



Food supply and individual quality influence seabird energy expenditure and reproductive success

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Abstract

Breeding animals trade off maximizing energy output to increase their number of offspring with conserving energy to ensure their own survival, leading to an energetic ceiling influenced by external, environmental factors or by internal, physiological factors. We examined whether internal or external factors limited energy expenditure by supplementally feeding breeding black-legged kittiwakes varying in individual quality, based on earlier work that defined late breeders as low-quality and early breeders as high-quality individuals. We tested whether energy expenditure increased when food availability decreased in both low- and high-quality birds; we predicted this would only occur in high-quality individuals capable of sustaining high levels of energy expenditure. Here, we find that food-supplemented birds expended less energy than control birds because they spent more time at the colony. However, foraging trips of food-supplemented birds were only slightly shorter than control birds, implying that food-supplemented birds were limited by food availability at sea similarly to control birds. Late breeders expended less energy, suggesting that low-quality individuals may not intake the energy necessary for sustaining high-energy output. Food-supplemented birds had more offspring than control birds, but offspring number did not influence energy expenditure, supporting the idea that the birds reached an energy ceiling. Males and lighter birds expended more energy, possibly compensating for relatively higher energy intake. Chick-rearing birds were working near their maximum, with highest levels of expenditure for early-laying (high-quality) individuals foraging at sea. Due to fluctuating marine environments, kittiwakes may be forced to change their foraging behaviors to maintain the balance between reproduction and survival.

Keywords Seabird · Foraging behavior · Daily energy expenditure · Reproductive success · Climate change

Introduction

Energy, a critical but often limited resource, must be allocated among competing individual needs, such as reproduction and self-maintenance (Stearns 1992). How an animal allocates energy to reproduction during the breeding season will have important effects on future reproduction and survival (Welcker et al. 2015) and individuals that acquire more resources over time are expected to have greater lifetime fitness (McAdam and Boutin 2003). As a result, differential access to food is one of the greatest sources of variation in “individual quality” that correlates positively with fitness (Wilson and Nussey 2010).

Foraging behavior strongly impacts the amount of food that an individual obtains (Laskowski et al. 2021), while simultaneously using both time and energy during the search for and capture of prey (Bautista et al. 1998; Chivers

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et al. 2012). The amount of energy an individual allocates towards reproduction and survival is therefore a function of both energy acquisition (i.e., energy intake) and energy expenditure (Bautista et al. 1998). This ‘energetic ceiling’ represents the balance between maximal energy expenditure and intake over time (Elliott et al. 2014b). Importantly, an individuals’ daily energy expenditure (DEE) may not correlate linearly with fitness (Elliott et al. 2014b). For example, low DEE is expected when food is both scarce [e.g., due to reductions in individual resting metabolic rate, RMR, to allow for more energy to go towards reproduction; (Welcker et al. 2009)] and abundant [e.g., due to a reduction in overall reproductive effort when foraging conditions are favorable; (Jodice et al. 2002)]. Therefore, extrinsic factors (e.g., food availability) and intrinsic traits (e.g., age) can influence energy expenditure and the overall ‘net’ energy budget for life-history allocation.

Within the set of intrinsic traits, different behaviors, including foraging, preening, and various types of locomotion contribute to overall DEE (Welcker et al. 2015). In the case of many seabirds, flapping flight is the most energetically expensive of these behaviors (Birt-Friesen et al. 1989), and the proportion of time spent flying during foraging periods can have consequential impacts on an individual’s net energy budget (Collins et al. 2020), especially during reproductive periods (Stearns 1992; Welcker et al. 2015), when seabirds increase their foraging efforts (Gremillet 1997; Golet et al. 2004). During this period, there can be increases in an individuals’ net energy budgets through elevated energy intake, despite increased expenditure on movement. In situations where prey is abundant, seabirds have lower DEE and are more successful breeders (Jodice et al. 2002). Conversely, individuals must increase foraging effort (energy expenditure) when food is scarce to successfully raise and fledge chicks (Osborne et al. 2020).

The interactions among environmental conditions, individual quality, and energetics remain poorly understood. An individual’s energy budget for life-history allocation correlates positively with both environmental food supply (extrinsic) and the ability to capture prey (intrinsic) yet, individuals may demonstrate behavioral plasticity to adapt to changing environmental conditions and optimize energy budgets (Portugal et al. 2016; Dunn et al. 2020). Variation in individual quality is challenging to quantify and it is unclear whether unlimited food access would suppress the effects of individual quality on fitness or if the effect of individual quality on fitness would persist due to variation in physiological constraints or life-history strategies.

In breeding birds, reproductive success usually declines with time of nest initiation during the breeding season, both as a function of clutch size and of offspring survival; early breeders tend to have higher breeding success (Supp Fig. 2) (Perrins 1970; Verhulst and Nilsson 2008). In black-legged

kittiwakes (*Rissa tridactyla*; hereafter “kittiwakes”), the timing of egg laying becomes earlier with age (Coulson and White 1959) and later breeding is associated with reduced individual reproductive success (Goutte et al. 2014), suggesting that phenological variables such as timing of egg laying are related to individual quality.

We used an individual-based food supplementation field experiment to investigate the effects of breeding phenology, a trait linked to individual quality, and food supply on energy expenditure of kittiwakes. During the breeding season, kittiwakes are central place foragers and nest in large colonies (Daunt et al. 2002; Ainley et al. 2003). Kittiwakes are long-lived, sexually dimorphic, piscivorous seabirds that exhibit plasticity in foraging behavior to seek more profitable prey patches in times of limited prey availability (Coulson and Thomas 1985; Jodice et al. 2000; Chivers et al. 2012; Osborne et al. 2020). It is often assumed that energy allocation underlies life-history theory, with limited energy available for reproduction and other life processes driving tradeoffs between reproduction and other fitness components. However, a key assumption is that DEE is associated with breeding success, which we test here.

