

## Why timing is everything: Energetic costs and reproductive consequences of resource mismatch for a chick-rearing seabird

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**Abstract.** Timing reproduction to overlap with peak prey availability is vital to success for many species. This may be especially true for species that rely on one or a few prey species that exhibit strong seasonal peaks in abundance. Any mismatch must be mediated by parents that provision offspring through flexible behavioral changes within the bounds of their physiological tolerances. In Newfoundland, common murre *Uria aalge* breeding coincides with the inshore movement of capelin *Mallotus villosus*—their primary prey—such that peak prey availability overlaps with chick-rearing, the most energy demanding phase of breeding. We use colony-based observations and temperature-depth recorders to track the behavioral responses of murrelets to temporal match and mismatch with capelin availability. Activity budgets, daily energy expenditure (DEE) and chick-provisioning rates were constant across years when chick and capelin timing matched. However, when capelin were late, despite increasing diving effort and DEE, parents delivered fewer fish to chicks per day and reduced breeding success was observed. While parents partially buffered the effects of variable capelin abundance by reducing co-attendance time (time spent at the colony with mates) and increasing foraging time, physiological constraints on energy output likely limited their ability to maintain chick-provisioning rates in a mismatch year. Such responses could have demographic consequences if ocean climate changes decouple the timing of chick-rearing and prey availability.

**Key words:** activity budget; behavioral flexibility; energy ceiling; forage fish; *Mallotus villosus*; match-mismatch; Northwest Atlantic; ocean climate change; parental effort; prey availability; *Uria aalge*.

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### INTRODUCTION

Birds that rely on seasonally abundant prey have a limited window to reproduce and, as such, time breeding to coincide with seasonal peaks in food availability (Lack 1954, Perrins

1970). Climate changes, however, are disrupting trophic interactions by altering prey phenology and generating mismatch between peak food supply and energetic demand for predators that fail to adjust their phenology accordingly (Visser et al. 1998, 2011). Mismatches between food

supply and energy demand must be mitigated by parents, affecting foraging costs and individual fitness (Thomas et al. 2001). The match-mismatch hypothesis predicts that reproductive success will be high when the adult's most energetically demanding phase of breeding matches peak prey availability (Cushing 1990, Durant et al. 2005). This hypothesis is of great interest today as there is growing concern that climate change is increasing the severity and frequency of phenological mismatch, thereby disrupting trophic interactions and population dynamics (Thackeray et al. 2010).

Predicting how any one system will be affected by climate driven asynchrony is difficult because responses vary by species, population and habitat. While increasing mismatch has reduced fitness and caused population declines for some species (Both et al. 2006, 2010, Saino et al. 2011, Reed et al. 2013), there are no apparent fitness consequences for others (Drever and Clark 2007, Dunn et al. 2011, Vatka et al. 2011). Selective forces ultimately dictate specific responses; reproductive timing will be under direct natural selection if mismatch limits a species' ability to successfully raise their young. Conversely, mismatch may be adaptive if selection is acting on another life-history trait (e.g., egg production; Visser et al. 2011). In either case, sufficient resources have to be available to sustain reproductive costs, whether they be for egg production or chick provisioning. The economics of parental foraging is therefore a key selective force shaping the evolution of seasonal breeding in birds (Thomas et al. 2001).

Species that rely heavily on one or a few prey species while breeding, such as many seabirds, may be particularly vulnerable to strong temporal mismatch since the availability of key prey species is vital to successful reproduction (Regehr and Montevecchi 1997, Durant et al. 2003, Hipfner 2008, Gaston et al. 2009, Watanuki et al. 2009). Indeed, population consequences have been documented in such systems (Both et al. 2006). Parental common murres *Uria aalge* breeding at Newfoundland colonies primarily rely on capelin *Mallotus villosus* for self-sustenance and chick provisioning (Piatt 1987, Wilhelm et al. 2003, Burke and Montevecchi 2008). Owing to this dependence, hatching generally coincides with the inshore movements of matur-

ing schools of capelin such that peak prey availability overlaps with the chick-rearing period, the murres' most energetically demanding phase of breeding (Cairns et al. 1987, Carscadden et al. 2002). Chick-provisioning rates, fledging weights and success therefore depend on the timing and abundance of capelin (Burger and Piatt 1990, Davoren and Montevecchi 2003b). Though flexible time budgeting allows common murres to maintain chick feeding rates across a wide range of prey densities (Harding et al. 2007), there are limits to their flexibility and mismatch with capelin can override their buffering capabilities (Wilhelm et al. 2008). Harding et al. (2007) showed that when prey density was low murres reduced co-attendance time (time mates spent together at the colony) and increased foraging time (time at sea) by more than 2 hr/day. In the northeast Atlantic, murres spent this extra time diving in an attempt to compensate for low prey abundance (Monaghan et al. 1994). Mistiming breeding in the northwest Atlantic would equate to low prey abundance inshore, however, the migratory behavior of capelin could mean that prey are in fact abundant further from the colony (Nakashima 1992). In Newfoundland, breeding murres could increase flying time to compensate for mismatch with peak inshore capelin availability. This strategy, however, may be difficult to sustain as murres experience the highest flight costs of any volant species and operate near physiological limits (Elliott et al. 2013b).

Though the mechanism remains unclear, sustainable energy budgets of vertebrates are generally limited to  $\leq 7$  times basal metabolic rate (BMR; Weiner 1992, Hammond and Diamond 1997, Speakman and Król 2011). Metabolic rates in excess of  $7 \times$  BMR can of course be achieved in the short-term, but such expenditures must be fuelled by lipid reserves and not concurrent energy intake (Hammond and Diamond 1997). Chick-rearing thick-billed murres *Uria lomvia* are thought to be operating near maximum intensity, leaving a small buffer between performance and capacity (Elliott et al. 2013b). Thus, continued investment in chick-rearing comes at a cost to lipid reserves if poor conditions force expenditures beyond sustainable limits. Handicap studies have shown that thick-billed murres either reduce investment in their offspring to maintain

energetic capability *or* they reduce investment in themselves by running energetic deficits (meta-analysis in Elliott et al. 2013b). The natural handicap generated by resource mismatch could impose a similar effect. The question then remains whether common murres will reduce investment in offspring or themselves when capelin timing and chick-rearing are decoupled? Moreover, how do behavioral responses and physical limitations interactively influence this decision? Here we present an analysis of parental murre behavior at the colony and at sea in response to mismatch with prey and we attempt to uncover the mechanistic links between behavior and prey availability.

