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Article

Limited consequences of infestation with a blood-feeding ectoparasite for the nestlings of two North Pacific seabirds

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The seabird tick *Ixodes uriae* parasitizes over 60 host species in the circumpolar regions of both hemispheres. To assess the impacts of these ticks on the growth and development of nestling seabirds, we used a logistic growth model to interpolate between successive measures of mass (g) and wing chord (mm) for 558 Cassin's auklet *Ptychoramphus aleuticus* and 344 rhinoceros auklet *Cerorhinca monocerata* chicks over 11 years (1997–2008, less 2003) on Triangle Island, British Columbia, Canada. From the model, we estimated the asymptotic measure and the age at inflection point for each chick's growth trajectory, and assessed their relationships with tick load relative to other sources of annual and seasonal variation in growth. Most chicks (72.4% of Cassin's auklets, 62.2% of rhinoceros auklets) hosted ≥ 1 ticks, and the median tick load on infested chicks was two in both species. Infestation rates varied by a factor of about two among years (0.42 to 0.87 overall), but were uncorrelated between species and with air temperatures over the preceding winter. The probability of hosting a tick declined strongly with chick age, mainly in the first 20 days after hatching, and to near zero by fledging. Asymptotic weights and/or wing lengths declined with tick load in both species, but at normal loads the reductions were minor relative to those imposed by other factors; only at very high loads, which were rare, were effects likely to be biologically relevant. Tick load and survival to fledging were unrelated in both species. While our study found little influence of ticks, we believe there is need for further study of the relationships between parasites and seabird demography, especially in light of ongoing environmental change.

Keywords: ticks, seabirds, growth, North Pacific Ocean

Introduction

Parasites and pathogens can be important underlying causes of variation in the physiological, behavioural and demographic traits of their hosts. As a result, these organisms play leading roles in the evolution of life histories (Monticelli 1985, Cable and van Oosterhout 2007). Hematophagous ectoparasites, a group that includes ticks, mites and insects, compete directly with their host for critical nutrients, and can act as

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vectors for bacterial and viral agents that challenge the hosts' immune system (Olsen et al. 1993, Szep and Møller 1999) while at the same time reducing the capacity of the host to mount an immune response to the challenge (Saino et al. 1998, Pryor and Castor 2015). These ectoparasites can affect the fitness of hosts through direct mechanisms, i.e., by causing the deaths of adults (Gaston et al. 2002, Devevey and Christe 2009) and juveniles (Hawlena et al. 2006, Hillegass et al. 2010); and through indirect mechanisms, such as retarding the rate at which offspring develop (Moss and Camin 1970, Merino and Potti 1995). The severity of the infestation with ectoparasites, the intensity of the host's responses, and the consequences for fitness all can vary with environmental conditions (de Lope et al. 1993, McCoy et al. 2002, Jones et al. 2016).

Avian species that breed at high density, and that reuse their nest sites, are especially prone to being infested with ectoparasites (Rifkin et al. 2012). Those are two characteristic life-history traits of colonial seabirds (Lack 1968), so it follows that haematophagus ectoparasites infest many species belonging to this group (Feare 1976, Duffy 1983). The seabird tick *Ixodes uriae* is the most widely distributed tick in the world, parasitizing over 60 host species in the circumpolar regions of both hemispheres, and acting as a vector for a number of potentially virulent pathogens (Dietrich et al. 2011, Muñoz-Leal and González-Acuña 2015). The consequences of infestation with seabird ticks can include retarded growth and mortality of offspring (Bergström et al. 1999, Mangin and Gauthier-Clerc 2003), and in extreme cases, adult mortality (Gauthier-Clerc et al. 1998). Recent studies suggest that the seabird tick may be expanding its range poleward (Coulson et al. 2009), and that infestation rates (Descamps 2013) and the period of time over which the ticks are active each year (Benoit et al. 2009) are both on the increase. Similar tendencies have been documented in other species of ticks (Jaenson et al. 2016), and typify the types of changes to host-parasite relationships that are widely expected to result from global warming (Harvell et al. 2002, Dantas-Torres 2015).

Demographic research on seabirds has largely focused on the role of bottom-up forcing, and this agenda has produced a wealth of information on the mechanisms by which environmental variation influences survival and productivity (Aebischer et al. 1990, Thompson and Ollason 2001). By comparison, the effects of parasites on seabird demography remain very poorly studied, especially in the context of environmental change using multi-year datasets. Yet evidence exists to suggest that seabird ticks can have significant population-level effects on their hosts, with one study linking higher levels of infestation to declining numbers of black-legged kittiwakes *Rissa tridactyla* on breeding colonies (Boulinier and Danchin 1996). Both the breeding site fidelity and the breeding success of adult kittiwakes were lower on colonies experiencing higher levels of tick infestation.

On Triangle Island, British Columbia, Canada, environmental variation has strong effects on breeding by seabirds including Cassin's auklet *Ptychoramphus aleuticus* and rhinoceros auklet *Cerorhinca monocerata* (Bertram et al. 2001). Nestlings of both species are parasitized by seabird ticks on Triangle Island (Dietrich et al. 2012), where a one-year study found that tick infestation was associated with reduced body condition at fledging in Cassin's auklets (Morbey 1996). In a close relative, the tufted puffin *Fratercula cirrhata*, individuals that fledged from Triangle Island with poor body condition (small wings, light in mass) on were less likely to be re-sighted at the colony in later years (Morrison et al. 2009), suggesting a mechanism by which ticks could impact fitness. Further, ticks could have stronger effects on nestling seabird hosts when feeding conditions are poor (McCoy et al. 2002).

Here, we examine the relationships between infestation with seabird ticks and the survival and growth in mass and wing length of nestling Cassin's and rhinoceros auklets on Triangle Island. Our 11-year study spanned a period of extreme environmental variation in the oceanic waters surrounding the colony (Mackas et al. 2007), and this was linked to dramatic interannual variation in offspring performance in both species (Wolf et al. 2009, Borstad et al. 2011). Our specific aim was to quantify the potential impacts of seabird ticks in relation to annual and seasonal factors that are known from previous work to impact offspring growth and survival in these two seabirds on Triangle Island.