We used GPS-tracking to estimate DEE of control (naturally foraging) and food-supplemented kittiwakes during three years of low natural food supply (Piatt et al. 2020; Osborne et al. 2020). If high resource availability can compensate for low individual quality, we predict little variation in DEE among food-supplemented birds but higher energy expenditure among early-laying controls. However, if high resource availability cannot compensate for low individual quality, we predict that energy expenditure would be highest among early-laying kittiwakes in both treatment groups. Lastly, we tested for associations between DEE and breeding success by examining number of offspring produced and number of chicks fledged.

Materials and methods

This study was conducted at a kittiwake colony on Middleton Island (59° 26.7′ N, 146° 20.7′ W) in the Gulf of Alaska (USA) from May through August 2015, 2017 and 2018. Kittiwake nests are built on platforms that line the circumference of an abandoned U.S. Air Force radar tower (Jodice et al. 2002; Gill et al. 2002; Hatch 2013). Each nest and platform has a one-way window that can be opened from the inside, allowing researchers to access chick-rearing adults and chicks [detailed description in (Gill and Hatch 2002)]. Throughout the breeding season, we monitored every nest site twice daily to determine the timing of egg laying, hatching, fledgling, and chick mortalities. Adult kittiwakes were sexed via behavioral observations in the pre-breeding season (Jodice et al. 2000). For kittiwakes that hatched on the

tower, we defined adult age as the number of years since the individual hatched. For immigrants of unknown age, birds banded as adults, we estimated age as the number of years since the individual was first captured on the tower in addition to the average age at first capture [5 years; (Elliott et al. 2014c)]. Chick age was defined as the number of days since hatching at deployment; if two chicks were present at deployment, the age of the oldest chick was used.

We defined fledging success as the total number of chicks that fledged or that remained on the tower on the last day of field observations. Egg-laying date was recorded as the date that the first or single egg was laid. We also recorded adult and chick age as well as the number of chicks per nest.

Food supplementation

A subset of kittiwakes were given thawed fish (capelin, *Mallotus villosus*) at approximately 9:00, 14:00, and 18:00 and fed to satiety (hereafter “food-supplemented” individuals). Nests were on artificial nest sites that each had a food delivery mechanism [5 cm diameter PVC pipe that was cut in half and passed through the wall into the nest; described in (Gill and Hatch 2002)]. We collected data from 69 food-supplemented birds across all three years: 14 food-supplemented individuals in 2015, 24 food-supplemented individuals in 2017, and 31 food-supplemented individuals in 2018. Supplemental feeding began in early May in all three study years and continued until chicks fledged the nest (or breeding failure). The commencement of supplemental feeding corresponds with the pre-breeding period (~1 month prior to mean laying date) for this kittiwake population. As in previous studies (Gill and Hatch 2002; Welcker et al. 2015), all food-supplemented individuals consumed provided food but also foraged naturally. Individuals that were not supplementarily fed and solely relied on foraging at-sea were considered “control” individuals. We collected data from 98 control individuals: 7 control individuals in 2015, 46 control individuals in 2017, and 45 control individuals in 2018. While a subset of ~70 kittiwakes pairs were food-supplemented every year in the long-term food supplementation program, not all birds were included in this study because only a subset were fitted with GPS loggers.

GPS deployments

We collected GPS data from chick-rearing adults using two different types of devices. In 2015 i-gotU GPS loggers (GT-120, Mobile Action Technology, Taiwan; 15 g) were attached to the dorsal feathers of individuals using marine adhesive tape (TESA) and zip-ties in a way that did not interfere with flight; these continuously recorded location every 5 min until recapture, 24–48 h later. In 2017 and 2018, GPS (AxyTrek, Technosmart, EU; 8–12 g) were deployed on two

central rectrices with marine cloth tape and cable ties for 96 h; GPS fix rate was once every 3 min. Although sampling intervals varied between years, intervals of up to 300 s have minimal effect on measurement parameters of flight speed (Elliott et al. 2014a) and reducing location frequency can extend battery life (Osborne et al. 2020). GPS loggers were removed from their original casing and sealed in heat-shrink plastic tubing for waterproofing (Chivers et al. 2012). We attached GPS loggers with a mass range of 2–4% of the total body mass of individuals. Prior to release, birds were weighed (± 0.1 g using an Ohaus triple beam balance). Upon recapture, the birds were weighed again, and morphometric measurements were taken. In total, we obtained GPS data from 186 unique deployments ($n=98$ control; 69 food-supplemented). Some deployments were less than 24 h in duration due to early recapture or device failure and were, therefore, excluded from models of DEE and fledging success. The final dataset after excluding deployments shorter than 24 h was 168 trials ($n=99$ control; 69 food-supplemented).

