



## Short-term survival of Steller sea lion (*Eumetopias jubatus*) pups: Investigating the effect of health status on survival

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### ABSTRACT

We estimated survival probabilities for Steller sea lion (*Eumetopias jubatus*) pups from 3 wk to 6 wk old and from 6 wk to 1 yr at three rookeries in southeastern Alaska. We also investigated the effect of mass, body condition, health variables, and the genetic origin on 3–6 wk survival. Survival differed substantially among rookeries and between sexes, with survival lowest at Hazy Islands, intermediate at White Sisters, and highest at Graves Rocks and survival lower for males than females. Body mass, body condition, and hematocrit were positively related to survival and blood %H<sub>2</sub>O and haptoglobin level (for females; no relationship for males) were negatively related to survival. Taking predictor variables collectively, sea lion pups at Hazy Islands, which had the lowest survival probability, had the lowest mass, hematocrit, and hemoglobin, and had high levels of blood %H<sub>2</sub>O, and hookworm infection. Values from Graves Rocks, which had the highest survival, were the opposite of those from Hazy Island (*e.g.*, high mass, body condition, hematocrit, and hemoglobin), while those from White Sisters (intermediate survival) had varying means (*e.g.*, high hematocrit and hemoglobin and low hookworms, but also low body condition); these patterns suggest that physiological factors potentially underlie rookery differences in survival.

Key words: Steller sea lion, *Eumetopias jubatus*, survival, pup, physiology, health, Alaska, branding, mark-resight.

Based on differing population trends and genetics (Bickham *et al.* 1996, Loughlin 1997), the National Marine Fisheries Service classifies the Steller sea lion (SSL; *Eumetopias jubatus*) in the United States into two Distinct Population Segments (DPS), Eastern (EDPS) and Western (WDPS) with the division at 144°W longitude. The SSL population of the WDPS (*e.g.*, Prince William Sound, central and western Gulf of Alaska, Bering Sea, Aleutian Islands) is listed as “endangered” under the U.S.

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Endangered Species Act (U.S. Federal Register 1997) due to a large population decline, that likely began in the late 1970s (Braham *et al.* 1980, Merrick *et al.* 1987, Trites and Larkin 1996, Fritz *et al.* 2013). In contrast, the SSL population in the EDPS (southeastern Alaska south through California) was initially listed as “threatened,” but subsequently was removed from the U.S. Endangered Species List in December 2013 (U.S. Federal Register 2013) after verification of sustained population growth (Calkins *et al.* 1999, Pitcher *et al.* 2007, Mathews *et al.* 2011).

SSLs have been the focus of many studies during the past ~30 yr in an effort to understand these differing population trajectories, including studies that have estimated age-specific survival probabilities (York 1994, Pendleton *et al.* 2006, Hastings *et al.* 2011, Fritz *et al.* 2014, Maniscalco 2014). However, fewer studies have estimated survival of very young (*i.e.*, <1 yr) SSLs in Alaska (Maniscalco *et al.* 2008, Kaplan *et al.* 2008, Hastings *et al.* 2009) or examined effects of marking operations on pup survival (Hastings *et al.* 2009).

A number of factors (*e.g.*, health, body condition, weather) can affect both short- and long-term survival of SSL pups (Maniscalco *et al.* 2008; Hastings *et al.* 2009, 2011; Maniscalco 2014). Physiological parameters (*i.e.*, blood chemistry, hematology) have been used previously to determine whether SSL pups showed evidence of poor health or starvation (Castellini *et al.* 1993, Rea 1995, Rea *et al.* 1998, Lander *et al.* 2013). Haptoglobin (Hp) concentrations are positively correlated with white blood cell counts and serum globulin levels in SSLs and a sensitive indicator of inflammation response (Thomton and Mellish 2007), and thus could be an index of general health status (Zenteno-Savin *et al.* 1997). Other than mass and a rough condition index measured at branding (Hastings *et al.* 2009, 2011; Maniscalco 2014), the effects of physiological factors and genetic origin on SSL survival have not been previously studied and have rarely been studied in any pinniped. Pup body mass has been shown to be a predictor of survival for the first 1–2 yr (Hastings *et al.* 2011, Maniscalco 2014), but the association was equivocal in one study of survival of very young SSLs (Hastings *et al.* 2009).

