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EFFECTS OF EXTREME CLIMATE EVENTS ON ADULT SURVIVAL OF THREE PACIFIC AUKS

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Abstract.—Climate change is predicted to increase the frequency and severity of extreme climate events, and it is important that we understand how this might affect natural systems. We examined the effects of extreme climate events on adult survival rates in three species of auks breeding on Triangle Island, British Columbia: Cassin's Auklet (*Ptychoramphus aleuticus*), Rhinoceros Auklet (*Cerorhinca monocerata*), and Tufted Puffin (*Fratercula cirrhata*). Our 15-year study period (1994–2008) included two extreme climate events: a strong El Niño event in 1997–1998 and an atmospheric blocking event in 2005. Neither event had any detectable effect on the annual adult survival rate (± 95% confidence interval) of either Tufted Puffins (females: 0.96 ± 0.05; males: 0.91 ± 0.06) or Rhinoceros Auklets (0.86 ± 0.02 in both sexes). By contrast, the adult survival of female Cassin's Auklets was halved during both extreme climate events (from a background rate of 0.84 ± 0.05 to 0.44 ± 0.10), whereas survival of males was low, but constant through time (0.75 ± 0.03). Our results, combined with those of previous studies, suggest that the major ongoing decline in the Cassin's Auklet population on Triangle Island is driven by negative effects of climatic variation on both reproductive success and the survival of adult females. Climate change may result in continued Cassin's Auklet population declines at this and more southerly colonies. By contrast, the relative stability of Rhinoceros Auklet and Tufted Puffin populations is likely attributable to the resiliency of adult survival rates to climatic conditions. *Received 22 August 2010, accepted 15 August 2011.*

Key words: Cassin's Auklet, *Cerorhinca monocerata*, climate change, El Niño, *Fratercula cirrhata, Ptychoramphus aleuticus*, Rhinoceros Auklet, seabird, sex difference, Tufted Puffin.

Effets des événements climatiques extrêmes sur la survie des adultes de trois pingouins du Pacifique

Résumé.—Les changements climatiques devraient augmenter la fréquence et la gravité des événements climatiques extrêmes, et il est important que nous comprenions comment cela peut affecter les systèmes naturels. Nous avons examiné les effets des événements climatiques extrêmes sur les taux de survie des adultes chez trois espèces de pingouins se reproduisant sur l'île Triangle, en Colombie Britannique : *Ptychoramphus aleuticus*, *Cerorhinca monocerata* et *Fratercula cirrhata*. Notre période d'étude de 15 ans (1994–2008) comprenait deux événements climatiques extrêmes : un épisode El Niño intense en 1997–1998 et un épisode de blocage atmosphérique en 2005. Aucun de ces événements n'a eu d'effet détectable sur le taux de survie annuelle (± intervalle de confiance de 95%) de *F. cirrhata* (femelles : 0,96 ± 0,05; mâles : 0,91 ± 0,06) et de *C. monocerata* (0,86 ± 0,02 chez les deux sexes). En revanche, la survie des femelles adultes de *P. aleuticus* a été réduite de moitié au cours des deux événements climatiques extrêmes (selon un taux historique de 0,84 ± 0,05 à 0,44 ± 0,10), alors que la survie des mâles était faible mais constante dans le temps (0,75 ± 0,03). Nos résultats, combinés à ceux d'études antérieures, suggèrent que le déclin majeur en cours dans la population de *P. aleuticus* de l'île Triangle est entraîné par les effets négatifs de la variation climatique sur le succès reproducteur et la survie des femelles adultes. Les changements climatiques peuvent causer des déclins continus de la population de *P. aleuticus* dans cette colonie ainsi qu'à d'autres colonies plus au sud. En revanche, la stabilité relative des populations de *C. monocerata* et *F. cirrhata* est probablement attribuable à la résilience des taux de survie des adultes face aux conditions climatiques.

Global climate change is altering the phenology, distribution, and demographic rates of species in a variety of ecosystems (Edwards and Richardson 2004). Climate projections suggest that global warming may increase the frequency or amplitude of El Niño and other extreme climate events, or even lead to permanent El Niño-like conditions (Timmermann et al. 1999, Easterling

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et al. 2000, Guilyardi 2006). Further understanding of why the demography of some species, but not others, is strongly affected by extreme climate events would allow us to predict how climate change will affect the population dynamics and extinction risk of wild populations (Clark et al. 2001, Thomas et al. 2004) and help focus conservation efforts (Walther et al. 2002).