Behavioral classification and foraging trip metrics

We used Residence in Space and Time models (Torres et al. 2017) to identify locations where kittiwakes exhibited area-restricted search behavior. Speed and distance from the colony was obtained from GPS data and used to classify movement behavior. Behavior categories included: flight (> 4 m/s), on colony (≤ 4 m/s and < 100 m from colony) and on water (≤ 4 m/s and ≥ 100 m from the colony) [methods adapted from Patterson et al. (2019)]. Time-activity budgets were calculated for every 24 h period during a deployment; data from incomplete days (< 24 h periods) were excluded (as above). We identified all departures from the colony (> 1 km) and calculated the duration (h), maximum distance from the colony (km), and nearest distance to the colony on the return leg (km) for each departure. We defined foraging trips as departures lasting at least 30 min, where individuals reached a maximum distance of at least 5 km. These distance and duration thresholds were necessary to exclude preening and loafing sites near the colony. We calculated the proportion of time spent on foraging trips for each deployment (sum of individual foraging trip durations divided by total duration of deployment). Then, we excluded incomplete foraging trips where the GPS device did not record a location within at least 10 km of the colony on the return trip ($n=702$ complete foraging trips, 288 by supplemented birds, 414 by control birds) before modeling trip duration and foraging distance.

Daily energy expenditure

To estimate DEE, we used time-activity budgets and activity-specific metabolic rates for Pacific black-legged

kittiwakes reported in Jodice et al. (2003). We converted the activity budget to hours by multiplying the proportion of time spent in each behavior by 24. We then multiplied by the cost of behaviors by the activity specific metabolic rates (flight: $(8.79 + 7.41)/2$ mL CO₂/g/h; on colony: 1.85 mL CO₂/g/h, on water: 2.27 mL CO₂/g/h) and converted the estimated CO₂ production to O₂ by dividing by the respiratory quotient (0.85). We converted mL O₂ into J by multiplying oxygen consumption and energy (20.1 J/mL O₂). Finally, the value was divided by 1000 to produce the units kJ/g/day. If the deployment was longer than one day, we averaged DEE across days to obtain one value per deployment.

Statistical analysis

We modeled the proportion of time spent in flight, on colony, and on water (using generalized linear mixed effects models, GLMM) and DEE (using linear mixed effects models, LMM) in response to food treatment (food-supplemented or control), study year (categorical), sex (female/male), relative laying date (clutch initiation date minus mean laying date of GPS-tagged birds in the study year). We controlled for body mass (mean of body mass at deployment and recapture), adult age (years; continuous), chick age (days; continuous), and number of chicks. We included an interaction term between food treatment and study year because the effect of food supplementation on reproductive success and behavior depends on annual environmental conditions (Gill et al. 2002; Gill and Hatch 2002). Finally, to test for drivers of reproductive success, we modeled the total number of chicks fledged (GLMM; Poisson distribution) in response to food treatment, DEE, study year, relative laying date, and an interaction between food treatment and DEE.

All data processing and statistical analysis was conducted in R (v 3.6.2 R Core Team, 2019). We used LMM and GLMM with bird identity as a random intercept. In models of foraging trip metrics, we also included a random effect of deployment ID because individuals could depart on multiple foraging trips during a single deployment. We fitted LMMs and binomial GLMMs with package *lme4* (Bates et al. 2015) and modeled proportional data with beta regression in package *glmmTMB* (Brooks et al. 2017). For LMMs, Kenward–Roger was used as an approximation for degrees of freedom and single term deletions were used to determine *p*-values [package *lmerTest*, (Kuznetsova et al. 2017)]. When we tested for an interactive effect that was non-significant, we removed the interaction term and tested for main effects only. For GLMMs, we used Type III Wald χ^2 tests to test for interactions; if the interaction term was

non-significant, we tested for main effects only with Type II Wald χ^2 tests. We modeled the overall proportion of time spent foraging (beta regression GLMM), foraging trip duration (LMM), and foraging distance (binomial GLMM) in response to food treatment, year, and a two-way interaction. Foraging trip duration was log-transformed to achieve a normal distribution. Maximum foraging distance followed an approximately tri-modal distribution, corresponding to three primary foraging patches used by the kittiwakes (~ 10 km, 40 km, and 100 km from the colony); we therefore defined foraging distances as short (< 50 km from colony) or long (> 50 km from colony).

Results

Foraging behavior

In all three years, most foraging trips occurred within 120 km of the breeding colony on Middleton Island (Fig. 1). Although there was some overlap across the foraging locations every year, each year has a distinct trend in foraging location (Fig. 1). Birds in 2017 almost exclusively flew north, compared to birds in 2018 which flew both north and south (Fig. 1). Overall, food-supplemented birds spent ~25% of their time on foraging trips, whereas control birds spent ~50% of their time on foraging trips (food treatment: -1.07 ± 0.12 ; $\chi^2_1 = 80.9$, $p < 0.0001$; Fig. 2a). The proportion of time spent on foraging trips did not vary significantly between years (food treatment*year: $\chi^2_2 = 3.59$, $p = 0.17$; year: $\chi^2_2 = 1.4$, $p = 0.50$). Foraging trips were shorter in duration among food-supplemented birds (-0.58 ± 0.10 h, $F_{1,134} = 33.88$, $p < 0.0001$; Fig. 2b), but trip duration did not vary across study years (food treatment*year: $F_{2,120} = 1.56$, $p = 0.21$; year: $F_{2,115} = 0.46$, $p = 0.63$). Control birds were more likely to undertake long distance foraging trips relative to supplemented birds (odds ratio: 6.4; treatment: $\chi^2_1 = 25.82$, $p < 0.0001$). Long trips were least likely in 2015, followed by 2018 (odds ratio: 1.1) then 2017 (odds ratio: 4.0; $\chi^2_2 = 13.2$, $p < 0.01$; Fig. S1), but the effect of food treatment on foraging distance did not depend on study year (food treatment*year: $\chi^2_2 = 3.65$, $p = 0.16$).