In this study, we estimate survival probabilities of SSL pups from branding to 3 wk postbranding (~6 wk old) and from 6 wk to 1 yr to provide more fine-scale information on population processes during the first year of life. We also evaluate the relationships between early pup survival probability and mass, body condition, physiological indices of pup health, and genetic stock of origin.

## METHODS

### *Field*

In June 2005, SSL pups were captured at their natal rookeries at approximately 3 wk of age at three of the four rookeries in southeastern Alaska: Hazy Islands (HI), White Sisters (WS), and Graves Rocks (GR) (see Pitcher *et al.* 2007 and Hastings *et al.* 2011 for descriptions of locations). Pups were captured by hand in hoop nets, anesthetized using isofluorane gas (Heath *et al.* 1996), weighed using a hanging load cell, and measured (*i.e.*, standard length, axillary girth). Pups with masses >20 kg were hot-branded (Merrick *et al.* 1996) with individually unique letter-number combinations, and a skin-punch sample was collected from an interdigital web of the hind flipper for genetic analyses; skin samples were immediately placed in 90% ethanol. For a subset of the branded pups from each rookery, blood samples were collected

from the caudal gluteal vein. More detailed descriptions of pup handling, sampling, and marking procedures are described by Hastings *et al.* (2009, 2011), Lander *et al.* (2013), and O'Corry-Crowe *et al.* (2014).

Approximately 3 wk after the marking operation, we surveyed each of the three rookeries 5–6 times over 3–4 d periods, photographing each branded pup seen. In subsequent years (2006–2009), we conducted annual surveys of SSL rookeries and haul-outs in southeastern Alaska between mid-May and late July with more intense effort (~6 surveys/summer) at rookeries (Hastings *et al.* 2009, 2011; Jemison *et al.* 2013). Photographs of branded SSLs were taken from skiffs and from land; additional photographs of branded SSLs from the U.S.-Canadian SSL range (*i.e.*, Oregon to the Bering Sea) were provided by other research groups, agencies, and individuals. We only used observations of branded animals in analyses if identity was photographically confirmed.

### Physiology

Blood samples were collected in tubes containing ethylenediaminetetraacetic acid (EDTA) or sodium heparin and were kept chilled for up to 6 h at pup capture sites until returned to the larger work vessel for processing. Hematocrit (Hct) was measured using a microhematocrit centrifuge, and hemoglobin (Hb) concentration was measured spectrophotometrically (Lander *et al.* 2013). Water content (%H<sub>2</sub>O) and specific gravity (SG) of the heparinized plasma were measured as described by Castellini *et al.* (1993). Concentrations of blood urea nitrogen (BUN, mM/L), nonesterified fatty acids (NEFA, mM/L), and  $\beta$ -hydroxybutyrate ( $\beta$ -HBA, mM/L) were measured in heparinized plasma using commercially available assay kits (Rea *et al.* 1998). Haptoglobin (Hp, mg/mL) concentration was measured in heparinized plasma using a Phase Haptoglobin Colorimetric Assay with a SpectraMax 340PC plate reader. The assay was incubated 10 min at 30°C in triplicate against a standard curve 0–2 mg/mL, and samples were diluted if concentrations were above 1.75 mg/mL.

### Parasites

Determination of hookworm infection was based on fecal samples collected from the rectums of a sample of pups at each rookery (Beckmen and Hughes 2006: appendix 1). The standard McMaster method (Henrikson and Aagaard 1976) was used to quantify the number of hookworm eggs/g in formalin-preserved fecal samples (Beckmen and Hughes 2006: appendix 1). No additional parasite samples were collected from pups in this study.

### Genetics

Two rookeries, WS and GR, in the Eastern DPS, have breeding females genetically originating from each of the DPSs (Jemison *et al.* 2013, O'Corry-Crowe *et al.* 2014). That is, some SSL females, or one of their direct-line female ancestors, immigrated from the WDPS range to breed in the EDPS range. Using genetic samples from pups branded at GR, we determined mitochondrial DNA haplotypes and assigned maternal stock of origin as described by O'Corry-Crowe *et al.* (2006, 2014).

All data used for this paper, including resight observations, blood chemistry and physiology, and hookworm loads, were collected for a variety of independent studies and used opportunistically in our analyses. Consequently, the design of the study

(*e.g.*, balanced samples, all relevant covariates measured) was not optimal with respect to definitively investigating all factors that affect early SSL pup mortality, as a study designed expressly for such a purpose would have had. But our analyses provide an initial attempt at elucidating such factors, given the available data; additional data might reveal other factors affecting SSL survival or improve estimated relationships for the variables we investigated, leading to clearer understanding of health-survival mechanisms.