Material and methods

Study site

Field work was conducted on Triangle Island (50°52′N, 129° 05′W) annually from 1996 to 2007 with the exception of 2003. Triangle Island supports the world's largest Cassin's auklet breeding colony (500 000 pairs in the 1980s), and a sizable colony (45 000 pairs) of rhinoceros auklets (Rodway 1991).

Avian and arthropod study species

Cassin's and rhinoceros auklets spend most of their lives at sea, returning to colonies in the North Pacific Ocean annually to breed. Both lay a single-egg clutch in an earthen burrow which they excavate and reuse from one year to the next. Nesting densities on Triangle Island average ~1.5 burrows m^{-2} in the 190 g Cassin's auklet, and ~0.9 burrows m^{-2} in the 500 g rhinoceros auklet (Rodway and Lemon 2011). Rates of pre- and post-embryonic growth are slow in both species compared to their closest relatives, the *Aethia* auklets and *Fratercula* puffins (Hipfner et al. 2010a). Slow development necessitates long breeding seasons: to complete incubation and chick-rearing takes ~80 d for a Cassin's auklet pair (typically, early April to late June on Triangle Island) and ~100 d for a rhinoceros auklet pair (early May to mid-August). Adult survival rates on Triangle Island during our study period averaged ~80% y^{-1} in Cassin's auklets and ~87% y^{-1} in rhinoceros auklets (Morrison et al. 2011).

The seabird tick parasitizes nestlings of both species on Triangle Island, occurring almost exclusively (> 99%) on the webs of the feet (Morbey 1996). Over the course of the ticks' two- to seven-year life-cycle, larvae, nymphs and adult females attach to a host to take a single blood meal for a period lasting from 3 to 12 d, then drop to the ground to develop further, or in the case of adult females, to lay eggs (Eveleigh and Threlfall 1974, McCoy and Tirard 2002). The ticks overwinter in the substrate in all life-stages from egg to adult (Lee and Baust 1987).

Field methods

Burrows located on pre-defined study plots in West Bay (Cassin's auklet) and South Bay (rhinoceros auklet) were inspected at 5 d intervals to determine laying dates. When an egg was found, the burrow was then left undisturbed for 35 d (Cassin's auklet) or 45 d (rhinoceros auklet) to allow birds to complete incubation. Thereafter, burrows were checked at 5 d intervals until the chick hatched. When first found, the wing length (± 0.5 mm) and mass (± 1 g) of each chick was measured, and its hatching date (age 0) estimated using a calibration of wing length vs age for known-age chicks. Cassin's auklet chicks were weighed and measured at 5, 10, 25 and 35 d of age, then every other day until they disappeared; rhinoceros auklet chick measures were at 5, 10, 40 and 45 d, then every other day to disappearance. We assumed that fledging occurred on the day between the last check before the chick disappeared and the first check after. The age at fledging averages 43 d in Cassin's auklets (Hipfner et al. 2010c), and 54 d in rhinoceros auklets (Hipfner et al. 2008). The chicks were thoroughly inspected for ticks every time they were measured, and the total number of ticks present tallied.

Analytical methods

We first provide a basic description of tick infestation by calculating the proportion of chicks that hosted one or more ticks at least once during the nestling period (infestation rate), and determining the maximum number of ticks present. We also examined how the prevalence of ticks varied within and among years. Using package 'lme4' in R (Bates et al. 2015), we fit a linear mixed model that had presence of ticks as binary response variable modelled as a function of chick age, which was included both as a fixed effect and as a random effect within chick identifier nested within year. Chick age in the fixed statement measures the average effect of chick age across all chicks, whereas chick age in the random statement measures the variance in the effects of chick age across all chicks.

Growth rates of chicks

Repeated measures of mass and wing length were considered to vary as a sigmoid curve with chick age (in days) using the basic logistic growth model (Ricklefs 1968). This model describes how measures increase non-linearly to a final asymptote, and was calculated as a three parameter model based on the following equation:

$$W[t] = \frac{Asym}{1 + \left(\exp(xmid - t)\right) / scal}$$

Under this parameterization, $W[t]=$weight of chick at age t in number of days, where hatch day is $t=0$, *Asym* is the chick weight at the asymptote, *xmid* is the age at the inflection point (*Asym**0.5), and *scal* is a scale parameter that controls the shape of the curve and also represents the number of days between 0.5 and 0.75 of final weight at the asymptote (Fig. 1). The same model was used for wing length.

We used package 'nlme' in R (Pinheiro et al. 2017) to fit a mixed effect model that had *Asym, xmid, scal* as fixed effects, with *Asym* and *xmid* as random slopes with individual chick identity nested within year as random intercepts. This approach assumed a general shape of the growth curve, but allowed each chick to follow its own trajectory with individual *Asym* and *xmid* values, as well as accounting for the repeated measures on individual chicks, and any annual environmental effects (e.g., weather, food supply) that may have determined how the entire population performed in any particular year. We assessed model fit as variance explained R^2, by comparing the residual variance of the full model against the residual variance of a (fixed) intercept-only null model (Xu 2003). To examine associations between tick load and growth rates, the estimated *xmid* and *Asym* values for weight and wing length for each chick were extracted from the model, and we then used the 'glm' procedure in R (Crawley 2013) to fit a general linear model (GLM) that regressed *xmid* and *Asym* values against year (as a factor), hatching date (as day of year, day 1 = 1 January), and maximum tick load for each chick. Significance of parameters was assessed using a likelihood ratio test (LRT) at $\alpha = 0.05$.

Survival of chicks

To examine associations between tick load and the probability of fledging, each chick was assigned a final fate (0 if not fledged, 1 if fledged). We then used the 'glm' procedure in R (Crawley 2013) to fit a binomial GLM model of fate as a function of year (as a factor), hatching date (as day of year, where day 1 = 1 January), and maximum tick load. This model thus allowed us to assess whether the probability of fledging varied with tick load after accounting for variation due to annual and within-season effects. We tested for significance using a likelihood ratio test (LRT).

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.cb76d28> (Hipfner et al. 2018).

Results

Extent and patterns of infestation with ticks

In Cassin's auklets, a total of 558 chicks was monitored in the 11 yr of study. Most (72.4%) hosted ≥ 1 tick at least once, and the annual infestation rate varied from 0.45 to 0.87 (Fig. 1). Among chicks that hosted ticks, the median number present was 2, with a range from 1 to 37 (Fig. 1).