Time-activity budgets and daily energy expenditure

Food-supplemented birds spent less time flying, more time on the colony, but a similar amount of time on water (Fig. 3; Table 1). These differences in time-activity budgets resulted

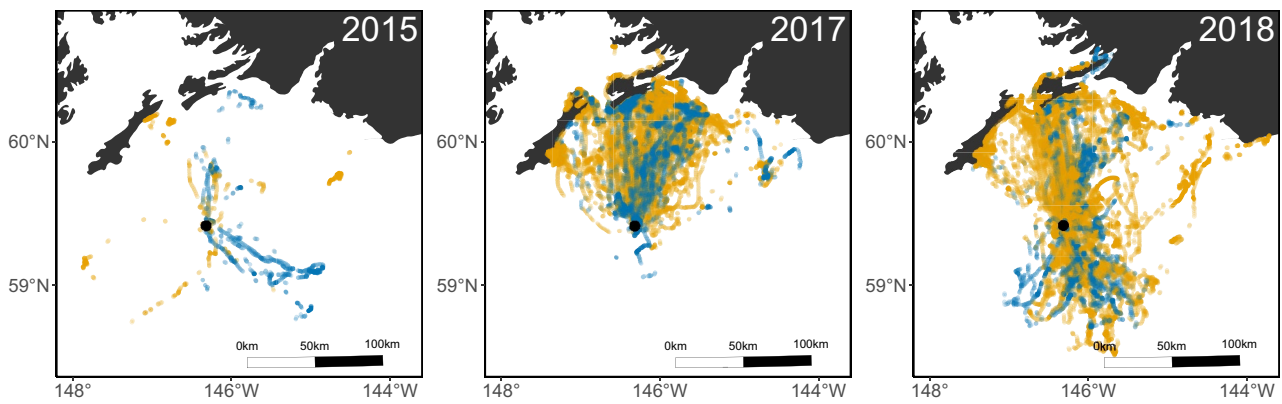
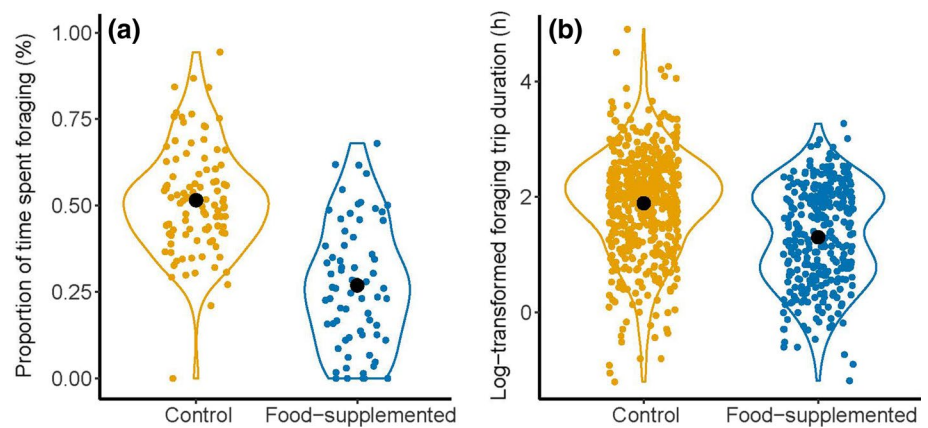


Fig. 1 Maps of foraging locations of food-supplemented (dark blue) and control (orange) black-legged kittiwakes tagged with GPS during chick-rearing in 2015 ($n=7$ control; 14 fed), 2017 ($n=46$ control; 24 fed), and 2018 ($n=45$ control; 31 fed). Black point indicates location of the Middleton Island breeding colony. Note that locations of food-

supplemented birds are overlaid on top of controls for visibility. In addition, two control birds also went to Icy Bay, Alaska (in 2015) and Glacier Bay, Alaska (in 2018) (outside the scope of the figure), which further demonstrates the greater energy expenditure in control birds

Fig. 2 Food-supplemented black-legged kittiwakes **a** spent a smaller proportion of time on foraging trips and **b** their individual foraging trips were shorter in duration, relative to controls. Violin plot indicates the distribution of data within each treatment group. Points show raw data (horizontal jitter added), where each point represents one individual of the entire GPS deployment in **(a)** and one foraging trip in **(b)**



in lower daily energy expenditure among food-supplemented than control birds (Table 2; Fig. 4). DEE was not associated with an interactive effect between food treatment and study year ($F_{2,149}=0.58, p=0.56$). Earlier breeders expended more energy than late breeders (Table 2). Additionally, males expended more energy than females (Table 2).

Breeding success

Food-supplemented birds fledged more chicks than the control birds (Table 3). Despite the annual variation, fledging success increased with food supplementation but not DEE ($\chi^2=0.01, df=1, p=0.92$) (Fig. 5).

Discussion

We used food supplementation and biologging to elucidate the effects of food availability and individual quality on movement and energy expenditure. We found that food-supplemented birds spent less time engaged in costly flight behavior, reducing their energy expenditure. We used biologging to confirm that the differences in energy expenditure between food-supplemented and control birds were driven by differences in time-activity budgets. Additionally, experimental food supplementation decreased natural foraging effort and increased breeding success in kittiwakes.