### Analyses

We constructed “capture” histories for each marked SSL using data from 2005 to 2009. To analyze these capture histories, we used robust design mark-resight models (Kendall *et al.* 1995, Williams *et al.* 2001) to estimate survival ( $\phi$ ) and sighting ( $p$ ) probabilities for the branded SSL pups. There were six primary “occasions” (hereafter “age”): branding (age  $\sim 3$  wk, initial release), approximately 3 wk postbranding (age 6 wk), and at 1, 2, 3, and 4 yr. We will reference  $p$  by age and  $\phi$ , which is survival between two ages, by the ending age (*e.g.*, survival between branding at  $\sim 3$  wk and sighting at 6 wk will be referred to as survival age-6-wk, survival from 6 wk to 52 wk is survival age-52-wk, and survival from  $\sim 3$  wk to 52 wk is age-1-yr). Only the second primary occasion, age-6-wk, had true secondary capture occasions (hereafter “pup surveys”), six at HI, and five each at WS and GR. It is important to include observations of animals older than 1 yr to avoid bias in survival estimates caused by movement of branded pups (with their mothers) away from the rookery of branding (Hastings *et al.* 2009). Before investigating the effects of morphometric, health, and genetic variables, we modeled  $\phi$  and  $p$  as functions of rookery, sex, age, and pup survey ( $p$  only). To reduce the number of models considered, we began with our most complex model and simplified the parameters sequentially, first considering 15 models for  $p$ , then 17 models for  $\phi$  for each of the top two models of  $p$  (34 total, Table 1). Second, using the best model from the first series of models, we fit 14 series of eight additional models for  $\phi$ ; each series included the effect of one covariate on  $\phi$  age-6-wk. The individual covariates, measured at branding, were mass, two condition indices (condition 1 [100\*axial girth/curvilinear length], condition 2 [the residual from the regression of mass on curvilinear length]), eight hematology and blood chemistry variables (Hct, Hb, %H<sub>2</sub>O, SG, BUN, NEFA,  $\beta$ -HBA, Hp), two measures of hookworm parasitization (egg abundance [hkwrn], presence/absence [hkwrn\_pa]), and a genetically-based DPS assignment (*i.e.*, EDPS or WDPS) for GR pups only. In these models,  $\phi$  could be a function of rookery, sex, or age, in addition to the covariate (Table 2); covariates were allowed to vary by sex (*e.g.*,  $\phi$ -mass slopes could differ between sexes). We included covariate models that did not include rookery or sex as predictors to investigate whether “rookery” or “sex” effects were actually caused by other factors (*e.g.*, health variables) that differed among rookeries. All of the individual covariates except mass and the condition indices were measured on only a sample (*i.e.*, 9%–21%) of the pups. To include covariates that had missing values in the models, we centered variable values (*i.e.*, subtracted the mean) and created indicator variables, one for each variable, which were 1 if we had a value for that variable and 0 if we did not. We then included the covariates as interactions of the centered covariate and the appropriate indicator variable (*i.e.*, a partial interaction model). Two of the variables had skewed distributions (hkwrn, Hp), so we transformed the variables to natural logarithms prior to analyses to be consistent with our among-rookery comparison of mean covariate values.

Table 1. Model selection results for parameters  $p$  and  $\phi$  (without covariates).  $\phi$ -models were fit using the top two  $p$  parameterizations. Bold type model names and AICc weights indicate top-ranked models for each variable.

<i>P</i> models	AICc weight <sup>a</sup>	$\phi$ Models	AICc weight	
			with <i>p</i> (ra)	with <i>p</i> (rao)
Constant	0	Constant	0	0
Rookery	0	Rookery	0	0
Sex	0	Sex	0	0
Age	0.11	Age	0	0
rookery*age	0.07	age234 <sup>b</sup>	0	0
<b>rookery+age</b> [model <i>p</i> (ra)]	<b>0.25</b>	rookery+sex	0	0
sex*age	0.13	rookery*sex	0	0
sex+age	0.04	rookery+age	0.05	0.04
age*pup survey	0	rookery*age234	0	0
age+pup survey	0.08	rookery+age234	0	0
rookery+(age*pup survey)	0	sex*age	0	0
<b>rookery+age+pup</b> survey [model <i>p</i> (rao)]	<b>0.28</b>	sex+age	0	0
sex+(age*pup survey)	0	sex*age234	0	0
sex+age+pup survey	0.03	sex+age234	0	0
rookery+sex+(age*pup survey)	0	<b>rookery+sex+age</b>	<b>0.50</b>	<b>0.40</b>
		rookery+sex+age234	0.01	0.01
		rookery*sex*age	0	0

<sup>a</sup>AICc weights are within parameters.