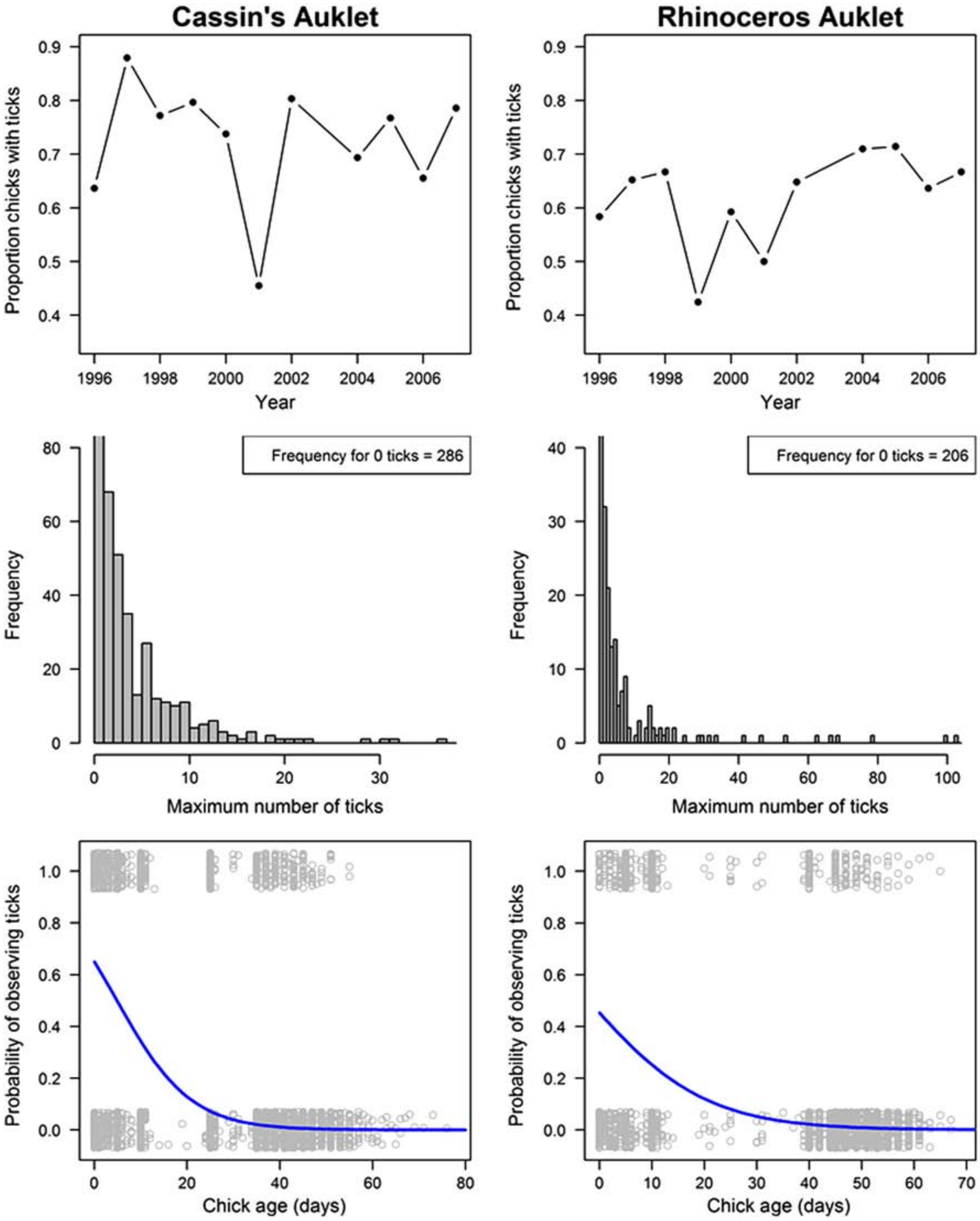

Figure 1. Frequency distributions of tick counts and incidence rate of ticks during burrow checks on individual auklet chicks on Triangle Island, British Columbia, 1996 to 2007. Top panels depict annual variation in the proportion of chicks that had at least 1 tick observed during repeated burrow checks. Middle panels present frequency distribution of maximum number of ticks counted per chick. Note that bar on histograms for frequency values for 0 ticks has been cut-off, and value appears in box within histogram. Bottom panels depict the probability of observing at least one tick on a chick during repeated burrow checks, as a function of chick age. A jitter of 0.35 was applied to observation (0 = no tick, 1 = tick present). Solid black line represents predicted value from binomial generalized linear mixed effects model (see text for details).

The probability of hosting a tick declined strongly with chick age ($\beta_{age}=-0.13$, SE = 0.010, t = –13.1, $p < 0.001$), with an initial probability of 0.65 on day 1 declining most strongly in the first 20 d post-hatching and to less than 0.01 on day 40 (Fig. 1).

A total of 344 rhinoceros auklet chicks was monitored over the 11-yr study. Most (62.2%) hosted ≥ 1 tick, and the annual infestation rate ranged from 0.42 to 0.71 (Fig. 1). For chicks that hosted ticks, the median number was 2, with a range from 1 to 103 (Fig. 1). The probability of hosting a tick declined with chick age ($\beta_{age}=-0.09$, SE = 0.01, t = –8.7, $p < 0.001$), from 0.45 on day 1 to less than 0.01 on day 45 (Fig. 1).

There was no significant correlation between annual infestation rates of Cassin's and rhinoceros auklets (Pearson's r = 0.33, p = 0.32). In addition, infestation rates were not correlated with median daily air temperature in the winter period (1 Dec to the end of Feb, as measured at the automated weather station on Sartine Island, 13 km southeast of Triangle Island) for either Cassin's auklet (Pearson's r = –0.09, p = 0.78) or rhinoceros auklet (Pearson's r = 0.24, p = 0.47).