## METHODS

### *Study site and field methods*

Archival temperature-depth recorders (TDRs; <5 g, Lotek LTD 1110, LAT 1500 or 2500 from Lotek Wireless, Canada) were deployed on chick-rearing common murres during July and August, 2007–2010 at Gull Island (47.26° N, 52.78° W), Witless Bay Ecological Reserve, Newfoundland, Canada (~100,000 breeding pairs in the reserve; Canadian Wildlife Service unpublished data). Adults were captured using a telescopic noose pole and were equipped with an archival tag secured to a plastic leg band (Pro-Touch Engraving, Canada) and attached to the left leg; a Canadian Wildlife Service metal band was attached to the right leg. TDRs were set to record temperature (accuracy < 0.2°C) and depth (accuracy < 1 m) every 2 s for each dive. A total of 39 TDRs were deployed of which 32 were retrieved (~3 days later [range 2–7 days]), 27 were successfully downloaded, and 25 captured chick-rearing foraging activity ( $N_{2007} = 3$ ,  $N_{2008} = 5$ ,  $N_{2009} = 12$ ,  $N_{2010} = 5$ ). Birds were weighed during each interaction using a Pesola scale. Handling time was ~3 min and ~6 min during logger deployment and recapture, respectively.

At the same site, ~50 focal breeding sites were observed each year from a bird blind situated <10 m from a large colony on the island (site 1; Mahoney 1979). Feeding and productivity watches were conducted to calculate prey delivery rates and fledging success, respectively. Feeding watches were conducted during daylight hours (~05:00 to 21:00; most spanned this period) and focused

on a subset of breeding sites (~10) that were continuously observed. Pairs in which individuals could be distinguished (e.g., bridled/un-bridled, banded/un-banded pairs) were observed preferentially; the time of arrival, change-over and departure were recorded. It was also noted whether a bird arrived with prey, and if so, the species was recorded. For productivity watches, the breeding status of each focal pair (unknown, empty, egg, chick) were noted nearly every day between the late egg laying and late fledging periods. Murre chicks were considered fledged if they disappeared from their nest site at  $\geq 16$  days of age – the minimum fledging age for murre chicks at Gull Island (Mahoney 1979). Hatching and/or fledging success was undetermined for many pairs that were difficult to observe from the blind. Productivity data at site 1 was supplemented with data from another site on the southeastern corner of Gull Island. At both sites, hatching and breeding success may be slightly biased as observations typically began in late-June, following the laying of most eggs; as such, losses of earlier eggs may have been missed.

### *Capelin timing and abundance*

Though quantitative data on the timing and abundance of capelin in the Witless Bay area are not available, data collected by Fisheries and Oceans Canada (DFO) on capelin spawning times and spring abundance were used as a rough index. The timing of capelin spawning has been monitored by DFO in Trinity Bay at Bellevue Beach, approximately 80 km from Gull Island, since the 1990s (DFO 2013). It is likely that capelin timing is relatively consistent between the sites as spawning has been shown to be synchronous at such a scale (Frank and Leggett 1981, Leggett et al. 1984). We therefore assume that the start and end of spawning activity at Bellevue Beach approximates the period during which capelin were available inshore to murres rearing chicks at Gull Island. Our proxy for capelin abundance involved the assumption that local abundance varied in accordance with abundance estimated annually from spring surveys conducted by DFO on the Grand Bank (see Mowbray 2013 for methods).

### *Data analysis*

The data collected in this study were processed

using R (R Core Team 2013) and analyzed using OpenBUGS (Lunn and Spiegelhalter 2009) via the R2OpenBUGS function in R (Sturtz et al. 2005); model building was largely guided by Kéry (2010). Credible intervals (95%) for all estimates were derived from the 2.5% and 97.5% quantiles of the MCMC results generated in OpenBUGS. Five chains were run concurrently with 15,000 repetitions, a burn in period of 5,000 and a thinning of 10. Each estimated variable had a Rhat value of 1.0 (where 1 is equivalent to convergence). Vague priors were used for all parameters. Here we consider a trend or difference “significant” if the credible interval of a parameter or contrast does not bound zero.

Activity budgets (proportion of time spent at the colony, sitting on water, diving and flying) were calculated for each logged individual on a daily basis using methods similar to Tremblay et al. (2003). To ensure typical activity budgeting was captured, the analysis was limited to days in which individuals were tracked for >12 h. Compositional data, such as activity budgets, are peculiar because the components sum to 1; attempts to apply statistical methods designed for unconstrained data may therefore lead to inappropriate inference. To account for this numerical constraint, we use a Dirichlet mixed model (log link) with activity budget set as the response, date and year set as explanatory variables and individual set as a random effect. As the multivariate generalization of the beta distribution, the Dirichlet distribution is quite useful for analyzing compositional data (Hijazi and Jernigan 2009). Applying this distribution allows for the simultaneous assessment of the effects of covariates on the relative contribution of multiple activities (Gueorguieva et al. 2008). So for year  $i$ , bird  $j$ , activity  $k$  and day  $x_{ij}$  we fit the following model for the observed vector of proportions  $p_{ijk} = p_{ij1}, \dots, p_{ij4}$ :

$$\text{Distribution} = p_{ijk} \sim \text{Dirichlet}(\alpha_{ijk})$$

$$\text{Linear predictor: } \log(\alpha_{ijk}) = \beta_{1,ijk} + \beta_{2,ijk} \times x_{ij}$$

$$\text{Random effects: } \beta_{1,ijk} \sim \text{Normal}\left(\mu_{\beta_1(ik)}, \sigma_{\beta_1(ik)}^2\right)$$

$$\beta_{2,ijk} \sim \text{Normal}\left(\mu_{\beta_2(ik)}, \sigma_{\beta_2(ik)}^2\right).$$

Random intercepts and slopes (hyperparameters) were applied to account for repeated measures across the same individuals (Schielzeth and Forstmeier 2009). This model was simplified using the following logic: (1) if there was a lack of covariance in slopes, the contrasting factor(s) were analyzed separately; (2) if there were no clear temporal trends in the global model or sub-models, day was removed as a covariate; and (3) if there were no annual differences, year was removed as a covariate.