<sup>b</sup>Models with age234 estimate a common annual survival for ages 2–4.

We used program MARK (White and Burnham 1999) with the RMark interface (Laake 2013) to fit models and calculate estimates. Because there are no goodness-of-fit procedures available for robust design models, we used the median  $\hat{c}$  method (Cooch and White 2014) to evaluate a CJS model equivalent to our most complex model ( $p$ [rookery+sex+age],  $\phi$ [rookery\*sex\*age]) to a simplified data set that pooled observations across pup surveys for age-6-wk. We ranked the models based on AICc weights (*i.e.*, the support for each model relative to the other models considered, Burnham and Anderson 2002). Final estimates were produced using model averaging (Burnham and Anderson 2002) of highly supported models that took into account uncertainty from model selection.

The mark-resight models produced interval survival estimates, from which we calculated additional estimates including age-1-yr survival and estimates scaled to 12 wk intervals for comparison with other studies (*e.g.*, Hastings *et al.* 2009). Variances and confidence intervals of product and rescaled estimates were calculated using the delta method (Williams *et al.* 2001) with confidence intervals calculated on the natural log scale prior to transformation to the probability scale. We adjusted weekly age-6-wk survival estimates for the rookery-specific intervals between branding and resighting (HI: 21 d, WS: 22 d, GR: 17 d).

We used linear models to estimate means for the individual covariates and compare means among rookeries. For each variable, we fit five combinations of predictors:

Table 2. Model selection results for  $\phi$  with covariates, compared to the best model (Table 1) for  $p$  and  $\phi$  without covariates (i.e., base model). Bold type AICc weights indicate the top-ranked model for each covariate.

Models fit	AICc weight <sup>a</sup>							
	$\phi$ -mass	$\phi$ -cond. 1	$\phi$ -cond. 2	$\phi$ -Hct	$\phi$ -Hb	$\phi$ -%H2O	$\phi$ -SG	
Sample size of individuals (HI/WS/GR) <sup>b</sup>	413 (223/147/43)	413 (223/147/43)	413 (223/147/43)	70 (26/29/15)	85 (35/31/19)	58 (20/20/18)	58 (20/20/18)	
rookery+sex+age (base model)	0.01	0.58	0.45	0.41	0.65	0.42	0.48	
$\phi$ -covariate models <sup>c</sup>								
rookery+sex+age+ (age-6-wk*covariate)	<b>0.71</b>	<b>0.24</b>	<b>0.35</b>	0.24	<b>0.24</b>	<b>0.37</b>	<b>0.30</b>	
rookery+sex+age+ (age-6-wk*sex*covariate)	0.26	0.14	0.16	<b>0.31</b>	0.09	0.15	0.18	
rookery+age+ (age-6-wk*covariate)	0.01	0.02	0.02	0.02	0.02	0.04	0.03	
rookery+age+ (age-6-wk*sex*covariate)	0.02	0.01	0.01	0.02	0.01	0.02	0.01	
sex+age+ (age-6-wk*covariate)	0	0	0	0	0	0	0	
sex+age+ (age-6-wk*sex*covariate)	0	0	0	0	0	0	0.01	

(Continued)

Table 2. (Continued)