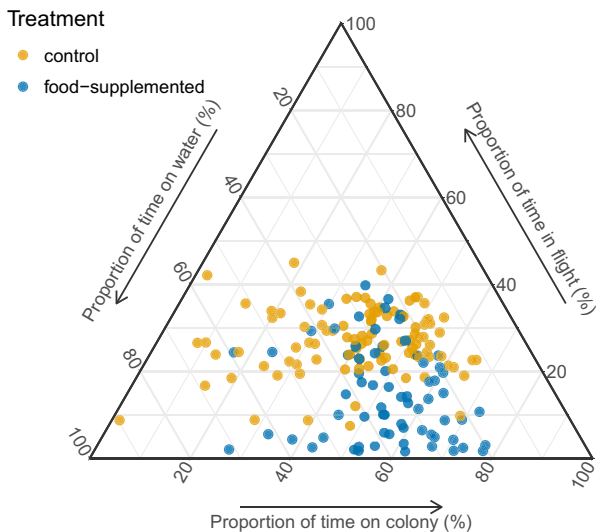


Fig. 3 Time-activity budgets showing the proportion of time that kittiwakes spent on the colony, in flight, and on water. Food-supplemented birds (dark blue) spent more time on the colony, less time in flight, but a similar amount of time on water, relative to controls (orange). Each point represents the time-activity budget of one individual over an entire GPS deployment

This result is consistent with previous supplementary feeding studies from our study site that show food-supplemented pairs fledge more chicks than controls (Gill and Hatch 2002; Whelan et al. 2020).

Across systems, early breeders often have greater breeding success (Perrins 1970; Verhulst and Nilsson 2008). In our study, within both the food-supplemented and control groups, we observed that early breeders expended more energy than late breeders. These ‘high quality’ birds also expended more energy regardless of food availability, supporting our prediction that only high-quality birds would sustain high levels of energy expenditure. In a previous long-term food-supplementation study, earlier breeders tended to have higher fledging success (Gill and Hatch 2002). However, in our study, laying date was not a predictor of fledging success among the GPS-tagged birds, likely because we only GPS-tagged birds that successfully hatched chicks, thus selecting for overall higher quality individuals. However, when we analyze the reproductive success of all the birds in the study years, including the birds that were GPS-tagged, we can see very strong effects of laying date on fledging success, where early breeders produce more fledglings (Supp Fig. 2).

Late-breeding birds appeared to have a lower energy ceiling (the balance between energy intake and expenditure), as seen by their lower energy expenditure, presumably

because they consume less energy themselves. Interestingly, food supplementation did not override this pattern, so access to prey resources is not the only factor underlying this relationship. However, we estimated DEE based only on time-activity budgets and previously published activity-specific metabolic rates, rather than direct measures via doubly labeled water. Access to unlimited resources may affect activity-specific metabolic rates (Trayhurn et al. 1982; Briga and Verhulst 2017; Halsey 2018). A recent study found that food-supplemented kittiwakes flew at slower airspeeds relative to controls during incubation (Lalla et al. 2020), suggesting that fine-scale flight behavior may be adjusted to food availability, which could influence the cost of flight. The low energy expenditure among food-supplemented birds observed in our study corresponds well with an earlier study that found lower energy expenditure in fed kittiwakes (Jodice et al. 2002). Furthermore, in our study males expended more energy than females, suggesting a need to compensate for higher energy demands by the heavier sex. Differences in energy expenditure between sexes were pronounced during past supplemental feeding experiments, which implies differences in reproductive roles and demands (Jodice et al. 2002).

Increased food supply decreased energy expenditure through changes in time-activity budgets. However, early breeders of higher quality expended more energy within both treatment groups, suggesting that high-quality individuals were spending energy to acquire greater resources. However, we did not find evidence that greater energy expenditure increased reproductive success. This paradox could indicate that high-quality individuals expend (and gain) more energy but invest it in self-maintenance and survival (e.g., body condition; Whelan et al. 2020) rather than reproduction.

Anthropogenic pressures will continue to change the energy landscape within the marine environment; it is important to consider how kittiwakes may adapt their reproductive strategies. As shown in our study, more time spent away from the nest and greater energy expended on flying has negative repercussions to breeding success, namely less chicks fledged. Similarly, Chivers et al. (2012) found that during breeding seasons with low prey availability near colonies, kittiwakes foraged at greater distances, spent more time away from the nest, and had lower breeding success rates relative to kittiwakes with access to prey closer to the colony. Changing food availability (Jodice et al. 2002), overfishing (Wanless et al. 2007), marine heat-waves (Frölicher and Laufkötter 2018), and ocean regime shifts (Birt-Friesen et al. 1989; Hatch 2013) will force seabirds to adjust their foraging patterns to ensure reproductive success.

Table 1 Model estimates for the proportion of time that kittiwakes spent in flight, on colony, and on water