In the marine environment, organisms at all trophic levels are being affected by increases in water temperatures and the frequency of extreme climate events (Hoegh-Guldberg 1999, Richardson 2008). Organisms can be affected by climate either directly, through an intolerance of extreme temperatures or weather conditions, or indirectly, via the cumulative effects of climate on lower trophic levels (Schreiber 2002, Mackas et al. 2007).

The effects of climate on top predators are usually indirect (Forcada et al. 2008, Saba et al. 2008). In the case of seabirds, local (e.g., sea-surface temperature) and large-scale (e.g., El Niño-Southern Oscillation) climate variables that influence prey availability often have dramatic effects on breeding performance (Schreiber 2002, Sandvik et al. 2008, Wells et al. 2008). However, the growth rate of a seabird population is most sensitive to changes in adult survival because seabirds have comparatively high survival rates and low annual fecundity (Wooller et al. 1992, Sæther and Bakke 2000). Consequently, determining why extreme climate events strongly affect the adult survival of some species of seabirds, but not others, is a critical area of current research (Grémillet and Boulinier 2009, Hamer 2010).

We compared the effects of extreme climate events on adult survival rates of three sympatric auks breeding on Triangle Island, British Columbia. The three species include two generalist feeders, the Tufted Puffin (*Fratercula cirrhata*; mean body mass ± SD = 744 ± 64 g, *n* = 95) and Rhinoceros Auklet (*Cerorhinca monocerata*; 491 ± 34 g, *n* = 1,477), and the smaller, more zooplanktivorous Cassin's Auklet (*Ptychoramphus aleuticus*; 174 ± 12 g, *n* = 1,981). Survival data were available for the periods 2002–2007 for Tufted Puffin and 1994–2008 for Rhinoceros and Cassin's auklets. The study period included two extreme climate events: the very strong 1997–1998 El Niño event (Schwing et al. 2002) and the atmospheric blocking event of 2005 (Schwing et al. 2006, Sydeman et al. 2006). Unlike an El Niño event, the 2005 event resulted from extra-tropical large-scale forcing, which suppressed upwelling-favorable winds (Kosro et al. 2006, Schwing et al. 2006). Both events were characterized by very warm sea-surface temperatures (SSTs), reduced total zooplankton biomass, and a shift from "northern" to "southern" species of zooplankton in the California Current System (Mackas et al. 2006).

Previous research at Triangle Island has shown that reproductive success of all three species is reduced in years of warm SSTs, especially during extreme climate events (Gjerdrum et al. 2003, Hipfner et al. 2007, Wolf et al. 2009, Borstad et al. 2011). Variation in climatic conditions is expected to have more severe effects on reproductive success than adult survival in seabirds (Drent and Daan 1980). Therefore, we focused on how adult survival varied in response to the two extreme climate events, and included sex as a predictor variable because sex differences in reproductive investment have been described in many socially monogamous seabirds (Weimerskirch et al. 2000, Fraser et al. 2002, Quillfeldt et al. 2004) and may influence responsiveness to climate variation (Jenouvrier et al. 2005). The present study is the first to examine how extreme climate events influence adult survival of the two puffin species; previous research demonstrated that the 1997–1998 El Niño event reduced adult survival in Cassin's Auklet (Bertram et al. 2005, Lee et al. 2007).

METHODS

Study site and species.—Triangle Island (50°52′N, 129°05′W) supports the world's largest Cassin's Auklet colony (~550,000 pairs in 1989; Rodway 1991), the largest Tufted Puffin colony in the Northeast Pacific outside Alaska (~26,500 pairs in 1984; Rodway 1991), and a large colony of Rhinoceros Auklets (~42,000 pairs in 1989; Rodway 1991). The Tufted Puffin and Rhinoceros Auklet populations at Triangle Island remained relatively stable between 1984 and 2009. By contrast, the Cassin's Auklet population declined by an estimated 40% between 1989 and 2009 (M. S. Rodway and M. J. F. Lemon unpubl. data), and declines of a similar or greater magnitude have occurred on the other large colony in the Scott Islands archipelago (Hipfner et al. 2010a), and at the Farallon Islands, California, well to the south (≥75%, 1971–2002; Lee et al. 2007). Population modeling indicates low reproductive success and adult survival related to warm SSTs are the primary drivers of the Cassin's Auklet population decline on the Farallon Islands (Wolf et al. 2010). The same variables are likely important contributors to the population decline on Triangle Island because reproductive success at Triangle Island and the Farallon Islands covaries and is significantly related to local oceanographic conditions (Wolf et al. 2009), and extreme climate events dramatically decrease adult survival at both sites (Bertram et al. 2005, Lee et al. 2007).