Nestling growth and relationships with tick loads

Mass and wing length increased non-linearly with age, and the logistic model provided a robust fit to the repeated measures. Variance explained values for each model were 0.96 (for mass) and 0.99 (for wing) in Cassin's auklets, and 0.92 (for mass) and 0.98 (for wing) in rhinoceros auklets. Growth parameters for mass and wing length (*Asym*, *xmid*), and their variation among years and individuals (i.e., random effects) are reported in Table 1; growth trajectories are depicted in Fig. 2; Table 2 reports the results of the GLMs for effects of year, hatching date and maximum tick load on growth parameters; and Table 3 reports the slopes of the lines from the GLMs relating growth parameters to hatching date and maximum tick load. Those slopes are used (below) to examine associations between median (2 in both species) and maximum (37 in Cassin's auklet; 103 in rhinoceros auklet) tick loads and asymptotic masses and wing lengths.

In Cassin's auklets, asymptotic mass (*Asym*) varied among years, and declined with later hatching and (marginally) with maximum tick load. The average difference in mass between a chick with no ticks and one with 2 ticks ($\beta = -0.29$ g tick^{-1} × 2 ticks = –0.6 g) was small relative to the variation among years and individuals: 28.8 and 20.0 g, respectively (Table 1). The maximum observed load of 37 ticks represented a potential loss of 10.7 g in asymptotic mass, but tick loads that high were rare (Fig. 1). Age at the midpoint of growth in mass (*xmid*) also varied among years and declined with hatching date, but the effect of tick load was not statistically significant (Fig. 3).

Table 1. Parameter estimates for non-linear mixed effects models depicting a logistic growth curve of mass and wing length of individual Cassin's auklet and rhinoceros auklet chicks on Triangle Island, British Columbia, 1996 to 2007.

	Cassin's auklet				Rhinoceros auklet			
Parameter	Value	SE	t	p	Value	SE	t	p
Mass								
Fixed Effects								
Asym	150.6	8.6	17.5	< 0.001	277.8	14.9	18.6	< 0.001
xmid	12.4	0.7	18.6	< 0.001	14.1	0.7	20.7	< 0.001
scale	7.2	0.1	99.0	< 0.001	9.8	0.2	55.4	< 0.001
Random effects								
Year variation								
Asym	28.2				48.2			
xmid	2.2				2.1			
Individual chick variation								
Asym	20.0				43.9			
xmid	1.5				2.6			
Residual	10.2				16.3			
Wing length								
Fixed Effects								
Asym	130.7	2.8	45.9	< 0.001	167.1	3.9	43.2	< 0.001
xmid	22.8	0.2	111.9	< 0.001	27.0	0.3	100.0	< 0.001
scale	10.1	0.1	199.4	< 0.001	12.5	0.1	223.3	< 0.001
Random effects								
Year variation								
Asym	9.3				12.4			
xmid	0.6				0.8			
Individual chick variation								
Asym	7.8				12.0			
xmid	1.5				1.2			
Residual	4.1				3.0			

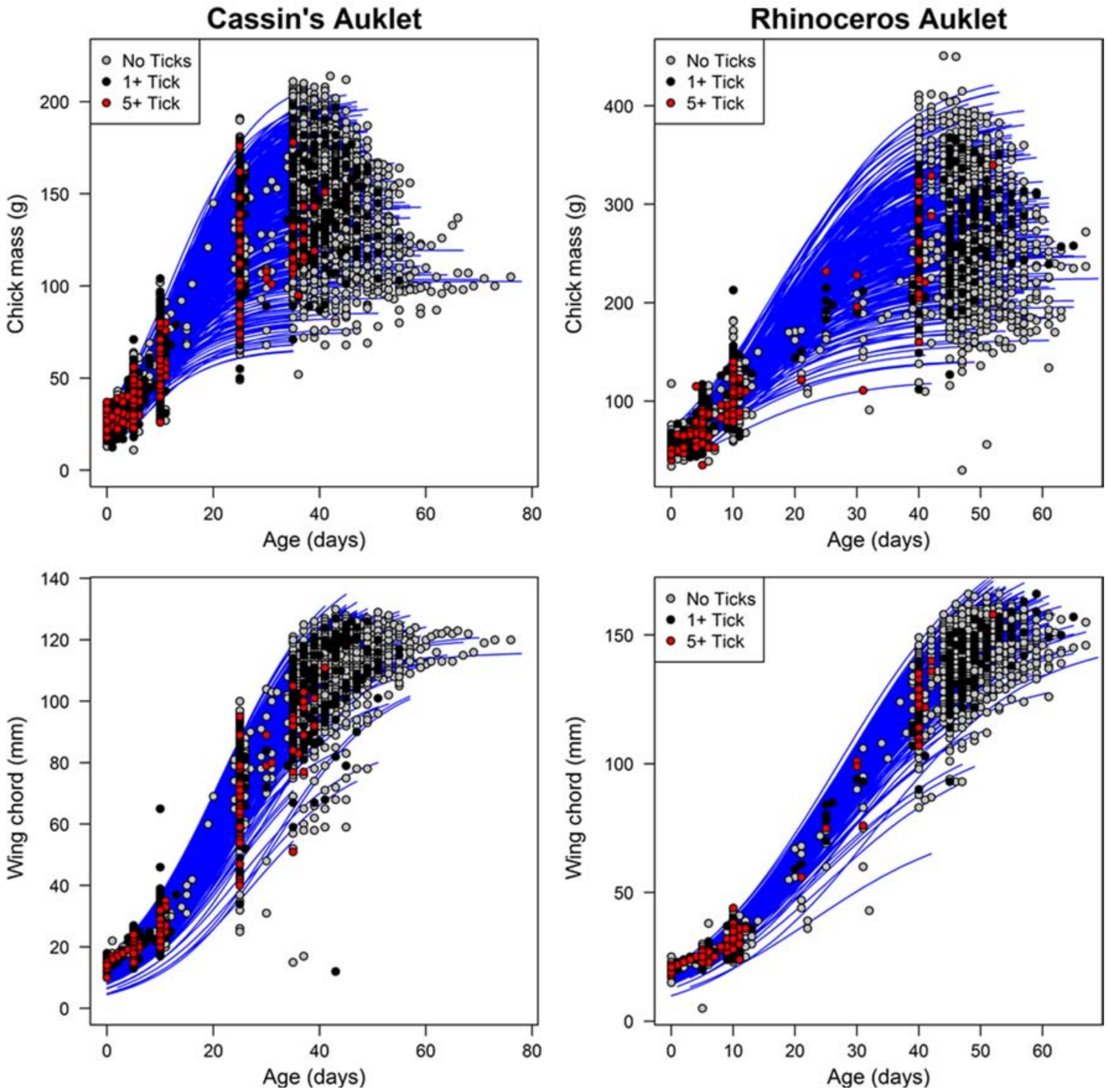

Figure 2. Growth patterns of chick mass and wing length of Cassin's Auklet and rhinoceros Auklet chicks on Triangle Island, British Columbia, 1996 to 2007, as a function of chick age (d). Color of dot indicates number of ticks observed during burrow checks (note that 0 counts may be covered by darker colors). Lines indicated mean predicted values from logistic growth models (see Material and methods).