The same covariates and model simplification rules were used to model trends in daily energy expenditure (DEE), diving frequency (dives/day), co-attendance time (hr/day), prey delivery rate (feeds/day) and prey composition (percent capelin). To estimate DEE, we first calculate total energy expenditure from the activity budgets of each bird for each day using the highest ranked activity specific energy expenditure model presented in Table 1 of Elliott et al. (2013a) for thick-billed murre. These values were scaled to DEE by dividing total energy expenditure by the proportion of the day captured by the TDR. Likewise, co-attendance time was scaled to hr/day by dividing the observed duration by the proportion of the day observed through feeding watches (feeding watches < 8 hr in duration were excluded). Both DEE and co-attendance time were analyzed using linear mixed models. Diving frequency and the number of prey delivered were analyzed using generalized linear mixed models with a Poisson error structure (log link); proportion of the day observed was used as an offset (feeding watches < 8 hr in duration were excluded) to scale the response to dives/day and feeds/day. Our prey composition analysis was limited to identified prey items from all feeding watches across all individuals; since capelin and sandlance, *Ammodytes* spp., constitute 99.7% of observed prey items (379/380; only one unidentified flatfish was delivered in 2010), these data were analyzed using a generalized linear model (binomial error, logit link) with proportion of capelin set as the response. Finally, hatching, fledging (proportion of chicks fledged), and breeding success (proportion of eggs resulting in fledged chicks) were analyzed using generalized linear models (binomial error, logit link) with year as the only explanatory variable.



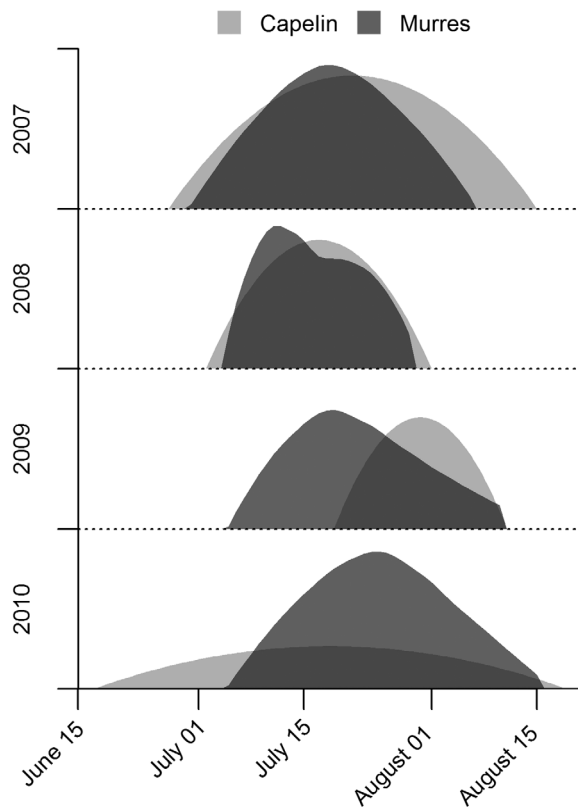


Fig. 1. Diagram of the timing and relative abundance of capelin and common murre chicks across years. Capelin curves were generated from best available proxies for local timing and abundance (see *Methods*), and murre chick curves were derived from direct observations conducted on Gull Island, Witless Bay Ecological Reserve, Newfoundland.

## RESULTS

Based on spawning times at Bellevue Beach, capelin were presumed to be inshore and therefore available to murres throughout the chick-rearing period at Gull Island in all years, except 2009 (Fig. 1). During 2009, chicks hatched before the onset of capelin spawning; capelin availability probably increased mid-way through the chick-rearing period (Fig. 1). Estimates of capelin spring abundance on the Grand Bank were similar from 2007 to 2009 (262,200–300,500 t), but dropped 10-fold in 2010 (23,200 t); we therefore assume that this translates into a large, perhaps 10-fold, decrease in inshore capelin abundance (Fig. 1).

Activity budgets, dive rates and DEE were obtained from 24 birds ( $N_{2007} = 2$ ,  $N_{2008} = 5$ ,  $N_{2009} = 12$ ,  $N_{2010} = 5$ ) across 25 unique dates ( $N_{2007} = 4$ ,  $N_{2008} = 4$ ,  $N_{2009} = 10$ ,  $N_{2010} = 7$ ), and co-attendance time and prey delivery rates were obtained from 66 sites ( $N_{2007} = 19$ ,  $N_{2008} = 20$ ,  $N_{2009} = 14$ ,  $N_{2010} = 13$ ) across 20 unique dates ( $N_{2007} = 7$ ,  $N_{2008} = 4$ ,  $N_{2009} = 6$ ,  $N_{2010} = 3$ ). Global models revealed that 2009 was the only year exhibiting significant within-season change in the proportion of time spent diving, diving rates, DEE and chick feeding rates; prey composition and co-attendance time were apparently constant through time in all years. Activity budgets, diving rates, DEE and feed rates were similar during 2007, 2008 and 2010 (Fig. 2a). From 2007 to 2010, chick-rearing common murres spent 51% (credible interval = 36–65%) of their time at the colony, 39% (credible interval = 26–53%) of their time sitting on the water, and just 6% (credible interval = 5–9%) and 5% (credible interval = 4–8%) of their time diving and flying, respectively. Each day, birds performed 52 dives (credible interval = 39–68 dives/day) and provided chicks with 2.8 prey (credible interval = 2.4–3.2 prey/day). Their activities resulted in an average DEE of 1969.9 KJ/day (credible interval = 1761.0–2184.0 KJ/day); this value is not far from their theoretical upper limit to sustainable energy expenditure of  $7 \times \text{BMR}$  ( $7 \times 350 = 2450$  KJ/day; Cairns et al. 1990). Annual co-attendance time ranged from a high of 4.9 hr/day (credible interval = 4.0–5.8 hr/day) during 2008 to just 1.4 hr/day (credible interval = 0.9–1.8 hr/day) during 2009. Co-attendance time increased by 2.3 hr/day (credible interval = 1.0–3.6 hr/day) between 2007 and 2008, it decreased by 3.5 hr/day (credible interval = 2.5–4.5 hr/day) from 2008 to 2009, and it was similar from 2009 to 2010 (–0.1 hr/day [credible interval = –0.9 to 0.7 hr/day]). The proportion of capelin fed to chicks was 99% (141/142), 99% (90/91), 97% (118/121) and 90% (47/52) for 2007, 2008, 2009, and 2010, respectively (Fig. 3). Contrasts revealed that percent capelin was significantly different only in 2007 and 2010, when it was reduced by 9% (credible interval = –2 to –18%).