All three study species are socially monogamous, with biparental care, delayed maturity, single-egg clutches, and strong breeding-site fidelity (Gaston and Jones 1998). Tufted Puffins and Rhinoceros Auklets feed on a mixed diet of zooplankton and fish, but nestlings are provisioned almost exclusively with fish (Williams et al. 2008, Davies et al. 2009). Cassin's Auklets feed themselves (Ainley et al. 1996, Sorensen et al. 2009) and their offspring (Ainley et al. 1996, Bertram et al. 2001) primarily with zooplankton. Males average 4–10% heavier than females in all three species. Tufted Puffins provision offspring several times per day, whereas Rhinoceros and Cassin's auklets provision offspring just once per parent per night (Manuwal and Thoresen 1993, Gaston and Dechesne 1996, Piatt and Kitaysky 2002). After breeding, Tufted Puffins disperse widely to winter in the North-central Pacific (Piatt and Kitaysky 2002), whereas Rhinoceros and Cassin's auklets generally move south to spend the winter off California (Manuwal and Thoresen 1993, Gaston and Dechesne 1996).

Mark–recapture data collection.—Tufted Puffins were captured using noose-carpets set near breeding burrows on Puffin Rock, an islet connected to Triangle Island at low tide, in 2002. Each individual was banded with a unique three-color band combination plus a federal band and weighed to the nearest 10 g using a 1-kg Pesola spring scale. A 1-cc blood sample was collected for molecular sexing. Banded Tufted Puffins were resighted using a 20–60× spotting scope during daily 2-h observation periods from mid-April to late August in 2003–2007. Observations included all daylight hours and were made on 46–123 days year^{-1}. Color-band combinations were readily identifiable, and no birds were observed that had lost a color band or federal band, which suggests that wear and loss of bands did not add bias to the data (Breton et al. 2006).

We used barrier nets to capture Rhinoceros and Cassin's auklets as they left nesting slopes in the early morning (0100–0400 hours PST) from April to July (Cassin's Auklets) or April to August (Rhinoceros Auklets) in 1994–2008. Rhinoceros Auklets were captured on 6–22 occasions year^{-1} in South Bay (but just 2 occasions in 1999), and Cassin's Auklets on 8–27 occasions year^{-1} in West Bay (see Bertram et al. 2000). All individuals were banded with a federal band and weighed (±10 g for Rhinoceros Auklets, ±5 g for Cassin's Auklets) using 1,000- or 300-g Pesola spring scales, and bill depth at the gonys (±0.1 mm) was measured with dial calipers.

Age and sex determination.—Most Tufted Puffins banded in 2002 had three bill furrows and showed strong burrow-site fidelity in subsequent years, which suggests that they were breeding adults ≥5 years of age (Tanaka and Ogi 1986, Piatt and Kitaysky 2002). Puffins were sexed from blood using a polymerase chain reaction [PCR]-based molecular technique (Fridolfsson and Ellegren 1999).

Rhinoceros Auklets cannot be aged using morphological criteria but were likely to have been ≥3 years old when banded, as this is thought to be the minimum age at first breeding (Gaston and Dechesne 1996). To assign sex, we applied rules developed from a PCR-based molecular analysis of 23 females and 26 males breeding on Triangle Island (Addison et al. 2008). Individuals with bill depth <16.0 mm were classified as females, and those with bill depth >16.5 mm were classified as males. For individuals of intermediate bill depth, those with body mass <500 g were classified as females and those with body mass >500 g as males. There was no evidence that bill depth increased in the year following first capture, given that the average change in bill depth (–0.2 mm ± 0.8 [SD], n = 29) was consistent with measurement error.

Cassin's Auklets with white-eyes were classified as adults (Manuwal 1978). Individuals were sexed from bill depth: female if <9.5 mm, male if >9.9 mm (Knechtel 1998). There was no evidence that bill depth increased with age, given that the average (± SD) change in bill depth (0.0 ± 0.6 mm, n = 28) was similar to measurement error. We excluded Cassin's Auklets that were not measured as adults and that had an intermediate bill depth.