Fixed effect	Estimate ± standard error	Degrees of freedom	χ^2	<i>p</i> -value
<i>Proportion of time in flight</i>				
(Intercept)	− 0.014 ± 0.582	–	–	–
Food treatment				
Control	0.72 ± 0.12	1	36.7	1.4 × 10 ^{−9}
Year				
2017	0.45 ± 0.15	2	9.6	0.0081
2018	0.29 ± 0.14			
Relative laying date	− 0.039 ± 0.011	1	13.7	0.00021
Sex				
Male	0.44 ± 0.11	1	16.1	6.1 × 10 ^{−5}
Adult age	− 0.0077 ± 0.0112	1	0.48	0.49
Adult mass	− 0.0051 ± 0.0013	1	15.7	7.5 × 10 ^{−5}
Number of chicks	0.12 ± 0.09	1	1.7	0.19
Chick age	− 0.018 ± 0.007	1	6.6	0.010
<i>Proportion of time on colony</i>				
(Intercept)	− 1.1 ± 0.6	–	–	–
Food treatment				
Control	− 0.56 ± 0.12	1	22.4	2.2 × 10 ^{−6}
Year				
2017	0.38 ± 0.15	2	6.6	0.036
2018	0.27 ± 0.14			
Relative laying date	0.0043 ± 0.0113	1	0.14	0.71
Sex				
Male	− 0.028 ± 0.121	1	0.055	0.82
Adult age	0.012 ± 0.013	1	0.91	0.34
Adult mass	0.0027 ± 0.0014	1	3.7	0.054
Number of chicks	− 0.0045 ± 0.1029	1	0.0019	0.97
Chick age	− 0.023 ± 0.007	1	9.6	0.0019
<i>Proportion of time on water</i>				
(Intercept)	− 0.52 ± 0.74	–	–	–
Food treatment				
Control	0.12 ± 0.11	1	1.2	0.27
Year				
2017	− 0.65 ± 0.12	2	29.0	5.0 × 10 ^{−7}
2018	− 0.41 ± 0.12			
Relative laying date	0.019 ± 0.010	1	3.7	0.054
Sex				
Male	− 0.22 ± 0.12	1	3.2	0.072
Adult age	− 0.013 ± 0.011	1	1.4	0.24
Adult mass	0.00017 ± 0.00164	1	0.011	0.92
Number of chicks	− 0.066 ± 0.090	1	0.55	0.50
Chick age	0.033 ± 0.007	1	24.8	6.4 × 10 ^{−7}

Proportion of time spent in each behavior was modeled via beta-regression

Table 2 Model estimates for daily energy expenditure (DEE) of kittiwakes

Fixed effect	Estimate ± standard error	F-value	degrees of freedom	p-value
(Intercept)	2.55 ± 0.30	–	–	–
Food treatment control	0.37 ± 0.06	37.5	1, 148	7.8 × 10 ⁻⁹
Year				
2017	0.17 ± 0.07	3.0	2, 141	0.055
2018	0.08 ± 0.07			
Relative laying date	-0.018 ± 0.006	10.1	1, 158	0.0018
Sex		9.3	1, 151	0.0027
Male	0.18 ± 0.06			
Adult age	-0.0034 ± 0.0063	0.3	1, 141	0.59
Adult mass	-0.0024 ± 0.006	14.2	1, 157	0.00023
Number of chicks	0.067 ± 0.052	1.6	1, 156	0.20
Chick age	-0.0069 ± 0.0038	3.3	1, 158	0.070

DEE was estimated using time-activity budgets and published activity-specific metabolic rates

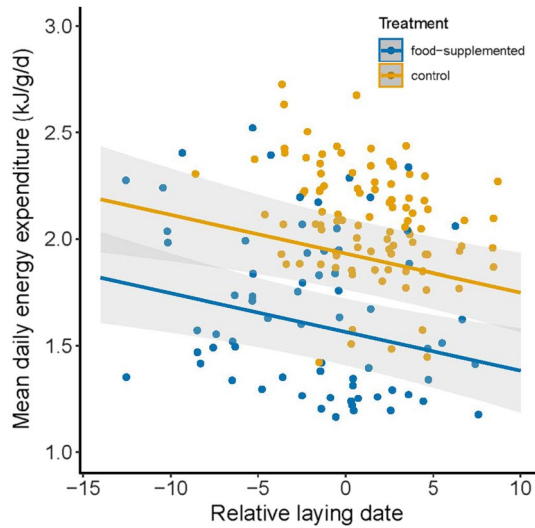


Fig. 4 Food-supplemented kittiwakes expended less energy per day than controls, and DEE was higher among early breeders, relative to late breeders. Lines represent model predictions and 95% confidence intervals (assuming mean continuous covariates of body mass, adult age, chick age, number of chicks; female sex, 2018 year). Points indicate raw estimates of DEE for each individual over the entire GPS deployment

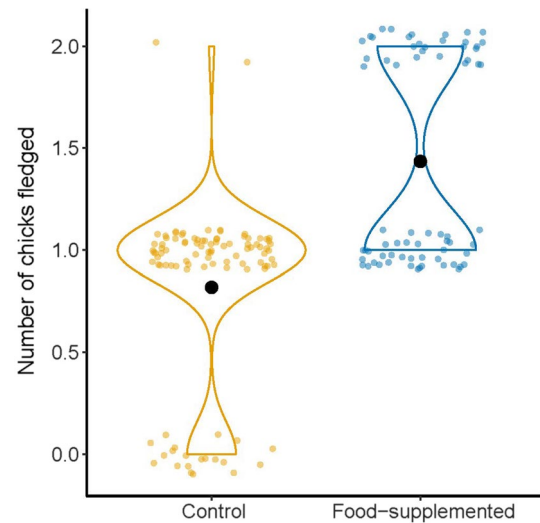


Fig. 5 Food-supplemented black-legged kittiwakes produced more fledglings than controls. Points show raw data (horizontal and vertical jitter added) and black point shows treatment mean over the study

Table 3 Model estimates for kittiwake fledging success (i.e., number of chicks fledged)

Fixed effect	Estimate ± standard error	χ ²	degrees of freedom	p-value
(Intercept)	0.21 ± 0.43	–	–	–
Daily energy expenditure	0.12 ± 0.24	0.25	1	0.62
Food treatment				
Control	-0.58 ± 0.20	8.3	1	0.0039
Year				
2017	-0.071 ± 0.235	0.16	2	0.92
2018	-0.090 ± 0.227			
Relative laying date	-0.0083 ± 0.0186	0.20	1	0.66

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Author contribution statement SRK-R, SW, JA, SAH, KHE, and SJ conceived and designed the experiments. SRK-R, SW, and JA conceived and developed the methodology. The formal analysis was conducted by SRK-R, SW, and JA while SRK-R, SW, SAH, and KHE curated the data. The investigation was conducted by SRK-R and SW. The funding acquisition was done by SRK-R, SAH, KHE, and SJ. The original draft was written by SRK-R, SW, and JA while all authors contributed to reviewing and editing the manuscript. The resources for this study were provided by SAH, KHE, and SJ. Lastly, KHE and SJ provided supervision.

