ENERGY INTAKE RATE INFLUENCES SURVIVAL OF BLACK OYSTERCATCHER *HAEMATOPUS BACHMANI* BROODS

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ABSTRACT

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The Black Oystercatcher *Haematopus bachmani* is a species of conservation concern that depends on marine intertidal prey resources. We examined diet, feeding rates, growth, and survival of Black Oystercatcher broods in southcentral Alaska, 2013–2014. To determine the importance of diet for brood survival, we modeled daily survival rates of broods as a function of energy intake rate and other ecological factors. We hypothesized that broods fed at higher energy intake rates would grow faster and fly earlier, and thus be less vulnerable to predators and have higher rates of survival. Consistent with our prediction, broods with higher energy intake rates had higher rates of growth and daily survival. Our best-supported model indicated that brood survival varied by energy intake rate and brood age. To understand how adults meet the increasing nutritional needs of developing chicks, we examined delivery rates, prey type, and prey size as a function of brood age. Delivery rates differed by age, but composition and size classes of prey items did not, indicating that adults respond to the rising energetic needs of broods by increasing parental effort rather than by switching prey. These findings demonstrate the importance of diet and provisioning to broods and, given the consequences of reduced energy intake on survival, indicate that climate change–related shifts in intertidal invertebrates could significantly impact Black Oystercatcher populations.

Key words: Alaska, brood survival, chick diet, growth, parental care, provisioning rates

INTRODUCTION

The Black Oystercatcher *Haematopus bachmani* has been designated as a species of conservation concern due to its small population size, unknown population trends, and limited distribution (Tessler *et al.* 2014). They range from Baja California, Mexico to the Aleutian Islands of Alaska and are reliant on nearshore marine habitats for all life history components, including feeding, nesting, and raising their semi-precocial young (Andres & Falxa 1995). This reliance on the nearshore environment throughout their annual life cycle has made them vulnerable to a number of threats such as predation of eggs and young; human disturbance; coastal infrastructure development; direct and indirect effects of shoreline contamination, including reduced food availability; and climate change, with resultant effects on nesting and feeding resources (Tessler *et al.* 2010).

Despite considerable research effort examining threats to nest survival, our understanding of factors influencing Black Oystercatcher post-hatch survival is limited (Vermeer *et al.* 1992, Gill *et al.* 2004). Although predation is thought to be the major cause of mortality in Black Oystercatcher broods (Tessler *et al.* 2014), there is some evidence to suggest that diet plays an important role in brood survival. For example, in a study in British Columbia, heavier Black Oystercatcher chicks had a better chance of survival than lighter chicks (Groves 1984). Similar patterns were documented for Eurasian Oystercatchers *H. ostralegus*, in that fledging success was positively correlated with growth rate (Kersten

& Brenninkmeijer 1995). Furthermore, in years of lower food availability, brood survival of Eurasian Oystercatchers decreased (Heg & van der Velde 2001).

Given the potential relationship between diet and brood survival, climate-induced changes in the abundance or composition of marine intertidal invertebrates may significantly affect Black Oystercatchers. Warming ocean temperatures alter the behavior, physiology, and demography of many invertebrates on which Black Oystercatchers depend (Grenon & Walker 1981, Menge *et al.* 2008). The breeding propensity of Black Oystercatchers is negatively correlated with sea-surface temperature, presumably due to warmer sea temperatures creating deficient feeding conditions that result in poor body condition of breeding adults (Hipfner & Elner 2013). Ocean acidification, sea level rise, and increased storm frequency may also affect marine invertebrate communities (Harley *et al.* 2006, Fabry *et al.* 2008). These changes may have profound implications for Black Oystercatchers, considering that their diet is relatively specialized and has remained constant over the past century (Carney 2013).

To assess the importance of diet on brood survival of Black Oystercatchers, we modeled daily survival rates of broods as a function of energy intake rate and other ecological factors. We hypothesized that broods fed a similar diet but at a greater frequency would grow faster and fly earlier, and thereby be less vulnerable to predators. Assuming that diet is an important factor influencing brood survival, we predicted that the energy intake rate of broods

would be positively correlated with survival rates. To understand how adults meet the increasing nutritional needs of developing chicks, we examined how delivery rates, prey composition, and prey size varied with chick age. Collectively, these findings will identify the importance of diet and provisioning to the survival of Black Oystercatcher broods in a rapidly changing marine ecosystem.

