not in breeding propensity, in Cassin's Auklets in the eastern North Pacific Ocean. Curvilinear age functions were more parsimonious than age-specific models for all three parameters.

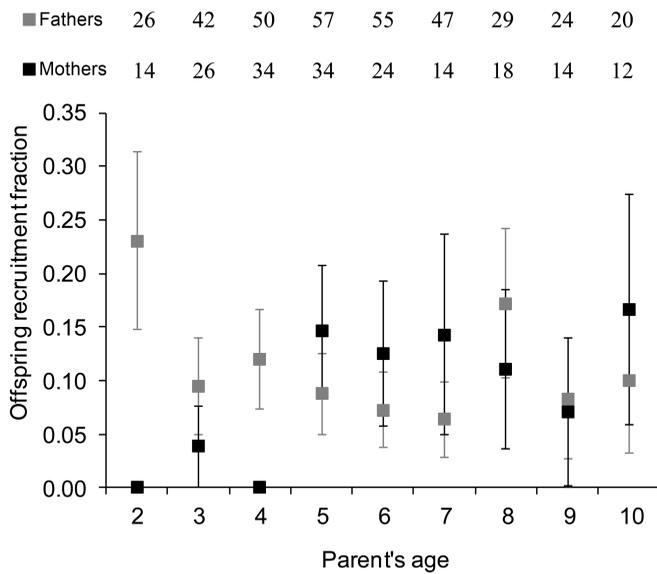


FIG. 3. Influence of parental age on probability of recruitment (\pm SE) in Cassin's Auklets fledged at Southeast Farallon Island, California, 1981–2009. Numbers across the top are sample sizes (number of fledglings released) in each sex and age category.

The probability of recruiting rose quickly and peaked at ages 4–6, but recruitment was a protracted process that included birds as old as 10. In seabirds in particular, the variation among individuals in the age of recruitment is quite large (see reviews in Bradley and Wooller 1991, Danchin et al. 1991). Our probabilistic estimates of recruitment age for this colony update estimates for this colony made a decade ago (Pyle 2001). Pyle (2001) found 24–29% of birds recruited at age 2, whereas we found that only 19% of a typical cohort recruited at age 2, whereas we found that only 19% of a typical cohort recruited at 2 years old. We also found larger proportions of birds recruited at ages ≥ 4 years old than Pyle (2001); however, Pyle truncated his data to exclude the oldest recruits. Our analytical approach differed from Pyle's (2001), so our results are not directly comparable; however, it appears that Cassin's Auklets may be delaying maturity in recent years compared with the 1980s and 1990s. Our age-specific estimates of recruitment indicate that there may be two waves of recruitment, the first from ages 2 to 7 and the second in ages >7 (Fig. 1). The latter wave may be birds that delayed recruiting; different life history strategies selected to increase fitness may coexist in the same population at evolutionary equilibrium (Ens et al. 1995).

It is also possible that true recruitment of the second wave was outside the study area's nest boxes and was undetected until the birds later moved into a nest box where they were recorded as new recruits. Breeding dispersal movements for this population have been shown to be toward the natal site (Pyle 2001). Because of high natal site fidelity in this species (Pyle 2001) and low density of natural burrow sites in the study areas (PRBO unpubl. data), we assumed that maturing local offspring were likely to recruit to boxes, but they also can use natural burrows and may move between the two, so our estimates of recruitment, survival, and breeding propensity may be conservative (biased low) because we could not document recruitment and breeding attempts in burrows. Thus, there is some possibility that we may have

TABLE 2. Table of model-selection results for parental age effects on return rate of fledgling Cassin's Auklets on Southeast Farallon Island, California, 1981–2009. We used AIC corrected for small sample size to rank models (AIC_c) and AIC_c weights (w_i) as a measure of the strength of evidence for a given model, but considered models with AIC_c differences (ΔAIC_c) < 2 as equivalent; k = number of parameters; LL = log likelihood.

Sex	Model	AIC_c	ΔAIC_c	w_i	k	LL
Females	2–4 differs from 5–10	102.0	0.0	0.95	1	-50.0
	2 differs from 3–10	109.3	7.3	0.02	1	-53.6
	Age-specific	109.5	7.5	0.02	6	-48.5
	Constant	111.8	9.8	0.01	1	-54.9
Males	2 differs from 3–10	234.5	0.0	0.66	1	-116.3
	2–4 differs from 5–10	236.6	2.1	0.23	1	-117.3
	Constant	238.2	3.7	0.10	1	-118.1
	Age-specific	245.9	11.4	0.00	8	-114.8

underestimated recruitment, survival, and breeding propensity and overestimated age at first breeding.