During 2009, chick-rearing murres initially spent ~15% of their time diving, but gradually decreased diving effort to ~2% later in the season (–0.4/day [credible interval = –0.6 to –0.2/day]; Fig. 2b). Diving frequency was concurrently

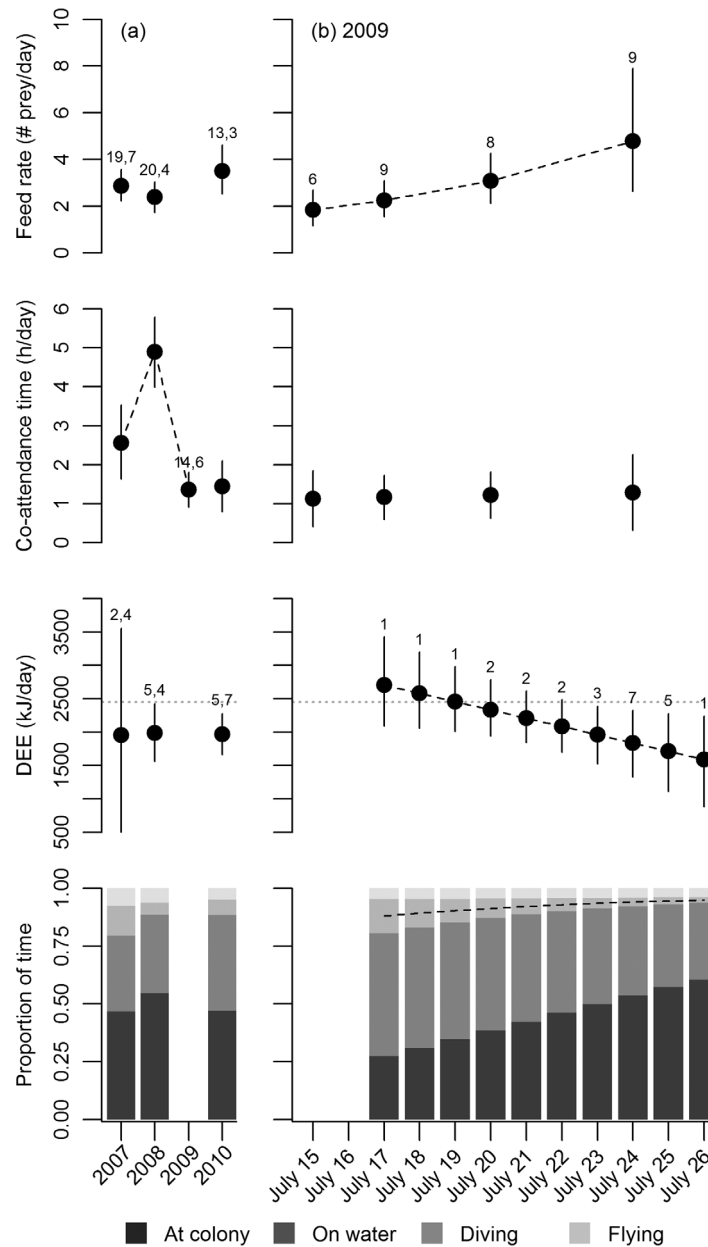


Fig. 2. Estimates of feed rates, co-attendance time, daily energy expenditure (DEE) and proportion of time spent at the colony, sitting on the water, diving and flying by chick-rearing common murres (a) across all years and (b) during 2009. Values indicate sample size (birds/sites, days) and dashed lines indicate significant trends. Grey dotted line indicates theoretical upper limit to sustainable energy expenditure ( $7 \times$  BMR of 350 KJ/day; Cairns et al. 1990).

reduced from  $\sim 100$  to  $\sim 20$  dives/day ( $-28\%$ /day  $-8.0$  KJ/day]) and an increase in chick feed rates from  $\sim 2$  to  $\sim 4$  fish/day (10 %/day [credible interval = 3–18%/day]; Fig. 2b). The proportion of time spent flying and co-attendance time was constant through the season (Fig. 2b). Coinci-

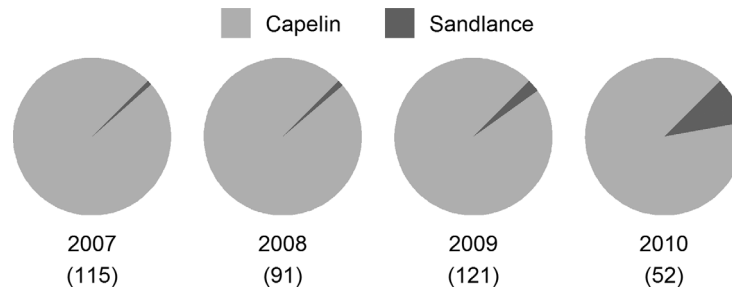


Fig. 3. Proportion of capelin and sandlance in chick diets at Gull Island from 2007 to 2010. Sample size indicated in brackets.

dently, hatching, fledging and breeding success in 2009 was reduced relative to 2008 (Fig. 4), declining from 72% to 55% ( $-17\%$  [credible interval =  $-3$  to  $-30\%$ ]), from 88% to 55% ( $-33\%$  [credible interval =  $-17\%$  to  $-49\%$ ]) and 62% to 29% ( $-33\%$  [credible interval =  $-19\%$  to  $-47\%$ ]), respectively.