STUDY AREA AND METHODS

Our field site was located within Kenai Fjords National Park in southcentral Alaska, USA, (59°51′18″N, 149°42′14″W). Specifically, we studied Black Oystercatchers (hereafter referred to as oystercatchers) nesting in Aialik Bay, a deep, glacially forged inlet in-cut by smaller coves and bounded by steep mountains (Cook & Norris 1998, Spencer & Irvine 2004). Shoreline topography varies from gravel beaches of low wave energy to rocky cliffs of high wave energy with a mean tide range of 1.7 m (NOAA 2008).

Field methods

From May to August in 2013 and 2014, we conducted systematic boat-based surveys of historically known nesting sites to locate breeding territories and oystercatcher broods. Upon detecting a territorial pair, we searched the surrounding area on foot. For all nests found, we recorded location and clutch size, and we floated eggs to determine the stage of incubation to estimate hatch dates (Mabee *et al.* 2006). To detect new nests throughout the breeding season, we periodically revisited sites where nests had failed, sites where territorial pairs were observed but had yet to initiate a nest, and historical breeding sites. Once nests were located, we monitored them every 3–5 d throughout the nesting period. As nests approached the estimated day of hatch, we visited them daily. After eggs hatched, we visited broods every 3–5 d until they fledged or failed, to determine growth rates, energy intake rates, and fledging success. We monitored six broods in 2013 and fourteen broods in 2014. Chicks were considered to have fledged when they were fully capable of sustained flight, which occurred at ~40 d after hatch.

We marked chicks with colored tape or colored plastic bands until their tarsi were large enough to be fitted with a metal band and two plastic alpha-numeric bands. We recaptured chicks every 3–5 d until they fledged or died, to measure relaxed wing length and thus determine growth rates. We used wing growth rather than body mass in our growth rate analysis because wing length determines when chicks can fly (Tjørve *et al.* 2007).

To estimate energy intake rates, we observed adults provisioning their broods for two hours at low tide, when intertidal feeding grounds became exposed. Upon arriving at a territory, we used binoculars to locate the brood from our boat. During the first few days after hatch, most broods remained at the nest. Later, they moved with their parents to intertidal feeding areas and throughout their territory. Broods stayed with and were fed by their parents throughout the entire chick-rearing period. After a brood was located, we set up a 20–60× spotting scope in a camouflaged blind ~50 m away and waited for the birds to resume normal activity, which typically occurred within minutes of us entering the blind. We recorded the taxa and size class of each prey item fed to a chick and the time at which the provisioning event occurred. We assigned prey items to a size class in relation to adult bill length, using four size classes: 1) less than one eighth of the bill length, 2) between one eighth and one quarter, 3) between one quarter and one half, and 4) one half or more. Prey items, in general, were easily identifiable to the genus or species level based on shape, size, and color, as well as on the handling behavior of the adults. If the observer was unsure of the prey or if vision was obstructed during a feeding event, the prey item was listed as 'unknown.' Two observers worked together throughout the study to reduce observer bias. All fieldwork was conducted under appropriate permits and with approval from the University of Alaska, Fairbanks, Institutional Animal Care and Use Committee (#436591).

Energy analysis

We collected intertidal invertebrates to measure the energy content of oystercatcher prey. In July 2014, we sampled from five intertidal feeding areas within our study site. We collected the four most common prey items that we observed being fed to chicks: limpets *Lottia* spp. (*n* = 22), mussels *Mytilus trossulus* (*n* = 45), barnacles *Semibalanus cariosus* (*n* = 15), and chitons *Katharina tunicata* (*n* = 10; Table 1). Samples were frozen at −4 °C for approximately one month prior to analysis. In the lab, we measured the length and mass of each frozen sample, then dried them in a freeze drier at −40 °C for at least 48 hours. After freeze-drying, we weighed the samples, removed shells, and reweighed the samples to determine dry mass. We combined samples of the same prey type to obtain three composite samples with minimum of 1 g of homogenized dry mass for each prey item; samples were then homogenized using scissors and a mortar and pestle. Energy content of composite samples was measured using a bomb calorimeter and corrected for the unburned fuse and acid by titration. We calculated the energy density of composite samples as kilojoules per gram dry mass (kJ·g^{-1} DM) and averaged composite samples of the same prey type to obtain mean energy densities.