Models fit	AICc weight <sup>a</sup>						
	$\phi$ -mass	$\phi$ -cond. 1	$\phi$ -cond. 2	$\phi$ -Htct	$\phi$ -Hb	$\phi$ -%H2O	$\phi$ -SG
age+(age-6-wk* covariate)	0	0	0	0	0	0	0
age+(age-6-wk* sex* covariate)	0	0	0	0	0	0	0
Models fit	AICc weight						
	$\phi$ -BUN	$\phi$ -NEFA	$\phi$ - $\beta$ -HBA	$\phi$ -Hp <sup>d</sup>	$\phi$ -hwkrm <sup>d</sup>	$\phi$ -hkwrmp/a	$\phi$ -east-west
Sample size of individuals (HI/WS/GR)	81 (34/29/18)	80 (33/29/18)	81 (34/29/18)	69 (24/27/18)	68 (23/31/14)	75 (30/32/14)	36 (0/0/36)
rookery+sex+age (base model)	0.57	0.58	0.56	0.22	0.58	0.60	0.64
$\phi$ -covariate models							
rookery+sex+age+ (age-6-wk* covariate)	<b>0.28</b>	<b>0.22</b>	<b>0.24</b>	<b>0.08</b>	<b>0.28</b>	<b>0.26</b>	<b>0.24</b>
rookery+sex+age+ (age-6-wk*sex* covariate)	0.11	0.16	0.17	<b>0.64</b>	0.11	0.10	0.09
rookery+age+(age-6-wk* covariate)	0.02	0.02	0.02	0.01	0.03	0.03	0.02
rookery+age+ (age-6-wk*sex* covariate)	0.01	0.01	0.01	0.05	0.01	0.01	0.01
sex+age+(age-6-wk* covariate)	0	0	0	0	0	0	0
sex+age+(age-6-wk*sex* covariate)	0	0	0	0	0	0	0
age+(age-6-wk* covariate)	0	0	0	0	0	0	0
age+(age-6-wk*sex* covariate)	0	0	0	0	0	0	0

<sup>a</sup>AICc weights are within variables.

<sup>b</sup>HI = Hazy Islands, WS = White Sisters, GR = Graves Rocks.

<sup>c</sup>Covariate interactions contain an indicator variable (not listed) to account for missing data.

<sup>d</sup>Covariate natural-log-transformed prior to analysis.

rookery\*sex, rookery+sex, rookery, sex, mean (*i.e.*, intercept only). We selected the best model using AICc. Estimated means are marginal means (*i.e.*, SAS least-squares means, Littell *et al.* 2006), which adjust means and variances for other factors in the model. We evaluated differences among means by estimating the difference between means with a confidence interval on the differences. To account for highly skewed distributions, Hp concentrations and hookworm egg counts were transformed using natural logarithms; resulting means transformed back to the original scale are geometric means.

## RESULTS

In 2005, 415 SSL pups were captured and branded: 225 at HI (223 used in the analyses), 147 at WS, and 43 at GR. Of these pups, 169 (64%) from HI were seen at least once after branding, compared with 113 (77%) from WS and 40 (93%) from GR.

We estimated  $\hat{c} = 1.22$  for our most complex CJS-equivalent model. Although this estimate is  $>1$ , it is not excessively so and is based on a simplified data set, consequently we did not adjust our results for lack of fit. Two models of  $p$  had very similar weight, with probabilities varying by rookery, age, and pup survey, or just by rookery and age (Table 1). We used the rookery+age+pup survey parameterization of  $p$  for evaluating  $\phi$  models incorporating covariates. Sighting probability varied among pup surveys from 0.27 to 0.36 for HI and from 0.31 to 0.44 for the other two rookeries; estimates of annual  $p$  for ages 1–4 varied from 0.64 to 0.72 for HI and from 0.70 to 0.78 for GR and WS.

Survival probability, but not  $p$ , differed between sexes (Table 1). As expected from the results of Hastings *et al.* (2011),  $\phi$  estimates varied among rookeries (Table 1) with estimates lowest at HI, highest at GR, and intermediate at WS (Table 3); sex and age effects on  $\phi$  also were strongly supported. We also found that survival was lower for young pups (*i.e.*, age-6-wk), increasing with age over the first year (Table 3).

Models with mass or Hp\*sex effects on  $\phi$  had higher AICc values than the base models (Table 2); for models containing condition 2, Hct, or %H<sub>2</sub>O effects, the sum of the AICc weights for the covariate and covariate\*sex models also exceeded the base model AICc weight (Table 2). Mass, condition 2, and Hct were positively related to  $\phi$ , while Hp (females only) and %H<sub>2</sub>O were negatively related to  $\phi$ . There was no support for other covariates individually accounting for variation in  $\phi$  (Table 2). However, sample sizes for covariates other than mass and condition were small, which does not invalidate the  $\phi$ -covariate relationships we found, but potentially masks other patterns due to poor precision.

For the GR animals with genetic samples, 13 (6 F, 7 M) had EDPS mitochondrial haplotypes and 23 (11 F, 12 M) had WDPS haplotypes. Genetic stock of matrilineal origin was not a predictor of  $\phi$  for this small sample (Table 2).