## DISCUSSION

While this research adds to the growing body of literature showing that flexible time budgets allow parental common murres to maintain chick feed rates across a wide range of local prey densities (Burger and Piatt 1990, Monaghan et al. 1994, Uttley et al. 1994, Harding et al. 2007, Wilhelm et al. 2008), it also highlights a staggering stability in foraging effort and daily energy expenditure across a wide range of conditions. It was only during severe mismatch with peak prey availability that limits to behavioral flexibility were apparent. When capelin arrived late in 2009, murres rearing chicks could not buffer chick provisioning rates despite increasing diving effort (cf. Monaghan et al. 1994). Contrary to expectation, they did not increase time spent flying, even though capelin were presumably more abundant offshore. High flight costs coupled with low dive costs (Elliott et al. 2013a) likely contribute to their apparent inability to increase flight time. Time and energy budget models postulate that foraging range has a strong influence on the ability of thick-billed murres to sustain the demands of chick-rearing (Houston et al. 1996). If the same applies to chick-rearing common murres, this could imply that flying time is highly constrained during chick-rearing. Increasing underwater search time must be the

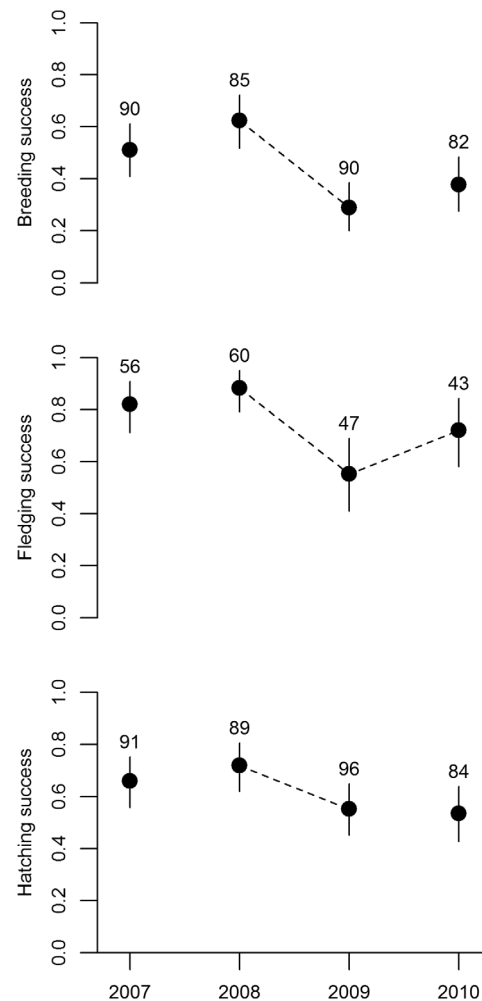


Fig. 4. Estimates of hatching, fledging and breeding success of common murres from 2007 to 2010. Values indicate sample size and dotted lines indicate significant trends.

more beneficial and economical foraging strategy.

Much of the murre's ability to buffer the effects of variable prey abundance is derived from flexible leisure time at the colony (minimum  $\approx$  45 min/day, maximum  $\approx$  3 hr/day) such that chick-rearing murre's can increase foraging time by up to 2 hr/day when prey abundance is low (Harding et al. 2007). If they spend this extra time flying, they would expend 1065 KJ, whereas 2 hr worth of diving would cost only 194 KJ (expenditures calculated using activity-specific rates [148 and 27 watts for flying and diving, respectively] from model 8, Table 1 in Elliott et al. 2013b). Though increased flight time may improve access to capelin, the associated costs could quickly outweigh the benefits. These extra costs would result in a DEE of 3035 KJ equating to nearly  $8.5 \times$  BMR (350 KJ/day; Cairns et al. 1990). A recently developed bio-energetics model for common murre's echoes the dramatic energetic consequences of increased flight time in response to dispersed prey (Thaxter et al. 2013).

Generally, vertebrates are unable to sustain energy budgets exceeding  $7 \times$  BMR, as very few species are capable of assimilating such large quantities of energy per day. The only way to afford such energy expenditure, if at all, would be to resort to running short-term energy deficits by utilizing lipid reserves (Weiner 1992, Hammond and Diamond 1997), a strategy adopted by the procellariiformes whose low wing-loading enables storage of substantial onboard lipid reserves (Chaurand and Weimerskirch 1994, Weimerskirch 1998). Such a strategy would be unsustainable in the long-term for species such as murre's that have limited capacity to store lipid (Jacobs et al. 2011), providing no fitness benefit to either the parent or chick. Increasing underwater search effort for sparse inshore capelin, or alternate prey, may be their only viable option.

Chick-rearing murre's have to consume substantial quantities of food each day to meet their energy demands (Cairns et al. 1990). Because foraging trips are short and flight costs are high, natural selection has favored rapid digestion – at the expense of digestive efficiency – to minimize mass retained and maximize energy turnover (Hilton et al. 2000a, 2000b). The reduction in digestive efficiency likely limits the murre's capacity to metabolize energy on a daily scale,

thereby imposing an energy ceiling ( $\sim$ 2000 KJ/day; Elliott et al. 2013b). In other words, the digestive track's capacity to assimilate food into energy constrains energy input which in turn imposes a ceiling on sustainable energy output (Weiner 1992). Murre's may be able to maximize energy intake, and subsequent output, by acquiring prey that are assimilated more efficiently. This may be a viable tactic since assimilation improves as fat content increases (Brekke and Gabrielsen 1994). Perhaps this is why common murre's select larger prey and/or supplement their diet with alternate prey during poorer conditions (Burger and Piatt 1990, Uttley et al. 1994, Burke and Montevecchi 2009, Buren et al. 2012). We were unable to measure the size of capelin delivered to chicks, yet we did observe an increase in the proportion of sandlance delivered during 2009 and 2010. The selection of larger capelin or alternate prey such as sandlance could, in theory, increase daily energy assimilation because fat content in capelin increases with size (Montevecchi and Piatt 1984) or because sandlance has a higher relative lipid content than capelin (Montevecchi et al. 1984). To exemplify this point, let us assume that murre's typically catch one capelin per dive; since they dive  $\sim$ 50 times each day, we assume they catch  $\sim$ 50 capelin/day. If these are gravid and spent female capelin measuring  $\sim$ 158 mm long and weighing  $\sim$ 24 g, as described in Montevecchi & Piatt (1984), then their assimilation efficiency will be  $\sim$ 72% given their fat content is  $\sim$ 3.4%; in contrast, the assimilation efficiency of smaller capelin ( $\sim$ 141 mm and  $\sim$ 15.9 g; Eaton et al. 1975) would be 70% given their fat content is 1.9% (assimilation efficiencies were estimated using equations in Brekke & Gabrielsen 1994). Given large capelin (158 mm, 24 g) have an energy density of  $\sim$ 4.2 KJ/g and small capelin (141 mm, 15.9 g)  $\sim$ 3.7 KJ/g, potential metabolized energy from small capelin would be  $\sim$ 2100 KJ/day whereas larger capelin would provide  $\sim$ 3600 KJ/day. This example indicates that mean catch per unit effort must be high ( $\sim$ 0.55–0.95 capelin/dive) to sustain a DEE of 1969.9 KJ/day. Assuming assimilation is the primary physiological bottleneck limiting energy output, this example also illustrates that a small shift in prey selection may make a big difference in the economics of murre foraging. It may be the case



that the murrelets studied here were able to increase energy output during the mismatch year by using this tactic rather than relying on energy reserves. Jacobs et al. (2011) suggest that trade-offs between flight costs and fasting endurance limit the murrelets' lipid stores, thereby constraining their energy buffer. Prey selection or switching may therefore serve as an alternate buffer to variable prey accessibility.