Since not all organic compounds in the diet are available to the consumer, we conducted a pepsin digestibility assay to determine

TABLE 1
Energy density (kJ·g^{-1}) and digestibility (g digested·g^{-1} dry mass (DM)) of intertidal marine invertebrates collected in Kenai Fjords National Park, Alaska, July 2014

Prey type	Energy density of composite samples						Mean energy density (kJ·g^{-1}) ± SD	Mean digestibility (g digested·g^{-1} DM) ± SD	Mean digestible energy density (kJ·g^{-1} DM)
	kJ·g^{-1}	*n*	kJ·g^{-1}	*n*	kJ·g^{-1}	*n*			
Barnacle	18.64	5	16.96	5	17.58	5	17.73 ± 0.69	0.49 ± 0.02	8.64
Chiton	18.68	3	18.38	3	19.65	4	18.90 ± 0.54	0.73 ± 0.11	13.75
Limpet	19.59	10	20.39	12	-	-	19.99 ± 0.40	0.78 ± 0.08	15.57
Mussel	17.84	15	18.06	15	17.94	15	17.95 ± 0.09	0.89 ± 0.04	16.02

the digestible energy density of prey items (Barboza *et al.* 2009). Approximately 1 g of homogenized dry mass of each prey type was placed in synthetic filter bags, inserted in jars, and immersed in an acid-pepsin solution of pH 1 in a 0.1 mol/L HCl solution containing 2 g/L pepsin (VanSomeren *et al.* 2015). The jars were placed in an incubator for six hours, then filter bags were removed, rinsed, and dried in an oven. We reweighed the samples to determine the remaining mass. Digestibility of prey was calculated by dividing the difference between total dry mass and remaining dry mass by the total dry mass. We calculated digestible energy density of prey items as the product of energy density and digestibility.

We estimated the energy intake rates of broods based on data from our provisioning observations and estimates of digestible energy density. For each prey type, we estimated the energy content of the four size classes to which observed prey was assigned. Energy content (kJ) of size classes was calculated as the product of digestible energy density (kJ·g^{-1}) for each prey type and dry mass (g). We estimated the dry mass of size classes using the length-to-mass regression of each prey type and the proportion of bill length that each size class represented. We used adult bill length data (see Jehl 1985 in Andres & Falxa 1995) and calculated length-to-mass regressions from our measurements (see Burgherr & Meyer 1997 in Baumgärtner & Rotthaupt 2003). The energy intake rate was calculated as the total energy content of prey fed to chicks per time observed (kJ·min^{-1}). Delivery rate was calculated as the total number of prey items fed to chicks per time observed. To account for variation in brood size, which ranged from one to three chicks, we divided energy intake and delivery rates by the number of chicks in a brood. We averaged energy intake rates to obtain a mean energy intake rate for each brood.

We calculated linear growth rate to quantify wing growth (Nisbet *et al.* 1995). Although birds exhibit a nonlinear pattern of growth (Ricklefs 1973), we were unable to capture chicks after they fledged, when growth rates begin to reach an asymptote. Therefore, we analyzed the linear phase of growth, which occurs when oystercatchers are 5–35 d old (Groves 1984, Hazlitt *et al.* 2002). Growth rate coefficients were calculated for broods by linear regression of age (in d) and wing length (in mm). Age and wing length values were log-transformed to meet assumptions of normality and equal variance. To test for a relationship between energy intake and wing growth, we conducted a linear regression of energy intake rate and wing growth rate coefficients.

We examined how delivery rate, prey composition, and prey size varied by chick age. We investigated these relationships by comparing between age classes: young (age ≤ 15 d) and old (> 15 d) chicks. We tested for a difference in delivery rates (number of prey items fed to chicks per minute) between the two age classes using a two-sample *t*-test. We conducted a chi-squared test of independence to determine if prey composition (limpets, mussels, barnacles, chitons, 'other' prey, unknown prey) differed between young and old chicks. We also conducted a chi-squared test to determine if the four size classes of prey consumed by chicks differed between age classes.

Survival analysis

We used an information-theoretic approach to examine the relative support for models that describe associations between daily survival rate of broods and variables of interest. A small set of candidate

models was selected from variables that we hypothesized might influence survival. These variables were age (as both a linear and quadratic trend), year (2013, 2014), minimum daily temperature, landform (island vs. mainland), and our primary variable of interest: energy intake rate. We included the landform covariate because we reasoned that: (1) survival would be higher for broods on islands than on the mainland due to the absence of mammalian predators on islands in our study area (Morse *et al.* 2006) and (2) composition of prey items delivered to chicks reared on rocky islands would differ from prey provisioned on mainland beaches (Robinson *et al.* 2018). In addition to models with a single variable of interest, we included additive models consisting of all two-covariate combinations (Table 2). Given that energy intake rates increase with brood age (Hazlitt *et al.* 2002) and that we did not have intake rates for many broods 20–40 d old because they did not survive to fledge, we limited our energy intake rates of broods to observations that occurred when broods were 15 days old or younger. We were unable to obtain energy intake rates for 7 of the 20 broods studied; to account for these missing data in the models that included energy intake rate, we applied the energy intake rate covariate to only the broods with energy intake data, and we applied the other covariates in the model to all broods (Cooch & White 2002). We used Akaike's information criterion, adjusted for small sample size (AIC$_c$) and normalized Akaike weights (w_i), to select the top-supported model in the candidate set. We conducted our survival analysis using