In the comparison of individual covariate means, “rookery” or “rookery\*sex” models were the best-supported for all but two of the covariates, SG and NEFA (Table 4), but for some variables, differences between means were small and not biologically meaningful (*e.g.*, condition 1). Means differed substantially among rookeries for several variables (Table 4). Pups from GR had high averages for mass, condition 2, Hct, and Hb (Table 4). Conversely, pups from HI had low averages for mass, Hct, and Hb, and high averages for %H<sub>2</sub>O, Hp, and hookworms. Values for WS pups did not



Table 3. Estimates of period and weekly survival probabilities (95% CI) for Steller sea lion pups branded at three rookeries in southeastern Alaska. Ages assume that pups were approximately 3 wk old when branded.

Rookery <sup>b</sup>	Sex	Period survival			Weekly survival <sup>a</sup>	
		age-6-wk	age-52-wk	age-1-yr	age-6-wk	age-52-wk
HI	F	0.831 (0.773–0.877)	0.671 (0.586–0.745)	0.558 (0.477–0.636)	0.940 (0.918–0.957)	0.987 (0.985–0.990)
	M	0.751 (0.680–0.811)	0.555 (0.467–0.640)	0.417 (0.341–0.498)	0.909 (0.878–0.932)	0.981 (0.977–0.984)
WS	F	0.910 (0.867–0.940)	0.796 (0.723–0.853)	0.724 (0.644–0.792)	0.971 (0.956–0.980)	0.993 (0.991–0.995)
	M	0.862 (0.807–0.903)	0.705 (0.623–0.775)	0.607 (0.524–0.684)	0.954 (0.934–0.968)	0.989 (0.987–0.991)
GR	F	0.951 (0.910–0.974)	0.856 (0.773–0.913)	0.815 (0.715–0.885)	0.980 (0.962–0.989)	0.996 (0.993–0.997)
	M	0.922 (0.865–0.957)	0.785 (0.679–0.863)	0.724 (0.604–0.819)	0.967 (0.942–0.982)	0.993 (0.990–0.995)

<sup>a</sup>Weekly survival estimates for age-6-wk are adjusted for the actual interval between branding and resighting (HI: 21 d, WS: 22 d, GR: 17 d).

<sup>b</sup>HI = Hazy Islands, WS = White Sisters, GR = Graves Rocks.

Table 4. Mean values for morphometric, hematological, and parasite-related variables for Steller sea lion pups from three southeastern Alaska rookeries in 2005; means were adjusted for sex differences if sex was in the model. Models considered were rookery\*sex, rookery+sex, rookery, sex, mean (i.e., no predictors). Means followed by the same letter have estimated differences whose 95% CI includes 0 (the estimated differences and their CIs are not shown).

Variable	Top model	HI <sup>a</sup>	WS <sup>a</sup>	GR <sup>a</sup>
mass (kg)	rookery*sex	26.7b (26.2, 27.2)	27.7a (27.0, 28.3)	29.0a (27.8, 30.2)
condition 1	rookery*sex	70.8a (70.4,71.2)	71.3a (70.4,72.3)	70.7a (70.2,71.2)
condition 2 (kg)	rookery*sex	0.07b (-0.23,0.38)	-0.60c (-0.99,-0.22)	1.31a (0.61,2.01)
Hct (%)	rookery*sex	31.6b (29.9, 33.4)	36.7a (35.1, 38.4)	36.4a (34.1, 38.7)
Hb (g/dl)	rookery*sex	11.2b (10.6, 11.7)	12.9a (12.4, 13.5)	12.9a (12.1, 13.6)
%H <sub>2</sub> O (%)	Rookery	92.9a (92.8,93.1)	92.5c (92.3,92.6)	92.7b (92.5,92.8)
SG (g/ml)	Mean	1.001a (1.0005, 1.0015)	1.001a (1.0005,1.0015)	1.001a (1.0005,1.0015)
BUN (mM/L)	rookery*sex	6.93a (5.68, 8.18)	6.40a (5.04, 7.76)	5.12a (3.41, 6.84)
NEFA (mM/L)	Mean	0.59a (0.52,0.65)	0.59a (0.52,0.65)	0.59a (0.52,0.65)
β-HBA (mM/L)	Rookery	0.25b (0.16, 0.34)	0.44a (0.35, 0.54)	0.22b (0.10, 0.34)
Hp <sup>b</sup> (mg/ml)	rookery*sex	2.70a (1.92,3.79)	1.46b (1.05,2.03)	2.18ab (1.47, 3.24)
hkwr <sup>b</sup> (eggs/g)	rookery*sex	1.01a (0.27,3.78)	0.16b (0.05, 0.51)	0.52ab (0.09, 2.90)
hkwr <sup>b, c</sup>		718 (188, 2752)	551 (45, 6696)	306 (47, 1970)
hkwr <sub>p</sub> /a <sup>d</sup>	Rookery	0.45a (0.29, 0.63)	0.09b (0.03, 0.25)	0.27ab (0.10, 0.53)