Murrelets substantially increased diving effort early during the 2009 chick-rearing period, presumably in response to limited access to capelin. Catch per unit effort must also have been significantly lower at this time. Assuming they were targeting large female capelin and they achieved energy balance, we estimate that catch per unit effort was  $\sim 0.4$  capelin/dive. Capelin likely became more accessible when spawning began, which is probably why diving effort decreased as the season progressed. Estimated catch per unit effort increased to  $\sim 1$  capelin/dive later in the season. Though prey availability apparently improved, parents did not increase co-attendance time, rather they continued to devote effort to foraging. Crucially, the ensuing increase in parental effort and chick investment may have helped buffer fledging success. The effects of mismatch, however, must not have been as dramatic as that felt by handicapped thick-billed murrelets (Elliott et al. 2013b) because it did not force parental common murrelets to trade-off chick survival for self-preservation.

Elliott et al. (2013b) demonstrated that older handicapped parents were more likely to run energy deficits because their prospects for future reproduction are relatively limited. Given older murrelets are much more likely to persist and successfully hatch chicks (Hedgren 1980, de Forest and Gaston 1996, Elliott et al. 2013b), it seems likely that low hatching success during 2009 was primarily caused by younger individuals abandoning their breeding attempt in response to poor prey accessibility. Though our study area was colonized relatively recently (early 2000s; GJR personal observations), our sample was probably biased towards the oldest individuals at the site (i.e., experienced breeders [ $>10$  years]), which may explain why we observed continued investment in chick-provisioning. Perhaps only the 'best birds' could sustain the extra investment while others aban-

doned their breeding attempt. More experienced breeders are more proficient foragers than young and naïve seabirds (Daunt et al. 2007); perhaps their knowledge of the prey base and its distribution minimized required efforts (Regular et al. 2013).

#### *Comparisons with previous studies*

Comparing the parameters observed in this study to those from other relevant studies, there are a mix of striking similarities and disconcerting differences. First, mean activity budget and DEE values of chick-rearing murrelets in Witless Bay during 1984 and 1985 (Cairns et al. 1987, 1990) all lie within the credible intervals reported here, and activity budgets in particular were similar with point estimates differing by less than 1%. Feed rates were also similar to those recorded in Witless Bay from the 1980s and late 1990s/early 2000s, differing by less than 1 fish/day (Burger and Piatt 1990, Davoren and Montevecchi 2003a, Wilhelm et al. 2008). Co-attendance times, however, were more divergent; with the exception of 2008, durations recorded by Burger & Piatt (1990) during the 1980s were up to 4 h greater than the values reported here (i.e., murrelets are currently working harder). These differences lend further support to the argument that an abrupt state change in capelin timing and abundance following a regime shift in the early 1990s (Buren et al. 2014) caused breeding murrelets to be more constrained than they were in the 1980s (Wilhelm et al. 2008). Capelin biomass and timing are influenced by seasonal sea ice dynamics which are key determinants of the pelagic spring bloom and subsequent emergence of *Calanus finmarchicus*, capelin's primary prey, from diapause (Buren et al. 2014).

It is unclear how ocean climate change will influence sea ice dynamics and how these physical changes will influence biological match-mismatch dynamics in the system. Nevertheless, extreme ice conditions can create profound bottom-up food web effects (Buren et al. 2014). In fact, there were peaks in ice area (predictor for capelin timing) when murrelets and Atlantic puffins *Fratercula arctica* indicated late arrival of capelin during 2000 and 2009 (Doody et al. 2008, Wilhelm et al. 2008, Rector et al. 2012; this study), and slumps in the timing of ice retreat (predictor of capelin abundance) when

murres indicated low capelin abundance during 1984 and 2010 (Burger and Piatt 1990).

### Conclusions

Our study sheds light on the underlying mechanisms forcing previously reported behavioral thresholds and expands our understanding of the murres' buffering capabilities during difficult conditions. First, there appears to be an upper limit on the time murres can spend with their partner at the colony (~3 hr/day; Harding et al. 2007). The energetic demands of chick-rearing appear to force parental murres to operate near maximum intensity ( $7 \times \text{BMR}$ ), even during the best years, thus the above mentioned threshold may be imposed by the minimum amount of foraging time required to meet their chicks' and their own energetic requirements (time minimizing tactic; Schoener 1971). Second, when parents spend less than 45 min/day with their partner at the colony, chick-provisioning is reduced (Harding et al. 2007). As suggested by Harding et al. (2007), the extra foraging time gained by reducing discretionary time at the colony helps murres buffer variation in prey availability. Though this extra time often allows parents to maintain chick feeding rates, murres have to strategically adjust their time and energy budget since they lack a large safety margin between performance and capacity. In other words, chick-rearing murres have a limited energy buffer because they operate at or near their energy ceiling (Elliott et al. 2013b) and they have a limited capacity to store lipids (Jacobs et al. 2011). To improve their energy buffer, we hypothesize that murres employ foraging tactics that maximize energy turnover during prey shortages. More specifically, we suspect improvements to assimilation is why murres select larger prey during poor food years (Burke and Montevecchi 2009, Buren et al. 2012). If prey selection or switching is not a viable option or is insufficient, then murres, particularly older individuals, may rely on energy reserves to maintain chick investment (Elliott et al. 2013b). The final threshold response of chick abandonment is likely mediated by lipid stores, whereby murres decide to abandon in favor of replenishing their reserves when lipid stores are pushed below a minimum threshold (Gaston and Hipfner 2006, Jacobs et al. 2011). Put simply, when poor prey

accessibility causes parental murres to run out of time and energy, they abandon their chicks. The circumstances that cause such responses are rare because of multifaceted buffering capabilities, but our results suggest that mismatch with prey could be drastic enough to reduce breeding success.