TABLE 2
Model rankings for Black Oystercatcher brood survival at Kenai Fjords National Park, Alaska, 2013–2014

Model[a]	ΔAIC$_c$[b]	w_i	K	Deviance
Age^2 + Energy Intake Rate	0.00	0.95	7	62.29
Age^2	8.92	0.01	3	79.35
Energy Intake Rate	10.22	0.01	3	80.66
Age^2 + Year	10.70	<0.01	4	79.11
Age^2 + Min Daily Temp	10.72	<0.01	4	79.13
Energy Intake Rate + Min Daily Temp	10.87	<0.01	5	77.24
Age^2 + Landform	10.93	<0.01	4	79.34
Energy Intake Rate + Landform	11.45	<0.01	4	79.86
Year	11.94	<0.01	2	84.40
Constant	12.12	<0.01	1	86.59
Energy Intake Rate + Year	12.73	<0.01	5	79.11
Age	13.28	<0.01	2	85.73
Landform	13.96	<0.01	3	84.40
Min Daily Temp + Year	13.96	<0.01	3	84.40
Min Daily Temp	13.97	<0.01	2	86.43
Landform	14.01	<0.01	2	86.47
Min Daily Temp + Landform	15.87	<0.01	3	86.31

[a] Models were ranked by differences for small sample size (ΔAIC$_c$) values. Normalized Akaike weight (w_i), number of parameters (*K*), and model deviance (Deviance) are also shown for each model.
[b] The lowest AIC$_c$ score in the model set was 76.48.

the nest survival module in program MARK (White & Burnham 1999). All other statistical analyses were done in program R (R Development Core Team 2014).

RESULTS

We monitored 20 oystercatcher broods in 2013 and 2014. The mean brood size was 2.3 ± 0.7 chicks (mean ± standard deviation (SD)), with a range of 1–3 chicks per brood. Of 20 nests that hatched, 10 fledged at least one chick (fledging success of 50 %).

We observed 1 979 prey items fed to chicks in the 20 broods. Limpets were the most common prey consumed, followed by mussels, barnacles, and chitons. Of the common prey consumed by oystercatcher broods, limpets had the highest energy density (mean ± SD; 19.99 ± 0.40 kJ·g^{-1} DM) of the four prey items we analyzed (Table 1). However, mussels had the highest digestibility (0.89 ± 0.04 g digested·g^{-1} DM) and digestible energy density (16.02 kJ·g^{-1} DM). Prey items of size class 2 (1/8–1/4 bill length) made up the majority (53 %) of prey items fed to chicks. Digestible energy content of this size class was highest for limpets (1.13 kJ), followed by chitons (0.66 kJ), barnacles (0.59 kJ), and mussels (0.35 kJ).

Delivery rates were higher for old chicks than for young chicks ($t_{17} = -3.39$, $P = 0.004$; Fig. 1). However, neither the composition ($X^2_{25} = 30$, $P = 0.22$) nor the size classes ($X^2_9 = 12$, $P = 0.21$) of prey items fed to chicks by their parents differed between old and young chicks.

We calculated wing growth rates for broods during the linear phase of growth. The mean wing growth rate coefficient was 1.12 (± 0.12 SD) with a range of 0.87–1.27. Energy intake rate to day 15 varied among broods, ranging from 0.01–1.01 kJ·min^{-1} with a mean of 0.28 (± 0.26 SD; $n = 13$). Energy intake rates were positively correlated with wing growth rate coefficients ($F_{1,9} = 14.87$, $P = 0.004$; Fig. 2).

We modeled daily survival rates of 20 oystercatcher broods. The best-supported model indicated that brood survival varied by energy intake rate and brood age (Table 2). Support for a model with energy intake rate was strong; normalized Akaike weight indicated a 0.95 probability that it was the best of the candidate models. This model was 8.92 AIC$_c$ units better than the next best model, which did not include energy intake rate. Energy intake rates were positively correlated with daily survival rates (Fig. 3). The age covariate in the top-ranking model was quadratic, with daily survival rates increasing for the first two weeks post-hatch and decreasing after three weeks (Fig. 4).