<sup>a</sup>HI = Hazy Islands, WS = White Sisters, GR = Graves Rocks.

<sup>b</sup>Analyses performed on natural-log transformed data; means are geometric means.

<sup>c</sup>Means of nonzero observations.

<sup>d</sup>Presence/absence of hookworms; estimates are proportion infected.

have as consistent a pattern (*i.e.*, high or low) across variables with high values for Hct and Hb and low values for hookworms and Hp, but they also had a high mean  $\beta$ -HBA and the lowest condition 2 (Table 4). Viewed as a whole, these variables suggest that pups from HI were on average in the poorest health, while those from GR and WS were much less so, paralleling the pattern of survival probability.

## DISCUSSION

Other studies have shown that sex, rookery of origin, mass, and body condition affect annual survival of SSLs to 1 yr or older (Pendleton *et al.* 2006, Hastings *et al.* 2011, Fritz *et al.* 2014, Maniscalco 2014); this study shows that early pup survival, while pups were still on the natal rookery (*i.e.*, age-6-wk), also was affected by these factors. In particular, lower survival of males than females, of smaller than larger pups, and lower survival of HI-born pups than WS and, especially, GR pups, as previously reported by Hastings *et al.* (2011), were also apparent at this very young age. These results provide more fine-scale information about first-year survival patterns. For example, Hastings *et al.* (2009) found no sex or age effects, and only weak support for a mass effect, on survival from 3 wk to 1 yr at Lowrie Island, part of the Forrester Island rookery (FI), the southernmost, oldest, and largest rookery in southeastern Alaska (3,060 pups in 2002, Pitcher *et al.* 2007). Similarly at a small rookery (~90 breeding animals) in the eastern Gulf of Alaska, Maniscalco *et al.* (2008) documented little variation in pup survival after 2 wk of age. Pup mortality can vary greatly among years (Maniscalco *et al.* 2008) and the 2005 cohort, which included all animals in our study, had the poorest survival to ages 1 and 2 yr compared with the four preceding year cohorts (Hastings *et al.* 2011). Therefore, particularly poor early survival at rookeries, relative to later survival during the first year, might have been especially apparent in our sample.

In addition to mass and body condition, our results suggest that health-related effects potentially affected early pup survival probability. Even with our small sample of pups with blood chemistry, hematology, and health-related measurements, we found evidence of reduced early survival based on Hct, %H<sub>2</sub>O, and, for females, Hp. The association of Hp with female, but not male, survival was unexpected and should be verified with more samples. Also due to small samples, we only fit models where survival was a linear (on the logit scale) function of health-related covariates, rather than other, potentially more realistic, nonlinear or threshold functions (Lander *et al.* 2013), thus reducing our chances of detecting patterns. Other factors, including Hb and hookworm infection, that were not useful singly as predictors of individual survival varied in a manner consistent with rookery differences in survival probability. In particular, the lowest Hct, Hb, and body mass, coupled with the highest %H<sub>2</sub>O, Hp, and hookworm infection occurred in HI pups that had particularly low survival probabilities (Table 3, 4); mean Hct and Hb values for HI were at or below the lower threshold for the normal range reported for this species (Lander *et al.* 2014). HI is the largest and slowest growing rookery of the three in this study, and low survival probabilities and patterns in mean health covariate values are consistent with population crowding. The survival-health variable association is somewhat less clear for the other rookeries. GR and WS pups had equally high mass, Hct, and Hb means, but WS pups had low hookworm and Hp levels with GR intermediate for both of these. GR

pups had high body condition and WS pups had low body condition, and WS pups had high  $\beta$ -HBA; survival was higher at GR than at WS. As with survival estimates for SSL  $\geq 1$  yr (Hastings *et al.* 2011), we found rookery effects still apparent even with strongly supported individual covariates in the models (Table 2). Of course, the rookery itself does not affect survival, but is a placeholder for proximate causes, possibly unmeasured, that vary among rookeries and affect population processes, including differences in food availability, population density, disease exposure, or exposure to storms.