If ocean climate changes increase the incidences of anomalous ice events, then the potential increase in variability in capelin timing and abundance could have negative population consequences for murres. Gaining a better understanding of threshold responses, and the environmental conditions that invoke them, is key to predicting the consequences of climate driven mismatch on energy flow and population dynamics of different species in different systems.

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### LITERATURE CITED

- Both, C., S. Bouwhuis, C. M. Lessells, and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* 441:81–83.
- Both, C., C. A. M. Van Turnhout, R. G. Bijlsma, H. Siepel, A. J. Van Strien, and R. P. B. Foppen. 2010. Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society B* 277:1259–66.
- Brekke, B., and G. W. G. Gabrielsen. 1994. Assimilation efficiency of adult kittiwakes and Brunnich's guillemots fed capelin and Arctic cod. *Polar*

- Biology 14:279–284.
- Buren, A. D., M. Koen-Alonso, and W. A. Montevecchi. 2012. Linking predator diet and prey availability: Common murres and capelin in the Northwest Atlantic. *Marine Ecology Progress Series* 445:25–35.
- Buren, A. D., M. Koen-Alonso, P. Pepin, F. K. Mowbray, B. S. Nakashima, G. Stenson, N. Ollerherd, and W. A. Montevecchi. 2014. Bottom-up regulation of capelin, a keystone forage species. *PLoS ONE* 9:e87589.
- Burger, A. E., and J. F. Piatt. 1990. Flexible time budgets in breeding common murres: Buffers against variable prey abundance. *Studies in Avian Biology* 14:1–83.
- Burke, C. M., and W. A. Montevecchi. 2008. Fish and chicks: Forage fish and chick success in co-existing auks. *Waterbirds* 31:372–384.
- Burke, C. M., and W. A. Montevecchi. 2009. The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. *Journal of Zoology* 278:354–361.
- Cairns, D. K., K. A. Bredin, and W. A. Montevecchi. 1987. Activity budgets and foraging ranges of breeding common murres. *Auk* 104:218–224.
- Cairns, D. K., W. A. Montevecchi, V. L. Birt-Friesen, and S. A. Macko. 1990. Energy expenditures, activity budgets, and prey harvest of breeding common murres. *Studies in Avian Biology* 14:84–92.
- Carscadden, J. E., W. A. Montevecchi, G. K. Davoren, and B. S. Nakashima. 2002. Trophic relationships among capelin (*Mallotus villosus*) and seabirds in a changing ecosystem. *ICES Journal of Marine Science* 59:1027.
- Chaurand, T., and H. Weimerskirch. 1994. The regular alternation of short and long foraging trips in the blue petrel *Halobaena caerulea*: A previously undescribed strategy of food provisioning in a pelagic seabird. *Journal of Animal Ecology* 63:275–282.
- Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. *Advances in Marine Biology* 26:249–293.
- Daunt, F., V. Afanasyev, a Adam, J. P. Croxall, and S. Wanless. 2007. From cradle to early grave: juvenile mortality in European shags *Phalacrocorax aristotelis* results from inadequate development of foraging proficiency. *Biology Letters* 3:371–374.
- Davoren, G. K., and W. A. Montevecchi. 2003a. Consequences of foraging trip duration on provisioning behaviour and fledging condition of common murres *Uria aalge*. *Journal of Avian Biology* 34:44–53.
- Davoren, G. K., and W. A. Montevecchi. 2003b. Signals from seabirds indicate changing biology of capelin stocks. *Marine Ecology Progress Series* 258:253–261.
- De Forest, L. N., and A. J. Gaston. 1996. The effect of age on timing of breeding and reproductive success in the thick-billed murre. *Ecology* 77:1501–1511.
- DFO. 2013. Assessment of capelin in SA2 + Div. 3KL in 2013. DFO Canadian Science Advisory Secretariat Research Document 2013/011.
- Doody, L. M., S. I. Wilhelm, D. W. McKay, C. J. Walsh, and A. E. Storey. 2008. The effects of variable foraging conditions on common murre (*Uria aalge*) corticosterone concentrations and parental provisioning. *Hormones and Behavior* 53:140–8.
- Drever, M. C., and R. G. Clark. 2007. Spring temperature, clutch initiation date and duck nest success: A test of the mismatch hypothesis. *Journal of Animal Ecology* 76:139–148.
- Dunn, P. O., D. W. Winkler, L. A. Whittingham, S. J. Hannon, and R. J. Robertson. 2011. A test of the mismatch hypothesis: How is timing of reproduction related to food abundance in an aerial insectivore? *Ecology* 92:450–461.
- Durant, J. M., T. Anker-Nilssen, and N. C. Stenseth. 2003. Trophic interactions under climate fluctuations: The Atlantic puffin as an example. *Proceedings of the Royal Society B* 270:1461–1466.
- Durant, J. M., D. O. Hjermmann, T. Anker-Nilssen, G. Beaugrand, A. Mysterud, N. Pettorelli, and N. C. Stenseth. 2005. Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecology Letters* 8:952–958.
- Eaton, C. A., R. G. Ackman, C. S. Tocher, and K. D. Spencer. 1975. Canadian capelin 1972–1973. Fat and moisture composition, and fatty acids of some oils and lipid extract triglycerides. *Journal of the Fisheries Board of Canada* 32:507–513.
- Elliott, K. H., R. E. Ricklefs, A. J. Gaston, S. A. Hatch, J. R. Speakman, and G. K. Davoren. 2013a. High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. *Proceedings of the National Academy of Sciences* 110:9380–9384.
- Elliott, K. H., M. Le Vaillant, A. Kato, A. J. Gaston, Y. Ropert-Coudert, J. F. Hare, J. R. Speakman, and D. Croll. 2013b. Age-related variation in energy expenditure in a long-lived bird within the envelope of an energy ceiling. *Journal of Animal Ecology* 83:136–146.
- Frank, K. T., and W. C. Leggett. 1981. Prediction of egg development and mortality rates in capelin (*Mallotus villosus*) from meteorological, hydrographic, and biological factors. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1327–1338.
- Gaston, A. J., H. G. Gilchrist, M. L. Mallory, and P. A. Smith. 2009. Changes in seasonal events, peak food availability, and consequent breeding adjustment in a marine bird: A case of progressive mismatching. *Condor* 111:111–119.