DISCUSSION

Our results supported our hypothesis that broods fed at higher energy intake rates would grow faster and have higher rates of survival. Consistent with our prediction, broods with higher energy intake rates had higher daily survival rates. The addition of an energy intake rate covariate to the top-ranked model improved fit and strongly decreased deviance. Broods provisioned at higher energetic rates had higher rates of wing growth, presumably enabling them to fly at an earlier age and possibly making them more adept at evading predators. In another study that examined chick survival of oystercatchers before and after fledging, all mortalities occurred before chicks began to fly (Groves 1984). Birds that can minimize the period in which they are most vulnerable to predators can increase their chances of survival. However, under conditions of restricted energy intake, growth is compromised, leading to negative effects on survival. Our results underscore the importance of diet and provisioning to the growth and survival of oystercatcher broods.

The relationship that we found between energy intake rate, growth, and survival is consistent with findings from other shorebird studies. Arctic shorebird chicks that had access to more prey had higher growth rates than chicks with lower prey availability (McKinnon *et al.* 2012). African Oystercatchers *H. moquini* with low biomass available in their territories had decreased energy intake rates and were less likely to successfully raise two chicks (Leseberg
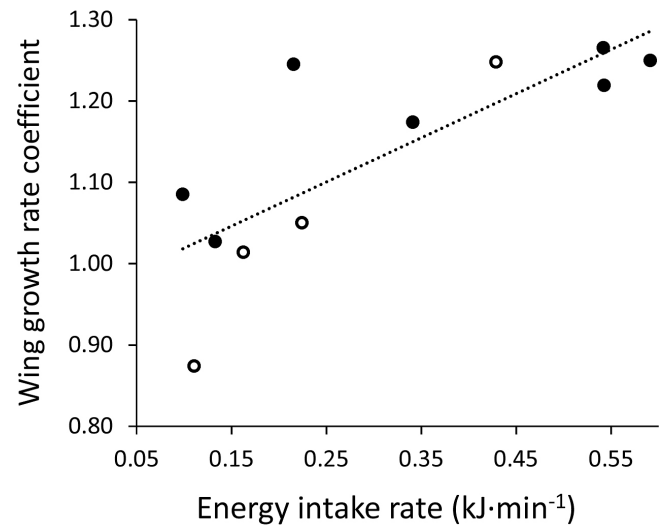

Fig. 1. Log-transformed delivery rates (prey items consumed per minute) differ between young (age ≤ 15 d) and old (> 15 d) Black Oystercatcher chicks in Kenai Fjords National Park, Alaska. Boxes represent the distances between the first and third quartiles; center bars represent the medians.

Fig. 2. Wing growth rate coefficients as a function of energy intake rate for Black Oystercatcher broods that survived to fledge (closed circles) and died before fledging (open circles) in Kenai Fjords National Park, Alaska, 2013–2014: slope = 0.55 (± 0.14 SD), $R^2 = 0.58$, $n = 11$).
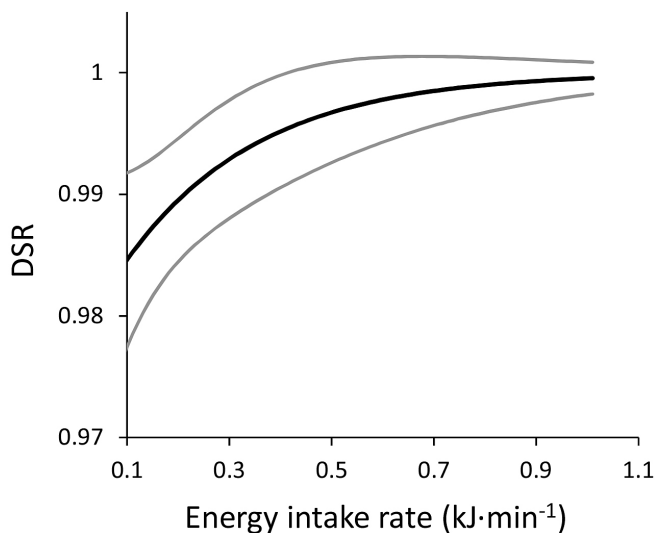
Fig. 3. Predicted daily survival rates (DSR) as a function of energy intake rate of Black Oystercatcher broods in Kenai Fjords National Park, Alaska, 2013–2014. Grey lines represent ± SD.