Modeling survival and recapture probabilities.—Standard methods (Lebreton et al. 1992, Cooch and White 2010) were used to estimate local adult annual survival (φ) and recapture–resighting (p) rates for each of the three species in separate analyses using Program MARK (White and Burnham 1999). First, global models were defined that allowed survival and recapture rates to vary among years of the study and to differ between the sexes. The global models allowed survival and recapture rates in the first year after initial capture to be modeled independently from those in subsequent years. This model structure, referred to as "time-since-marking (TSM)" models by Cooch and White (2010), accounts for a "transient effect": the expected lower site fidelity (and, hence, lower estimated survival rate) of transient than of resident individuals in the data set that our capture methods are known to include (Bertram et al. 2000). Residents' survival rate is a better approximation of true survival (Pradel et al. 1997). Second, reduced parameter models were constructed and evaluated to examine support for a transient effect and the hypotheses that survival differed between extreme-climate years (1997–1998 and 2005–2006) and non-extreme-climate years (all other years) and between the sexes. To reduce the number of models compared, we used the method of Lebreton et al. (1992) by first finding the best-supported parameterization of recapture rate and then keeping it unchanged while finding the best-supported parameterization of survival rate. Models were included in the Rhinoceros Auklet and Cassin's Auklet analyses, which allowed survival to differ in the year following each extreme-climate year (1-year time lag; i.e., 1998–1999 and 2006–2007), but the shorter time-series of the Tufted Puffin data set prevented consideration of a lagged climate effect. Model notation used is similar to that in Lebreton et al. (1992) and Cooch and White (2010).

Goodness-of-fit and model selection.—Goodness-of-fit was evaluated with the median $\hat{c}$ procedure (Cooch and White 2010), and the estimated variance inflation factor $\hat{c}$ was used to adjust standard errors and calculate QAIC$_c$, Akaike's information criterion adjusted for lack of fit and small sample bias (Burnham and Anderson 2002). Model adjustment for $\hat{c}$ was not required for all models, but we report QAIC$_c$ for all candidate model sets for consistency. Models were ranked according to Δ_i, the difference in QAIC$_c$ value from that of the top-ranked (most parsimonious) model. Adjusting for $\hat{c}$ did not change model rankings in the analyses where $\hat{c}$ was estimated to be close to 1. We also calculated QAIC$_c$ weights (w_i), which provide a relative index of the plausibility of each model, given the data and candidate model set. In addition to survival estimates from the best-supported model in each analysis, we present model-averaged survival estimates and 95% confidence intervals derived from unconditional standard errors, which incorporate model-selection uncertainty (Burnham and Anderson 2002). Because recapture rates were modeled before survival rates, the model-averaged estimates of recapture rates did not differ from those of the best-supported model. We present the effective sample size used for each analysis produced by MARK. The sin link function and second-part variance estimation were used throughout these analyses. Survival and resighting rates are reported ± 95% confidence intervals. We provide descriptions of the full set of models considered for each species, and their corresponding hypotheses, in Appendices 1–6 (online Supplementary Materials; see Acknowledgments).

RESULTS

Tufted Puffins.—The survival analysis included 96 individuals (50 females and 46 males). Ninety-one individuals (95%) were encountered in multiple years (48 females and 43 males). The effective sample size was 390. The global model explained the data adequately ($\hat{c}$ = 1.458). The best-supported model in the candidate set included a constant survival rate that differed between the sexes (Table 1). The second-ranked model had one fewer parameter (no sex effect) and was also well supported (low Δ_i and similarly high proportion of the QAIC$_c$ weights).

The best-supported model suggested that the survival rate of females tended to be higher than that of males, although their 95% CIs overlapped (0.96 ± 0.05 vs. 0.91 ± 0.06; Fig. 1). The second-ranked model estimated the same constant survival

Table 1. Model rankings and ranking criteria from Program MARK (White and Burnham 1999) for the predominant hypotheses to explain adult Tufted Puffin survival during 2002–2007 on Triangle Island, British Columbia. Δ_i is the difference in QAIC_c value from that of the top-ranked model, QAIC_c is Akaike's information criterion adjusted for small sample size and corrected for $\hat{c}$, QDeviance is the model deviance after correcting for $\hat{c}$, and w_i is the Akaike weight. Models with $\Delta_i > 10$ are not shown because they lack meaningful support (Burnham and Anderson 2002). See online Supplementary Material for the full set of models (Appendix 1) and corresponding hypotheses (Appendix 2).