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Availability of data and code Data and statistical code were uploaded as supplementary materials for review during the initial submission. If accepted, these will be published as supplementary materials.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Ethics approval All experiments were conducted in adherence with animal care protocols from the institutional affiliates in this study: University of Guelph (University of Guelph Animal Care Committee #3317) and McGill University (Animal Use Protocol #7599).

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References

- Ainley DG, Ford RG, Brown ED et al (2003) Prey Resources, competition, and geographic structure of kittiwake colonies in Prince William sound. *Ecology* 84:709–723. [https://doi.org/10.1890/0012-9658\(2003\)084\[0709:PRCAGS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0709:PRCAGS]2.0.CO;2)
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bautista LM, Tinbergen J, Wiersma P, Kacelnik A (1998) Optimal foraging and beyond: how starlings cope with changes in food availability. *Am Nat* 152:543–561. <https://doi.org/10.1086/286189>
- Birt-Friesen VL, Montevecchi WA, Cairns DK, Macko SA (1989) Activity-specific metabolic rates of free-living northern gannets and other seabirds. *Ecology* 70:357–367. <https://doi.org/10.2307/1937540>
- Briga M, Verhulst S (2017) Individual variation in metabolic reaction norms over ambient temperature causes low correlation between basal and standard metabolic rate. *J Exp Biol* 220:3280–3289. <https://doi.org/10.1242/jeb.160069>
- Brooks ME, Kristensen K, van Benthem KJ et al (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9:378–400. <https://doi.org/10.32614/RJ-2017-066>
- Chivers LS, Lundy MG, Colhoun K et al (2012) Foraging trip time-activity budgets and reproductive success in the black-legged kittiwake. *Mar Ecol-Prog Ser* 456:269–277. <https://doi.org/10.3354/meps09691>
- Collins PM, Green JA, Elliott KH et al (2020) Coping with the commute: behavioural responses to wind conditions in a foraging seabird. *J Avian Biol* 51:e02057. <https://doi.org/10.1111/jav.02057>
- Coulson JC, Thomas CS (1985) Changes in the biology of the kittiwake *Rissa tridactyla*: a 31-year study of a breeding colony. *J Anim Ecol* 54:9–26. <https://doi.org/10.2307/4617>
- Coulson JC, White E (1959) The Post-fledging mortality of the kittiwake. *Bird Study* 6:97–102. <https://doi.org/10.1080/00063655909475939>
- Daunt F, Benvenuti S, Harris MP et al (2002) Foraging strategies of the black-legged kittiwake *Rissa tridactyla* at a North Sea colony: evidence for a maximum foraging range. *Mar Ecol Prog Ser* 245:239–247. <https://doi.org/10.3354/meps245239>
- Dunn RE, Wanless S, Daunt F et al (2020) A year in the life of a North Atlantic seabird: behavioural and energetic adjustments during the annual cycle. *Sci Rep* 10:5993. <https://doi.org/10.1038/s41598-020-62842-x>
- Elliott KH, Chivers LS, Bessey L et al (2014a) Windscape shape seabird instantaneous energy costs but adult behavior buffers impact on offspring. *Mov Ecol* 2:17. <https://doi.org/10.1186/s40462-014-0017-2>
- Elliott KH, Le Vaillant M, Kato A et al (2014b) Age-related variation in energy expenditure in a long-lived bird within the envelope of an energy ceiling. *J Anim Ecol* 83:136–146. <https://doi.org/10.1111/1365-2656.12126>
- Elliott KH, O'Reilly KM, Hatch SA et al (2014c) The prudent parent meets old age: A high stress response in very old seabirds supports the terminal restraint hypothesis. *Horm Behav* 66:828–837. <https://doi.org/10.1016/j.yhbeh.2014.11.001>
- Gill VA, Hatch SA (2002) Components of productivity in black-legged kittiwakes *Rissa tridactyla*: response to supplemental feeding. *J Avian Biol* 33:113–126. <https://doi.org/10.1034/j.1600-048X.2002.330201.x>
- Gill VA, Hatch SA, Lanctot RB (2002) Sensitivity of breeding parameters to food supply in Black-legged Kittiwakes *Rissa tridactyla*. *Ibis* 144:268–283. <https://doi.org/10.1046/j.1474-919X.2002.00043.x>
- Golet GH, Schmutz JA, Irons DB, Estes JA (2004) Determinants of reproductive costs in the long-lived Black-legged Kittiwake: a multiyear experiment. *Ecol Monogr* 74:353–372. <https://doi.org/10.1890/02-4029>
- Goutte A, Angelier F, Bech C et al (2014) Annual variation in the timing of breeding, pre-breeding foraging areas and corticosterone levels in an Arctic population of black-legged kittiwakes. *Mar Ecol Prog Ser* 496:233–247. <https://doi.org/10.3354/meps10650>
- Gremillet D (1997) Catch per unit effort, foraging efficiency, and parental investment in breeding great cormorants (*Phalacrocorax carbo carbo*). *ICES J Mar Sci* 54:635–644. <https://doi.org/10.1006/jmsc.1997.0250>
- Halsey LG (2018) Keeping slim when food is abundant: what energy mechanisms could be at play? *Trends Ecol Evol* 33:745–753. <https://doi.org/10.1016/j.tree.2018.08.004>