Table 2. General linear models for growth in mass and wing length of individual Cassin's auklet and rhinoceros auklet chicks in relation to year, hatch date and tick load on Triangle Island, British Columbia, 1996 to 2007.

		Year LRT			Hatch date			Ticks LRT		
Species	Parameter	χ^2	df	p	χ^2	df	p	χ^2	df	p
Cassin's auklet	Mass asymptote	948.2	11	< 0.001	98.4	1	< 0.001	98.4	1	0.07
	Mass midpoint	1112.7	11	< 0.001	12.8	1	< 0.001	12.8	1	0.99
	Wing asymptote	1188.1	11	< 0.001	68.7	1	< 0.001	68.7	1	< 0.001
	Wing midpoint	855.5	11	< 0.001	41.3	1	< 0.001	41.3	1	0.004
Rhinoceros auklet	Mass asymptote	333.8	11	< 0.001	18.3	1	< 0.001	2.7	1	0.10
	Mass midpoint	334.8	11	< 0.001	45.3	1	< 0.001	0.07	1	0.79
	Wing asymptote	314.1	11	< 0.001	0.1	1	0.91	2.9	1	0.09
	Wing midpoint	559.4	11	< 0.001	19.8	1	< 0.001	0.09	1	0.76

Table 3. Slopes of the lines (β, with Standard Error) from general linear models relating growth parameters to hatching date and tick load of Cassin's auklet and rhinoceros auklet chicks on Triangle Island, British Columbia, 1996 to 2007.

		Hatch date		Tick Load	
Species	Parameter	β_{date}	SE	$\beta_{max\ ticks}$	SE
Cassin's auklet	Mass asymptote	–0.63	0.06	–0.29	0.16
	Mass midpoint	–0.013	0.003	n.s.	–
	Wing asymptote	–0.20	0.02	–0.20	0.06
	Wing midpoint	0.03	0.004	0.03	0.01
Rhinoceros auklet	Mass asymptote	–1.37	0.32	–0.29	0.18
	Mass midpoint	–0.11	0.015	ns	–
	Wing asymptote	ns	–	–0.08	0.05
	Wing midpoint	–0.03	0.007	ns	–

The asymptotic wing length of Cassin's auklets varied among years, and declined with later hatching and with maximum tick load. The reduction in wing length linked to 2 ticks (–0.4 mm) was small relative to the variation among years (9.3 mm) and individuals (7.8 mm), although the maximum load of 37 ticks represented a potential reduction of 7.5 mm in wing length. Age at the midpoint of wing growth varied among years, and increased with both