An interesting finding was the extremely low return rate of offspring from young mothers (ages 2–4). This low return rate may have been related to the observed smaller egg sizes and lower fledging weights of offspring from young mothers, which may have contributed to elevated juvenile mortality. Other studies have found effects of parental age on breeding performance due to egg composition (Giron and Casas 2003, Bogdanova et al. 2006) or offspring-rearing capability (Weimerskirch 1990, Pugsek 1995). Egg size is positively correlated with offspring growth and survival in many groups of birds, including seabirds (Hipfner and Gaston 1999). Larger seabird eggs have been shown to contain proportionately more albumen and less yolk, indicative of increased water content, which may be important for seabird young because of the high salt content of their diet (Williams 1994). An increase in foraging efficiency with age and experience (Desrochers 1992, de Forest and Gaston 1996, Catry and Furness 1999, Limmer and Becker 2009), caused by improvements in foraging ability (Daunt et al. 1999), diet choice (Rutz et al. 2006), and access to better foraging territories (Pärt 2001), might explain the generally better performance of older mothers (constraint hypothesis or increased ability hypothesis; Curio 1983, Forslund and Pärt 1995, Daunt et al. 1999). Cassin's Auklets have the capacity to begin breeding as early as age 2, but mothers ages 2–4 may only produce viable offspring during periods of favorable oceanic conditions when resources are plentiful. The few offspring from young mothers survive to breed means that survival of young to fledging is not an accurate estimate of parents' true reproductive success.

An alternative explanation for a low return rate of offspring from young mothers is that natal dispersal is higher in these offspring. When offspring of older mothers return to their natal site to recruit, the site is more likely to be vacated because of maternal mortality, whereas young mothers are more likely to survive and remain in their breeding site, requiring their offspring to disperse.

The high rate of return for offspring of 2-year-old fathers is difficult to explain. Young fathers may expend a larger amount of energy provisioning their chicks, but this is not supported by fledgling-weight data. Alternatively, offspring of primiparous males may have higher natal-site fidelity, but we found no theory

to support this possibility. Young fathers tend to pair with similar-aged females, so there is no evidence for an older mate influencing young fathers' success (PRBO unpubl. data).

We found evidence that juvenile birds ages 0 to 2 had lower annual survival than breeding-age birds. Juvenile birds generally experience lower and more variable apparent survival than adults (Clutton-Brock 1988, Newton 1989), and this may be due to mortality or natal dispersal. Survival is the more likely explanation, given that young birds are typically less efficient or less competitive foragers than older birds (Wunderle 1991), and median natal dispersal has been found to be <10 m among birds nesting in nest boxes within this population (Pyle 2001).

We also found evidence of actuarial senescence, in that the oldest birds had lower survival rates than birds ages 5–10. Other studies of seabirds have reported patterns of senescence in survival (for a review, see Bennett and Owens 2002). However, we found no apparent senescent decline in breeding propensity, and age-specific breeding success of Cassin's Auklet increases as an inverse function of age up to age 15 (Lee et al. 2007), indicating a shift in allocation from survival to reproduction in older birds (Emlen 1970, Gadgil and Bossert 1970). Local apparent survival is composed of true survival and permanent emigration, but the high breeding-site fidelity of this species leads us to believe that variation in apparent survival is largely attributable to mortality (Pyle 2001). However, any permanent emigration (i.e., older birds shifting from nest boxes to natural burrows) would bias our survival estimates lower than the true survival probability.

Our estimates rely on the assumptions of our modeling approach, but we believe that the constraints necessary for this analysis are biologically reasonable (Reed et al. 2003, Crespín et al. 2006). We are confident that our results are not excessively biased because (1) the goodness-of-fit results were strong, (2) our estimate of mean survival for breeding-age Cassin's Auklets is similar to previous estimates from this and other colonies (Bertram et al. 2005, Lee et al. 2007, Wolf et al. 2010), and (3) our estimate of mean breeding propensity was similar to previous results from this colony (Lee et al. 2007). The greatest strength of our approach is the explicit modeling of recapture probabilities to estimate survival and recruitment that are less biased by unequal detection probabilities.

We explored age and recruitment in a long-lived seabird from the California current system using a long-term, 28-year data set. We encourage other researchers to adopt the multistate capture–mark–recapture approach when investigating recruitment because these methods estimate age-specific probabilities of becoming a breeder with less bias by explicitly modeling detection probabilities. An additional advantage is the ability to assess the effects of external and individual covariates on recruitment parameters. We suggest that researchers, managers, and population modelers consider the possibility that young breeding birds (apparent recruits) are not always true recruits (in the sense of producing viable offspring that will become breeders), as this possibility could have significant implications for research designs, population models, and management actions.

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