- Hatch SA (2013) Kittiwake diets and chick production signal a 2008 regime shift in the Northeast Pacific. *Mar Ecol-Prog Ser* 477:271. <https://doi.org/10.3354/meps10161>
- Jodice PGR, Lanctot RB, Gill VA et al (2000) Sexing adult black-legged kittiwakes by DNA, behavior, and morphology. *Waterbirds* 23:405–415. <https://doi.org/10.2307/1522177>
- Jodice PGR, Roby DD, Hatch SA et al (2002) Does food availability affect energy expenditure rates of nesting seabirds? A supplemental-feeding experiment with Black-legged Kittiwakes (*Rissa tridactyla*). *Can J Zool* 80:214–222. <https://doi.org/10.1139/Z01-221>
- Jodice PGR, Roby DD, Suryan RM et al (2003) Variation in energy expenditure among black-legged kittiwakes: effects of activity-specific metabolic rates and activity budgets. *Physiol Biochem Zool* 76:375–388. <https://doi.org/10.1086/375431>
- Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest Package: Tests in Linear Mixed Effects Models. *J Stat Softw* 82:1–26. <https://doi.org/10.18637/jss.v082.i13>
- Lalla KM, Whelan S, Brown K et al (2020) Accelerometry predicts muscle ultrastructure and flight capabilities in a wild bird. *J Exp Biol* 223:jeb234104. <https://doi.org/10.1242/jeb.234104>
- Laskowski KL, Moiron M, Niemela PT (2021) Integrating behavior in life-history theory: allocation versus acquisition? *Trends Ecol Evol* 36:132–138. <https://doi.org/10.1016/j.tree.2020.10.017>
- McAdam AG, Boutin S (2003) Effects of food abundance on genetic and maternal variation in the growth rate of juvenile red squirrels. *J Evol Biol* 16:1249–1256. <https://doi.org/10.1046/j.1420-9101.2003.00630.x>
- Osborne OE, O'Hara PD, Whelan S et al (2020) Breeding seabirds increase foraging range in response to an extreme marine heatwave. *Mar Ecol-Prog Ser* 646:161–173. <https://doi.org/10.3354/meps13392>
- Patterson A, Gilchrist HG, Chivers L et al (2019) A comparison of techniques for classifying behavior from accelerometers for two species of seabird. *Ecol Evol* 9:3030–3045. <https://doi.org/10.1002/ece3.4740>
- Perrins CM (1970) The timing of birds' breeding seasons. *Ibis* 112:242–255. <https://doi.org/10.1111/j.1474-919X.1970.tb00096.x>
- Piatt JF, Parrish JK, Renner HM et al (2020) Extreme mortality and reproductive failure of common murrelets resulting from the northeast Pacific marine heatwave of 2014–2016. *PLoS ONE* 15:e0226087. <https://doi.org/10.1371/journal.pone.0226087>
- Portugal SJ, Green JA, Halsey LG et al (2016) Associations between resting, activity, and daily metabolic rate in free-living endotherms: no universal rule in birds and mammals. *Physiol Biochem Zool* 89:251–261. <https://doi.org/10.1086/686322>
- Stearns S (1992) The evolution of life histories. Oxford University Press, Oxford
- Torres LG, Orben RA, Tolkova I, Thompson DR (2017) Classification of Animal Movement Behavior through Residence in Space and Time. *PLoS ONE* 12:e0168513. <https://doi.org/10.1371/journal.pone.0168513>
- Trayhurn P, Douglas JB, McGuckin MM (1982) Brown adipose tissue thermogenesis is “suppressed” during lactation in mice. *Nature* 298:59–60. <https://doi.org/10.1038/298059a0>
- Verhulst S, Nilsson J-A (2008) The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. *Philos Trans R Soc B-Biol Sci* 363:399–410. <https://doi.org/10.1098/rstb.2007.2146>
- Wanless S, Frederiksen M, Daunt F et al (2007) Black-legged kittiwakes as indicators of environmental change in the North Sea: evidence from long-term studies. *Prog Oceanogr* 72:30–38. <https://doi.org/10.1016/j.pocean.2006.07.007>
- Welcker J, Harding AMA, Kitaysky AS et al (2009) Daily energy expenditure increases in response to low nutritional stress in an Arctic-breeding seabird with no effect on mortality. *Funct Ecol* 23:1081–1090. <https://doi.org/10.1111/j.1365-2435.2009.01585.x>
- Welcker J, Speakman JR, Elliott KH et al (2015) Resting and daily energy expenditures during reproduction are adjusted in opposite directions in free-living birds. *Funct Ecol* 29:250–258. <https://doi.org/10.1111/1365-2435.12321>
- Whelan S, Hatch SA, Irons DB et al (2020) Increased summer food supply decreases non-breeding movement in black-legged kittiwakes. *Biol Lett* 16:20190725. <https://doi.org/10.1098/rsbl.2019.0725>
- Wilson AJ, Nussey DH (2010) What is individual quality? An evolutionary perspective. *Trends Ecol Evol* 25:207–214. <https://doi.org/10.1016/j.tree.2009.10.002>