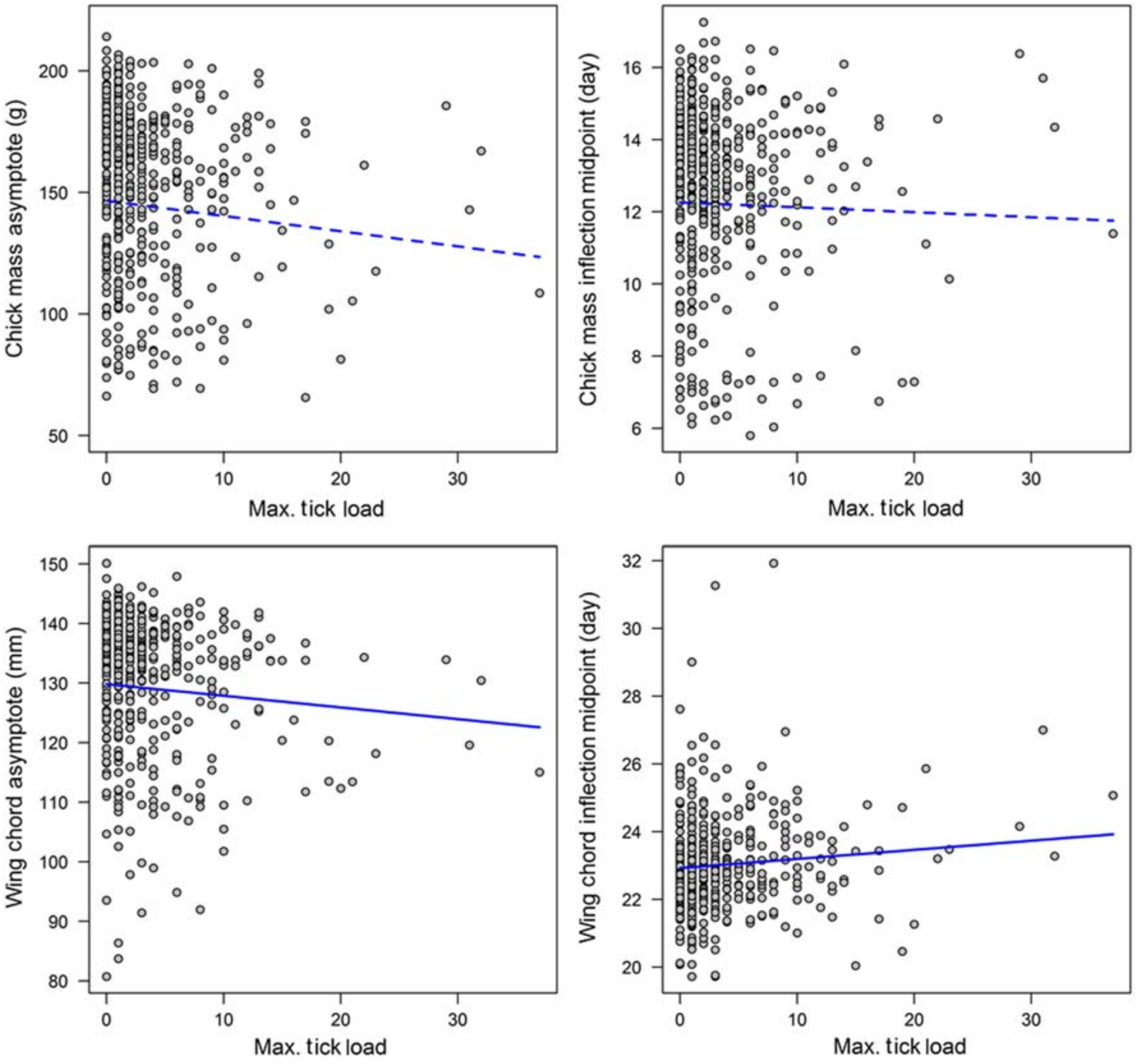

Figure 3. Effects of tick loads, measured as the maximum number of ticks observed on tick during its nestling period, on growth patterns of chick mass and wing length of Cassin's Auklet on Triangle Island, British Columbia, 1996 to 2007. Asymptote refers to the theoretical maximum value, and inflection midpoint refers to the age (in d) at which the chicks reached half its asymptote value. The lines indicate the effect of tick load assuming a median hatch date and averaged out all years. A dashed indicates a non-significant trend.

hatching date and tick load (Fig. 3). The difference was small for a load of 2 ticks (0.06 d), but considerable (1.1 d) for a load of 37 ticks.

In rhinoceros auklets, asymptotic chick mass varied among years, and declined with hatching date and (marginally) with maximum tick load. A load of 2 ticks represented just a 0.6 g loss in asymptotic mass, but a load of 103 ticks represented a potential reduction of ~30 g – comparable to the variation among years and individuals, 43.9 g and 40.2 g, respectively (Table 1). Tick loads that large were rare however (Fig. 1). Age at the midpoint for mass varied among years and declined with hatching date but with a non-significant effect of tick load (Fig. 4).

Asymptotic wing lengths of rhinoceros auklets varied among years, but not with hatching date and only marginally with maximum tick load. The reduction in wing length associated with a load of 2 ticks (–0.16 mm) was small, whereas the potential reduction linked to a load of 103 ticks (–8.8 mm) was comparable to the variation among years (12.4 g) and individuals (12.0 g). Age at midpoint of wing growth varied among years, and declined with hatching date with little effect of tick load (Fig. 4).

Nestling survival and relationships with tick loads

The median proportion of chicks that survived to fledge over the 11 yr of study was 0.86 (range 0.09 to 0.93) in Cassin's auklets, and 0.85 (range 0.40 to 1.00) in rhinoceros auklets (Fig. 5). Annual fledge rates were negatively but non-significantly correlated with annual infestation rates in both Cassin's (Pearson's r = –0.04, p = 0.89) and rhinoceros (Pearson's r = –0.42, p = 0.19) auklets.

In Cassin's auklets, the binomial GLM indicated that the probability of fledging varied among years, and declined