Our study contributes additional estimates of early pup survival for comparison with other studies. Our age-52-wk weekly survival estimate for females at HI was very similar to those from FI (in 2001–2002, 2005; Hastings *et al.* 2009) at 0.987 with slightly higher probabilities for GR and WS female pups ( $>0.992$ ). Hastings *et al.* (2009) also compared their 12 wk survival estimates for SSL pups from FI with published survival estimates (scaled to 12 wk) for unbranded pups of other otariid species. Our 12 wk estimates, averaged across sexes, ( $[\text{age-6-wk weekly estimate}]^{3*} [\text{age-52-wk weekly estimate}]^2$ ) were 0.685 for HI, 0.823 for WS, and 0.878 for GR. The estimate for FI, 0.868 (Hastings *et al.* 2009), is intermediate between our WS and GR estimates, possibly reflecting more favorable conditions in 2001–2002 compared with 2005 when all of our data were collected (Hastings *et al.* 2011). Our estimates from all three rookeries are within the range of published values for non-branded otariid pups (Hastings *et al.* 2009: table 2); even our low estimate for HI is in the 33rd percentile of the reported values.

SSL rookeries in southeastern Alaska have grown rapidly in both pup production and nonpup attendance following the transition from haul out sites to rookeries, with slower or no growth at the larger, older rookeries (Calkins *et al.* 1999, Pitcher *et al.* 2007, Mathews *et al.* 2011). The time since rookery establishment of our three study sites parallels their sizes with HI the oldest and largest, WS intermediate in size and age, and GR the newest and smallest of the three (Calkins *et al.* 1999, Pitcher *et al.* 2007, Mathews *et al.* 2011). If competition increases as more animals use a site, this could be reflected in lower survival probability, which is consistent with our results. Mathews *et al.* (2011) suggest that abundant fish stocks could have been an important factor in the establishment and growth of the GR rookery, of which high pup survival might be a proximate factor in the growth of the site; this is consistent with our results of high pup mass and survival at GR. The lack of a survival difference between pups with different genetic origins should be viewed cautiously because our sample size was very small and survival probabilities at GR, the only rookery with genetic data, was so high that any difference between stocks of origin would have had to have been small, if it existed at all. In addition, our stock assignments were based only on female lineages, so EDPS and WDPS pups might be genetically more similar depending on male line parentage.

A possible confounding factor in our interpretation would be if the age of the marked pups varied systematically among rookeries, for example if GR pups were older than HI pups, their mass and survival could be increased as a result. Survival probability of SSL pups was lower at Chiswell Island during their first 2 wk than for 4–10 wk; sources of mortality also differed between the two periods (Maniscalco 2014). SSL birth dates vary among rookeries throughout their range (Pitcher *et al.* 2001), but whether current timing of births varies systematically among our study rookeries is unknown. Branding dates varied by a maximum of 6 d among sites and is unlikely to have created significant age differences in the samples, and true rook-

ery differences likely accounted for patterns in survival probability and pup body mass.

Because our study is of branded animals only, we cannot partition the estimates between natural mortality and any mortality caused by the marking operation, including both physical effects of branding on individual pups and disturbance effects (*e.g.*, permanent separation of mothers and pups); this is also true for Hastings *et al.* (2009), the only other study that estimated short-term postbranding survival. Hastings *et al.* (2009) found that survival in the 2 wk postbranding was very similar to those >2 wk postbranding, consequently the maximum potential marking-caused (*i.e.*, branding+disturbance) mortality at FI was likely <1% of the pups branded. In contrast, using the same rationale we found greater differences between early (age-6-wk) and later (age-52-wk) survival in the first year, which could be a branding effect. However, our age-6-wk survival estimates are comparable to an estimate from FI in 2005 based on a small sample ( $n = 49$ ) of unbranded/undisturbed pups of branded mothers (Hastings *et al.* 2009). In our study, all marking operations were conducted by the teams of experienced branders, veterinarians, and research staff overseen by the same leaders, further suggesting that lower early *vs.* later survival during the first year in our 2005 sample was likely not attributable to marking.

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