Fig. 4. Daily survival rates (DSR) of Black Oystercatcher broods by age in Kenai Fjords National Park, Alaska, 2013–2014. Intervals represent ± SD.

et al. 2000). Food supply also strongly affected the growth and productivity of marine birds including kittiwakes *Rissa* spp. and skuas *Stercorarius* spp. (Gill & Hatch 2002, Ritz *et al.* 2005), and higher energy densities of Antarctic krill *Euphausia superba* result in higher growth rates and survival of Adelie Penguin *Pygoscelis adeliae* chicks (Chapman *et al.* 2010).

Although energy intake rates were positively correlated with wing growth, other mechanisms associated with feeding rates, aside from wing growth, may simultaneously influence survival. Chicks with higher energy intake rates may also have better body condition, making them more resistant to severe weather and disease (Møller *et al.* 1998); however, we did not encounter any diseased chicks. Additionally, parents that feed chicks at higher rates may attend to chicks more frequently and be able to defend them from predators more often. Since we were not able to test these hypotheses, we cannot rule out the possibility that additional mechanisms associated with intake rate, aside from growth, impact brood survival.

In addition to energy intake rate, brood age was a parameter in the best-supported survival model. The age trend in this model was quadratic, with low daily survival rates at hatch that increased for the first two weeks, then leveled off and decreased after three weeks. The pattern of lower survival among younger chicks has also been found in other shorebirds including American Oystercatchers *H. palliatus*, Snowy Plovers *Charadrius nivosus*, and Western Sandpipers *Calidris mauri* (Ruthrauff & McCaffery 2005, Colwell *et al.* 2007, Schulte & Simons 2015). Young chicks are slow and small, making them more vulnerable to predators and severe weather. Yet, in our study, after survival rates increased, they leveled off and decreased after three weeks. Chicks become less vulnerable to weather as they develop and begin to thermoregulate; however, they also become more active and conspicuous to predators. These combined factors may explain the quadratic relationship between age and survival.

Our findings also highlight how adults respond to the increasing nutritional needs of developing chicks. Adults did not adjust the types or size classes of prey brought to young versus old chicks;
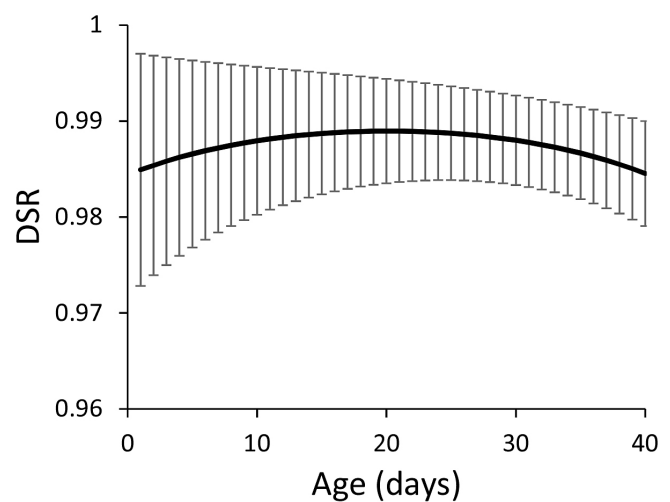
instead they increased the frequency by which they delivered prey. Experimental studies of chick provisioning in other species revealed a similar trend: individuals adjusted their feeding rate to account for temporary changes in the energetic demands of broods but did not adjust the size of food items brought to the nestlings (Koenig & Walters 2012). Together, these results show that adults respond to the rising energetic needs of broods by increasing parental effort.

Our study demonstrates the importance of diet and provisioning to the survival of oystercatcher broods. In the Gulf of Alaska, mussel populations can undergo dramatic shifts in abundance across time (Bodkin *et al.* 2018). During years when mussel abundance is low, oystercatchers may have difficulty provisioning their young and survival may be compromised. Less is known about the population dynamics of other species of oystercatcher prey and the implications of changing ocean conditions. Given the consequences of reduced energy intake on brood survival, shifts in composition and abundance of intertidal invertebrates as a result of climate change may significantly affect oystercatcher populations. Brood survival, productivity, and recruitment into the breeding population may decline if marine intertidal invertebrates respond negatively to changing ocean conditions. To better understand the biology underlying oystercatcher conservation, future research should address how climate-driven changes in nearshore ecosystems will affect food resources and predator communities with respect to oystercatcher populations.

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