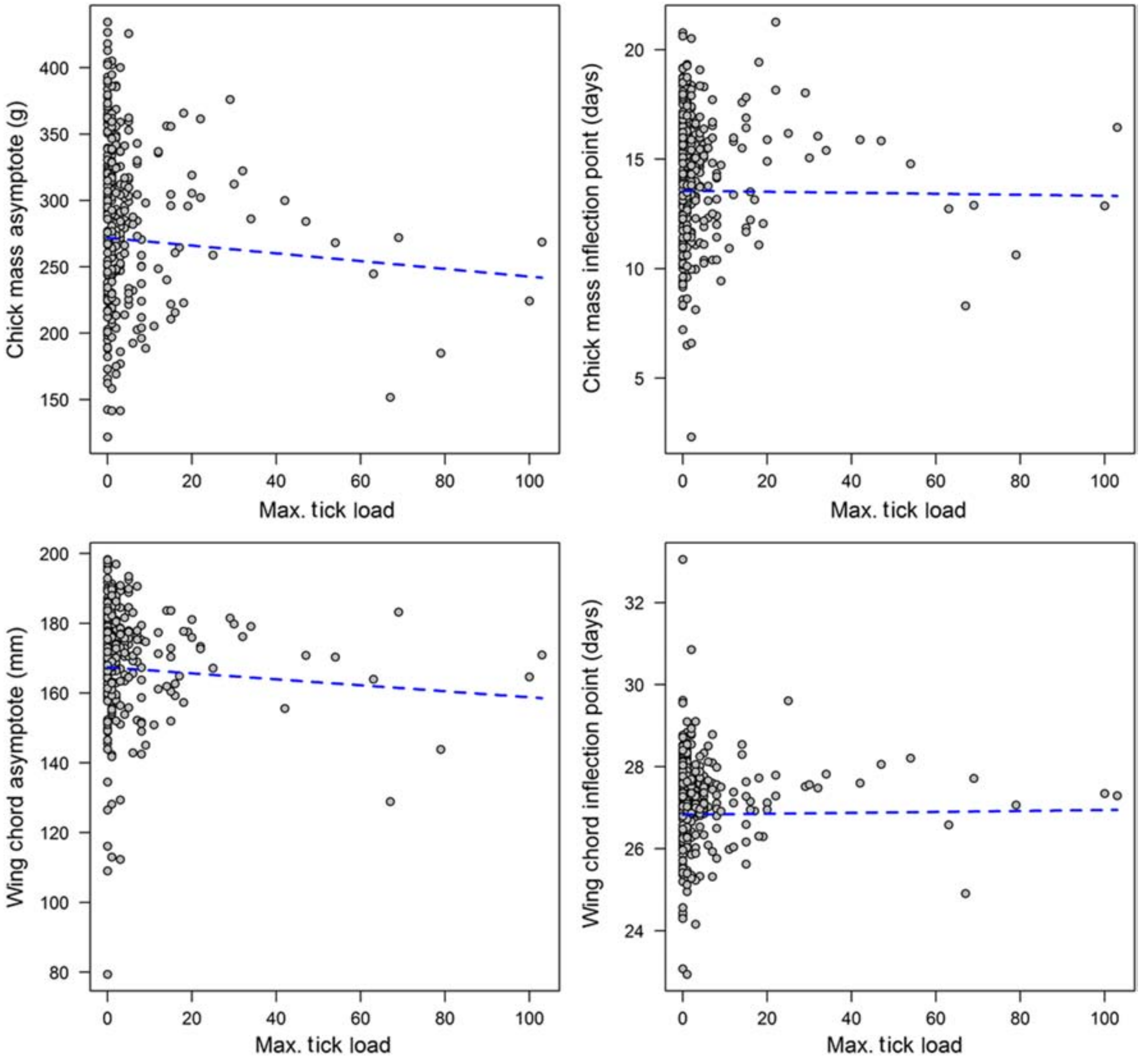

Figure 4. Effects of tick loads, measured as the maximum number of ticks observed on tick during its nestling period, on growth patterns of chick mass and wing length of rhinoceros Auklet on Triangle Island, British Columbia, 1996 to 2007. Asymptote refers to the theoretical maximum value, and inflection midpoint refers to the age (in d) at which the chicks reached half its asymptote value. The lines indicate the effect of tick load assuming a median hatch date and averaged out all years. A dashed indicates a non-significant trend.

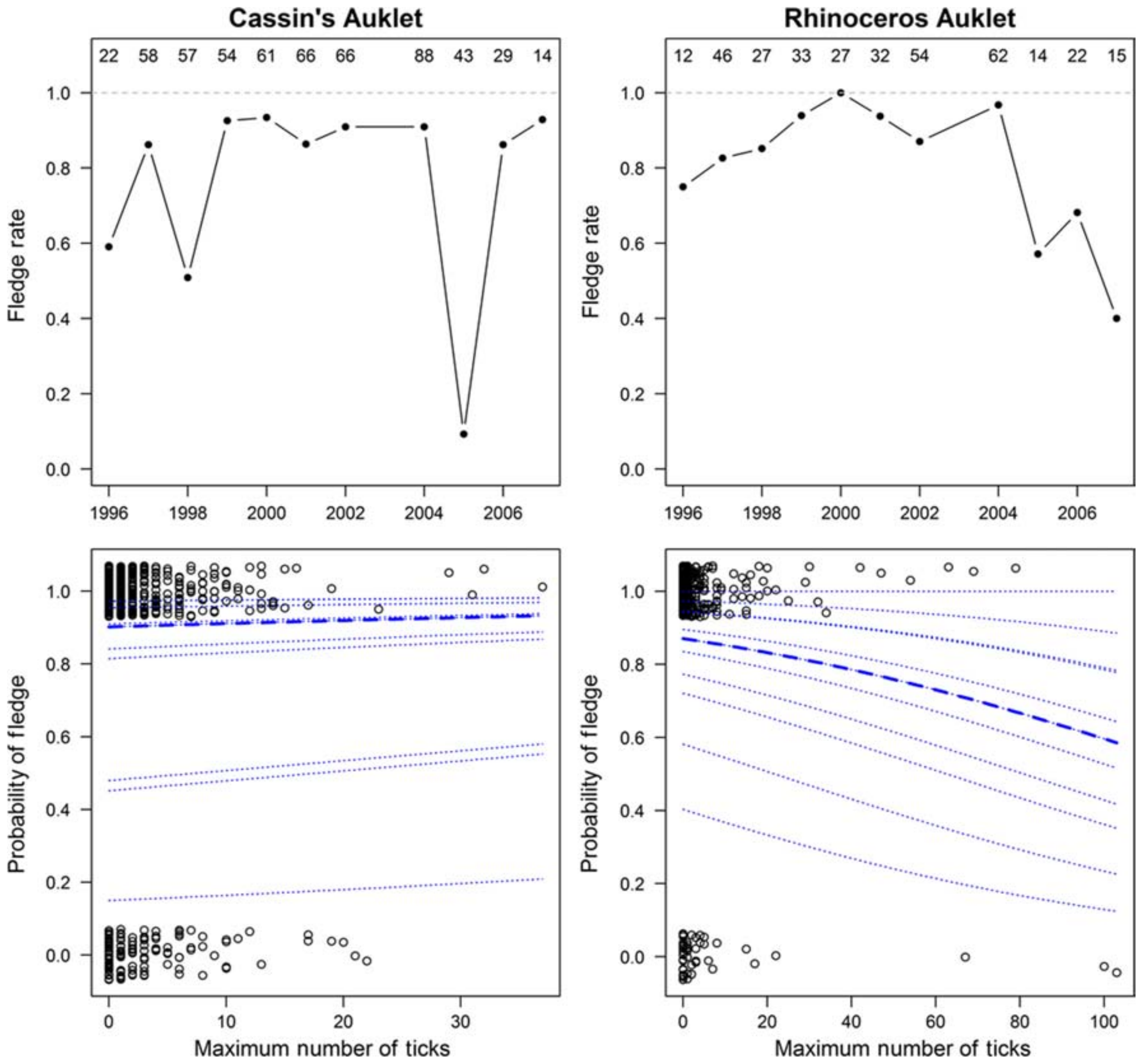

Figure 5. Annual fledge rates, and probability of fledge of individual auklet chicks as a function of tick load, observed during burrow checks on individual auklet chicks on Triangle Island, British Columbia, 1996 to 2007. A jitter of 0.35 was applied to fate (0 = not fledge, 1 = fledge). Values on top portion of upper panels indicated the number of chicks followed each year. Lines on lower panels indicate predicted probability of fledge based on tick load and median hatch day for each year, and thick lines indicates the median probability across all years. A dashed line indicates a non-significant result.

with hatch date ($\beta = -0.074$, SE = 0.011), but not tick load ($\beta = 0.01$, SE = 0.03) (Table 4). In rhinoceros auklets, the probability of fledging varied among years and declined with hatch date ($\beta = -0.052$, SE = 0.026), while tick load had a non-significant negative effect ($\beta = -0.015$, SE = 0.01) (Table 4). Removing the two chicks with very high loads (> 100 ticks) resulted in a reversal of the sign of the effect (LRT: $\chi^2 = 0.6$, df = 1, $p = 0.81$; $\beta = 0.005$, SE = 0.02) (Fig. 5).