Model rank	Model[a]	Δ_i	K	QDeviance	w_i
1	$\varphi_{(\text{sex})}\, p_{(\text{sex})}$	0.00	4	25.95	0.35
2	$\varphi_{(.)}\, p_{(\text{sex})}$	0.23	3	28.22	0.32
3	$\varphi_{(\text{climate})}\, p_{(\text{sex})}$	2.17	4	28.12	0.12
4	$\varphi_{(\text{sex, climate})}\, p_{(\text{sex})}$	2.75	5	26.65	0.09
5	$\varphi_{(\text{M2-sex/sex})}\, p_{(\text{sex})}$	3.61	6	25.45	0.06
6	$\varphi_{(\text{sex, sex*climate})}\, p_{(\text{sex})}$	3.87	6	25.70	0.05
7	$\varphi_{(\text{t})}\, p_{(\text{sex})}$	7.24	7	27.00	0.01

[a] Model notation follows Lebreton et al. (1992) and Cooch and White (2010): φ = survival probability, p = recapture probability, sex = sex effect, t = differs through time, (.) = constant through time, climate = extreme-climate-year effect, M2 = inclusion of a time-since-marking effect (comprising two time-since-marking periods; effects on the first year after initial marking [includes "transient" and "resident" individuals] precede the "/" and effects on any subsequent year [includes only "resident" individuals] follow the "/"), and asterisk indicates interaction between factors.

rate in males and females (0.93 ± 0.04). The model-averaged survival rate of females was 0.95 ± 0.03 in all years except the extreme-climate year (2005–2006), when it was 0.94 ± 0.04. The model-averaged survival rate of males was 0.92 ± 0.04 in all years. The best-supported structure of resighting rate varied only by sex, being 0.86 ± 0.11 in females and 0.98 ± 0.12 in males.

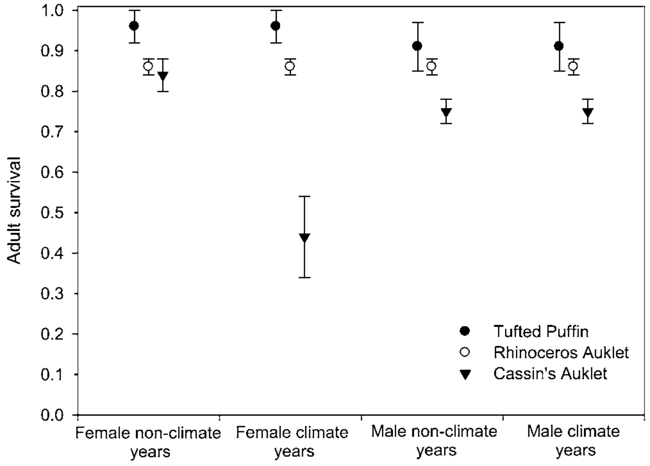

Fig. 1. Adult survival estimates of female and male Tufted Puffins, Rhinoceros Auklets, and Cassin's Auklets on Triangle Island, British Columbia, from 1995–1996 to 2007–2008. "Non-climate years" include all years, excepting the "climate years" of 1997–1998 and 2005–2006 that are defined by extreme climate events. The Tufted Puffin data set includes only the period from 2002–2003 to 2006–2007. The survival estimates presented are from the best-supported model from each analysis with 95% confidence intervals.

Rhinoceros Auklets.—The survival analysis included 1,290 individuals (585 females and 705 males). Three hundred and seventy-one individuals (29%) were encountered in multiple years (136 females and 235 males), giving an effective sample size of 2,059. The global model explained the data well ($\hat{c} = 1.082$). The best-supported model in the candidate set included constant adult survival that was equal between the sexes (Table 2). This model received about 2.5× the support of both the second-ranked model, which allowed survival to differ in extreme-climate years, and the third-ranked model, which allowed survival to differ in the year following each extreme-climate year (1-year time lag). However, the maximized log likelihood values of the second- and third-ranked models were essentially the same as that of the top-ranked model (both –2,209.05, vs. –2,209.15), which indicates that both additional terms were unimportant "pretending variables" (Burnham and Anderson 2002, Anderson 2008).

The best-supported model estimated the survival rate of adult Rhinoceros Auklets to be 0.86 ± 0.02 (Fig. 1). Model-averaged survival estimates were very similar to those from the best-supported model and were the same between the sexes. Survival in both extreme-climate years was 0.87 ± 0.06, whereas survival in the year following and in all other years was 0.85 ± 0.06 and 0.86 ± 0.03, respectively.