Discussion

Extent and patterns of infestation with ticks

The majority of Cassin's auklet (72%) and rhinoceros auklet (62%) chicks hosted seabirds ticks during the course of development on Triangle Island, British Columbia. Morbey (1996) recorded a very similar infestation rate (73%) on

Table 4. General linear models for survival of individual Cassin's auklet and rhinoceros auklet chicks in relation to year, hatch date and tick load on Triangle Island, British Columbia, 1996 to 2007.

	Year LRT			Hatch date			Ticks LRT		
Species	χ^2	df	p	χ^2	df	p	χ^2	df	p
Cassin's auklet	167.8	10	< 0.001	47.0	1	< 0.001	0.14	1	0.71
Rhinoceros auklet	25.0	10	< 0.001	3.9	1	0.047	1.6	1	0.20

Cassin's auklet nestlings at the same site in an earlier study. However, over the 11 yr of our study, the annual proportion of nestlings that experienced infestation varied by a factor of about two in both species. In Brünnich's guillemot *Uria lomvia*, an Arctic-nesting auk, more adult birds were infested with seabird ticks in breeding seasons following warmer winters, suggesting the existence of a simple relationship between environmental conditions and overwinter tick survival (Descamps 2013). In contrast, we found that infestation rates on Cassin's and rhinoceros auklet nestlings were unrelated to air temperatures in the preceding winter months, and that they were not correlated between the two species. Winter temperatures at our study site were mild, however, with a typical range from 4 to 8°C – insufficiently cold, perhaps, to cause mortality of ticks. Seabird ticks do show strong adaptation to specific seabird host species, even on multi-species seabird colonies (Dietrich et al. 2014), so the selective forces operating on ticks that feed on different species could differ even at small spatial scales.

Among infested chicks, the maximum tick loads present at any point during development were highly variable: 1 to 37 in the smaller Cassin's auklet and 1 to 103 in the larger rhinoceros auklet. We do not know which life-stages of ticks infested the nestlings, but all individuals collected from Cassin's auklet nestlings by Morbey (1996) were nymphs. Despite the difference in body size of the two seabird species, however, the median load per infested chick was a modest 2 ticks in both. The probability of hosting ticks declined strongly with chick age in both species, especially over the first 20 d post-hatching, and to near zero by the last few days prior to fledging. Morbey (1996) recorded a similar range (1–45) in maximum tick loads on Cassin's auklet nestlings on Triangle Island in 1994, but in that year, the relationship with age was quite different: tick loads increased gradually to 15 d of age, then declined gradually to fledging. Chicks were monitored at 5 d intervals through development in that study, however, which makes comparison with our study difficult. But that same pattern of an initial increase to near mid-development, then a decrease to fledging, was observed both in black-legged kittiwake chicks parasitised by seabird ticks (Boulinier and Danchin 1996), and for blue-footed booby *Sula nebouxii* chicks parasitised by the tick *Carios denmarki* (Ramos and Drummond 2017).

Nestling growth and survival and relationships with tick loads

Previous studies indicate that nestling seabirds infested with ticks of a variety of species experience reduced growth and survival, especially at high levels of infestation (Bosch and Figuerola 1999, Merino et al. 1999, Ramos et al. 2001, Monticelli and Ramos 2012). Studies involving the seabird tick have produced mixed results, however. In some, tick-infested chicks experienced no (Haemig et al. 1998, Descamps 2013) or only weak and inconsistent (Bergström et al. 1999) reductions in survival, while in others, infested chicks experienced overt reductions in growth but not survival (Morbey 1996). In that latter study, conducted in a single year on Triangle Island, Cassin's auklets infested with ten or more ticks reached asymptotic body masses at older ages, experienced slower wing growth, and delayed their fledging. A link between slow wing growth and delayed fledging has been found in other auks (Hipfner and Gaston 1999), including rhinoceros auklets (Deguchi et al. 2004), as has reduced post-fledging survival of individuals that leave the nest light in mass and with short wings (Morrison et al. 2009).

Growth and survival of nestling Cassin's and rhinoceros auklets varied markedly among the 11 yr of our study, and declined among individuals that hatched late. Previous studies on Triangle Island have concluded that interannual variations in growth and survival are direct consequences of oceanographic conditions, operating via effects on the prey base: ocean temperature for Cassin's auklet, which affects the abundance and timing of life-cycle events in their primary prey, the subarctic copepod *Neocalanus cristatus* (Bertram et al. 2001, Hipfner 2008); and the timing and intensity of the spring bloom for rhinoceros auklets, which affects the survival of their primary prey, young-of-year Pacific sand lance *Ammodytes personatus* (Borstad et al. 2011). And experimental studies have shown that the seasonal declines in offspring performance result from one or both of seasonal environmental effects and the reduced parental capacities of individuals that breed late (Hipfner et al. 2008, 2010c).

Relative to these primary environmental and parental influences on growth and survival, there was little additional impact from tick infestation (or not). Thus survival to fledging and age at the midpoint of growth in mass were unrelated to tick load in both species, while asymptotic mass and tick load were only marginally related in both. Consequences of infestation with ticks for wing growth were more apparent, as found by Morbey (1996), but only in the smaller of the two species, Cassin's auklet: higher tick loads were linked to reduced asymptotic wing length and older age at the midpoint of growth in that species. But even those associations were weak at normal levels of infestation – a median load of 2 ticks caused a < 0.5 mm reduction in wing length, and a < 0.1 d delay in the age at midpoint of wing growth.

Only at the very highest levels of tick infestation observed in our study did the magnitude of projected effects on growth approach those attributable to environmental and parental effects. This modest virulence may reflect a coevolution between the *Ixodes* ticks and their hosts (McCoy et al. 2002, Alizon et al. 2009), although our study methods permit only a coarse examination. We did not consider subtle effects that could result from the transmission of pathogens from ticks to birds; seabird ticks on Triangle Island are known to harbour the bacterium *Coxiella*, for example (Duron et al. 2014). We also did not consider post-fledging effects, such as impairments that might result from the small holes that we observed that ticks sometimes left in the webs of the feet of nestlings. Many species of ticks are expanding their range poleward and having increasingly severe effects on wildlife species worldwide as global temperatures warm (Dantas-Torres 2015). Air temperatures have warmed on Triangle Island over recent decades (Hipfner et al. 2010b), and while we found no link between winter temperatures and infestation levels, we suggest that the interplay between ticks and their seabird hosts should continue to be investigated in light of ongoing environmental change.

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