The best-supported structure of recapture rate varied through time without transient or sex effects and produced estimates from 0.18 ± 0.06 to 0.47 ± 0.08 (but 0.08 ± 0.03 in 1999, when sampling effort was reduced). The average recapture rate was 0.32 ± 0.07. The support for a recapture rate that varied through time was not a result of the low sampling effort in 1999, because a model that allowed recapture rate in 1999 to be estimated separately from all other years received less support than models in which recapture rate varied through time (ranked 8th; online Appendix 3).

Cassin's Auklets.—The survival analysis included 1,366 individuals (765 females and 601 males). We encountered 446 individuals (33%) in multiple years (207 females and 239 males), resulting in an effective sample size of 2,320. The global model explained the

Table 2. Model rankings and ranking criteria from Program MARK (White and Burnham 1999) for the predominant hypotheses to explain adult Rhinoceros Auklet survival during 1994–2008 on Triangle Island, British Columbia. Δ_i is the difference in QAIC_c value from that of the top-ranked model, QAIC_c is Akaike's information criterion adjusted for small sample size and corrected for $\hat{c}$, QDeviance is the model deviance after correcting for $\hat{c}$, and w_i is the Akaike weight. Models with $\Delta_i > 10$ are not shown because they lack meaningful support (Burnham and Anderson 2002). See online Supplementary Material for the full set of models (Appendix 3) and corresponding hypotheses (Appendix 4).

Model rank	Model[a]	Δ_i	K	QDeviance	w_i
1	$\varphi_{(\text{M2-t/.})}\, p_{(\text{t})}$	0.00	29	1,192.09	0.46
2	$\varphi_{(\text{M2-t/climate})}\, p_{(\text{t})}$	1.84	30	1,191.86	0.19
3	$\varphi_{(\text{M2-t/climate\_lag1})}\, p_{(\text{t})}$	1.89	30	1,191.92	0.18
4	$\varphi_{(\text{M2-t/sex})}\, p_{(\text{t})}$	2.02	30	1,192.04	0.17

[a] Model notation follows Lebreton et al. (1992) and Cooch and White (2010): φ = survival probability, p = recapture probability, M2 = inclusion of a time-since-marking effect (comprising two time-since-marking periods; effects on the first year after initial marking [includes "transient" and "resident" individuals] precede the "/" and effects on any subsequent year [includes only "resident" individuals] follow the "/"), sex = sex effect, t = differs through time, (.) = constant through time, climate = extreme-climate-year effect, climate_lag1 = extreme-climate-year effect with a 1-year time-lag, and asterisk indicates interaction between factors.

data well ($\hat{c}$ = 1.057). The best-supported model in the candidate set included female survival that was equal through time in non-extreme-climate years and similarly low in both extreme-climate years (Table 3). Male survival was equal across all years. The combined support for the top two best-supported models, which suggest that only female survival varied in extreme-climate years, was 3.6× that of the third-ranked model in which males were also affected by climate events. The second-ranked model differed from the top-ranked model only by the addition of an extra parameter that allowed female survival to differ between the two extreme-climate years (Table 3). The addition of this parameter did not improve upon the fit of the top-ranked model, because both models have essentially the same maximized log likelihood value (–2,264.05 vs. –2,264.09), which indicates that the added parameter is a "pretending variable" that is not important (Burnham and Anderson 2002, Anderson 2008).

The top-ranked model estimated the survival rate of adult female Cassin's Auklets to be 0.84 ± 0.04 in non-extreme-climate years, but only 0.44 ± 0.10 in extreme-climate years. The estimated constant survival rate of males was 0.75 ± 0.03. Parameter estimates averaged across all models were identical to those of the best-supported model alone for female survival rate in non-extreme-climate years and male constant survival rate. Model-averaged parameter estimates of female and male survival during extreme-climate years differed only slightly from those of the best-supported model (1997–1998: female, 0.45 ± 0.12; male, 0.74 ± 0.04; 2005–2006: female, 0.41 ± 0.08; male, 0.74 ± 0.04; Fig. 1). In each of the models with at least moderate support ($\Delta_i < 4$; Burnham and Anderson 2002), survival of both sexes in the first time-since-marking interval (first year after initial capture, including transient individuals) varied through time.

TABLE 3. Model rankings and ranking criteria from Program MARK (White and Burnham 1999) for the predominant hypotheses to explain adult Cassin's Auklet survival during 1994–2008 on Triangle Island, British Columbia. Δ_i is the difference in QAIC_c value from that of the top-ranked model, QAIC_c is Akaike's information criterion adjusted for small sample size and corrected for $\hat{c}$, QDeviance is the model deviance after correcting for $\hat{c}$, and w_i is the Akaike weight. Models with $\Delta_i > 10$ are not shown because they lack meaningful support (Burnham and Anderson 2002). See online Supplementary Material for the full set of models (Appendix 5) and corresponding hypotheses (Appendix 6).

Model rank	Model[a]	Δ_i	K	QDeviance	w_i
1	$\varphi_{(\text{M2-t/sex, female climate})}\ p_{(\text{M2-./t})}$	0.00	31	1,000.71	0.41
2	$\varphi_{(\text{M2-t/sex, female climate2})}\ p_{(\text{M2-./t})}$	0.34	32	999.00	0.35
3	$\varphi_{(\text{M2-t/sex, sex*climate})}\ p_{(\text{M2-./t})}$	1.35	32	1,000.00	0.21
4	$\varphi_{(\text{M2-t/., sex*climate})}\ p_{(\text{M2-./t})}$	6.65	31	1,007.35	0.01
5	$\varphi_{(\text{M2-t/., female climate})}\ p_{(\text{M2-./t})}$	8.17	30	1,010.93	0.01
6	$\varphi_{(\text{M2-t/., sex*climate2})}\ p_{(\text{M2-./t})}$	8.95	33	1,005.55	0.00

[a] Model notation follows Lebreton et al. (1992) and Cooch and White (2010): φ = survival probability, p = recapture probability, M2 = inclusion of a time-since-marking effect (comprising two time-since-marking periods; effects on the first year after initial marking [includes "transient" and "resident" individuals] precede the "/" and effects on any subsequent year [includes only "resident" individuals] follow the "/"), sex = sex effect, t = differs through time, (.) = constant through time, climate = extreme-climate-year effect, climate2 = extreme-climate-year effect that differs between the two extreme-climate years, and asterisk indicates interaction between factors.

The best-supported model structure for recapture rate included a transient effect, did not differ between the sexes, and was constant through the first time interval and varied with time in subsequent years. The estimated recapture rates of Cassin's Auklets in the years following the year after their initial capture ranged from 0.23 ± 0.08 to 0.66 ± 0.09 and averaged 0.45 ± 0.11.

DISCUSSION

The extreme climate events of 1997–1998 and 2005–2006 resulted in greatly elevated SSTs, decreased zooplankton biomass, and altered zooplankton community composition in the California Current System (Mackas et al. 2006). Nonetheless, we found no evidence that either event influenced the adult survival rates of Tufted Puffins or Rhinoceros Auklets at Triangle Island. By contrast, both events had similarly large effects on the adult survival rate of female, but not male, Cassin's Auklets. Our results are consistent with previous work that demonstrated a link between extreme climate events and adult survival in Cassin's Auklets (Bertram et al. 2005, Lee et al. 2007) but are novel in revealing a sex difference in how extreme climate events influenced adult survival in that species.

Our conclusion that extreme climate events had less effect on adult survival rates of Rhinoceros Auklets than of Cassin's Auklets is consistent with other data sources. In Rhinoceros Auklets, burrow occupancy changed little from 2005 to 2006 at Triangle Island (from 64% to 65%; Hipfner et al. 2008). By contrast, burrow occupancy rates decreased dramatically between those two years in Cassin's Auklets (from 77% to 44%; Hipfner et al. 2010b), and occupancy remained low in 2007 (51%; Triangle Island Seabird Research Station [TISRS] unpubl. data), which suggests that the decrease was due to mortality rather than skipped breeding. In addition, beached-bird surveys in November 2005 in southern Washington and Oregon found anomalously high encounter rates for Cassin's Auklets, but average or below-average rates for Rhinoceros Auklets (Parrish et al. 2007: fig. 2). Likewise, beaching rates of Cassin's Auklets were unusually high in December 2005 and January 2006 along the coast of British Columbia, an area well north of the expected midwinter distribution off California of Cassin's Auklets breeding in Alaska and British Columbia (Manuwal and Thoresen 1993). Typical counts of beached Cassin's Auklets were 3 to 7 birds for every 3 km of beach in Pacific Rim National Park Reserve on the west coast of Vancouver Island (P. Clarkson, Parks Canada, pers. comm.), although high tides, beach debris, and scavenging were thought to have resulted in low detectability of beached birds. Cassin's Auklets were also found among other seabird species beached along the east coasts of Graham and Moresby islands, Haida Gwaii (A. Cober, B.C. Ministry of Environment, pers. comm.). Necropsies on 14 of the Haida Gwaii birds, which unfortunately were not sexed, indicated that they died of starvation (B.C. Ministry of Environment unpubl. data).

Our results raise three important questions. First, why was the survival of female Cassin's Auklets strongly affected by extreme climate events, whereas that of males was not? Jenouvrier et al. (2005) argued that sex differences in adult survival rate, and the effects of environmental covariates, might be explained by sex differences in breeding investment. For example, in the extreme year of 2005, most Cassin's Auklet chicks died within a week of hatching

(Sydeman et al. 2006, TISRS unpubl. data); therefore, in that year reproductive costs were borne largely by egg-laying females. Alternatively, male Cassin's Auklets perhaps limit the effect of extreme climate events on their survival by reducing provisioning effort or abandoning the care of the nestling to the female.

Second, why did male Cassin's Auklets—and, to a lesser extent, male Tufted Puffins—have a lower constant survival rate than the female survival rate in non-extreme-climate years? A higher survival rate in females is not an uncommon pattern in long-lived birds (Aebischer and Coulson 1990, Tavecchia et al. 2001, Robertson et al. 2006). In other auks, males spend more time than females defending nests and guarding offspring (Creelman and Storey 1991), and this is suggested by the higher resighting rate of male Tufted Puffins in our study. As a result, males may be involved more frequently in intra- and interspecific conflicts (Fraser et al. 2002) and may be more exposed to predators (Hipfner et al. 2011). Alternatively, Tavecchia et al. (2001) proposed that if first reproduction is a stronger selective force on female rather than male quality, then, among experienced breeders, females would have a higher survival rate than males.

Third, why was there no detectable survival response to the extreme climate events by Tufted Puffins or Rhinoceros Auklets? The ability of these species to maintain high adult survival rates during extreme climate events may be related to their greater expected life span, larger body size, and more piscivorous diet compared with auk species that respond strongly to climate extremes (Jones et al. 2002, 2007; Bertram et al. 2005; Lee et al. 2007), including the Cassin's Auklet. Life-history theory suggests that longer-lived species should be more reluctant to increase their investment in reproduction during extreme climate events to minimize threats to future breeding opportunities (Drent and Daan 1980, Sandvik and Erikstad 2008), and longevity is positively correlated with body size in birds (Lindstedt and Calder 1976). However, body size may have independent effects because small birds have to feed at a higher rate than large birds to support their high metabolic rates (Peters 1983, Furness and Ainley 1984) and because starvation is a more imminent threat to small birds (Peters 1983). Smaller seabirds also have reduced diving depth, which potentially reduces their access to prey (Piatt and Nettleship 1985, Furness and Tasker 2000); Cassin's Auklets, for example, do not dive as deep as the larger Rhinoceros Auklets (40 m vs. 60 m; Burger and Powell 1990, Burger et al. 1993). Furthermore, Bertram et al. (2005) argued that seabirds that feed at a higher trophic level (fish instead of zooplankton) may be less responsive to climate variation because they have access to multiple annual cohorts of prey (Bertram et al. 2005).

The divergent population trends of the three species that we studied on Triangle Island between 1984 and 2009 (M. S. Rodway and M. J. F. Lemon unpubl. data) may be related to how climatic variation has influenced reproductive success and adult survival. In all three species, reproductive success is strongly affected by annual variation in climatic conditions through effects on the prey base. The temperature of the water column is particularly important for Cassin's Auklets (Wolf et al. 2009) because it affects the timing of the bloom of the copepod *Neocalanus cristatus* (Hipfner 2008). The timing of the phytoplankton bloom is most important for Rhinoceros Auklets because it affects the availability of Pacific Sandlance (*Ammodytes hexapterus*; Borstad et al. 2011), which Tufted Puffins also rely heavily on while breeding (Gjerdrum et al. 2003). We suggest that populations of Rhinoceros Auklets and Tufted Puffins, buffered as they are by relatively high adult survival rates that were insensitive to recent extreme climate events, have experienced enough years with high productivity to maintain themselves at Triangle Island. By contrast, the Cassin's Auklet population, with lower adult survival rates that are dramatically reduced in females during occasional extreme climate events, have not maintained their numbers. Climate change and predicted increases in the frequency and amplitude of extreme climate events (Timmermann et al. 1999, Easterling et al. 2000, Guilyardi 2006), suggest that continued Cassin's Auklet population declines are likely at Triangle Island and at colonies at more southerly locations (Wolf et al. 2010).

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