- Gaston, A. J., and J. M. H. Hipfner. 2006. Adult Brunnich's Guillemots *Uria lomvia* balance body condition and investment in chick growth. *Ibis* 148:101–109.
- Gueorguieva, R., R. Rosenheck, and D. Zelterman. 2008. Dirichlet component regression and its applications to psychiatric data. *Computational Statistics and Data Analysis* 52:5344–5355.
- Hammond, K., and J. Diamond. 1997. Maximal sustained energy budgets in humans and animals. *Nature* 386:457–462.
- Harding, A. M. A., J. F. Piatt, J. A. Schmutz, M. T. Shultz, T. I. Van Pelt, A. B. Kettle, and S. G. Speckman. 2007. Prey density and the behavioral flexibility of a marine predator: The common murre (*Uria aalge*). *Ecology* 88:2024–2033.
- Hedgren, S. 1980. Reproductive success of guillemots *Uria aalge* on the island of Stora Karlsö. *Ornis Fennica* 57:49–57.
- Hijazi, R. H., and R. W. Jernigan. 2009. Modelling compositional data using Dirichlet regression models. *Journal of Applied Probability & Statistics* 4:77–91.
- Hilton, G. M., R. W. Furness, and D. C. Houston. 2000a. A comparative study of digestion in North Atlantic seabirds. *Journal of Avian Biology* 31:36–46.
- Hilton, G. M., G. D. Ruxton, R. W. Furness, and D. C. Houston. 2000b. Optimal digestion strategies in seabirds: A modelling approach. *Evolutionary Ecology Research* 2:207–230.
- Hipfner, J. M. 2008. Matches and mismatches: Ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. *Marine Ecology Progress Series* 368:295–304.
- Houston, A. I., W. A. Thompson, and A. J. Gaston. 1996. The use of a time and energy budget model of a parent bird to investigate limits to fledging mass in the thick-billed murre. *Functional Ecology* 10:432–439.
- Jacobs, S. R., D. B. Edwards, J. Ringrose, K. H. Elliott, J.-M. Weber, and A. J. Gaston. 2011. Changes in body composition during breeding: Reproductive strategies of three species of seabirds under poor environmental conditions. *Comparative Biochemistry and Physiology, Part B* 158:77–82.
- Kéry, M. 2010. Introduction to WinBUGS for ecologists: A Bayesian approach to regression, ANOVA and related analyses. Academic Press, Burlington.
- Lack, D. 1954. The natural regulation of animal numbers. Oxford University Press, Oxford, UK.
- Leggett, W. C., K. T. Frank, and J. E. Carscadden. 1984. Meteorological and hydrographic regulation of year-class strength in capelin (*Mallotus villosus*). *Canadian Journal of Fisheries and Aquatic Sciences* 41:1193–1201.
- Lunn, D., and D. Spiegelhalter. 2009. The BUGS project: Evolution, critique and future directions. *Statistics in Medicine* 28:3049–3067.
- Mahoney, S. P. 1979. Breeding biology and behaviour of the common murre on Gull Island, Newfoundland. Dissertation. Memorial University of Newfoundland, St. John's, Newfoundland, Canada.
- Monaghan, P., P. Walton, S. Wanless, J. D. Uttley, and M. D. Bljrs. 1994. Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding guillemots *Uria aalge*. *Ibis* 136:214–222.
- Montevecchi, W. A., and J. F. Piatt. 1984. Composition and energy contents of mature inshore spawning capelin (*Mallotus villosus*): Implications for seabird predators. *Comparative Biochemistry and Physiology Part A: Physiology* 78:15–20.
- Montevecchi, W. A., R. E. Ricklefs, I. R. Kirkham, and D. Gabaldon. 1984. Growth energetics of nestling northern gannets (*Sula bassanus*). *Auk* 110:334–341.
- Mowbray, F. K. 2013. Some results from soring acoustic surveys for capelin (*Mallotus villosus*) in NAFO Division 3L between 1982 and 2010. DFO Canadian Science Advisory Secretariat Research Document 2012/143.
- Nakashima, B. S. 1992. Patterns in coastal migration and stock structure of capelin (*Mallotus villosus*). *Canadian Journal of Fisheries and Aquatic Sciences* 49:2423–2429.
- Perrins, C. M. 1970. The timing of birds' breeding seasons. *Ibis* 112:242–253.
- Piatt, J. F. 1987. Behavioural ecology of common murre and Atlantic puffin predation on capelin: Implications for population biology. Dissertation. Memorial University of Newfoundland, St. John's, Newfoundland, Canada.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rector, M. E., A.-L. Kouwenberg, S. I. Wilhelm, G. J. Robertson, D. W. McKay, M. G. Fitzsimmons, C. R. Baker, M. L. Cameron-Macmillan, C. J. Walsh, and A. E. Storey. 2012. Corticosterone levels of Atlantic puffins vary with breeding stage and sex but are not elevated in poor foraging years. *General and Comparative Endocrinology* 178:408–16.
- Reed, T. E., S. Jenouvrier, and M. E. Visser. 2013. Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *Journal of Animal Ecology* 82:131–44.
- Regehr, H. M., and W. A. Montevecchi. 1997. Interactive effects of food shortage and predation on breeding failure of black-legged kittiwakes: Indirect effects of fisheries activities and implications for indicator species. *Marine Ecology Progress Series* 155:249–260.
- Regular, P. M., A. Hedd, and W. A. Montevecchi. 2013. Must marine predators always follow scaling laws?



- Memory guides the foraging decisions of a pursuit-diving seabird. *Animal Behaviour* 86:545–552.
- Saino, N., et al. 2011. Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B* 278:835–42.
- Schielzeth, H., and W. Forstmeier. 2009. Conclusions beyond support: Overconfident estimates in mixed models. *Behavioral Ecology* 20:416–420.
- Schoener, T. W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2:369–404.
- Speakman, J. R., and E. Król. 2011. Limits to sustained energy intake. XIII. Recent progress and future perspectives. *Journal of Experimental Biology* 214:230–241.
- Sturtz, S., U. Ligges, and A. Gelman. 2005. R2WinBUGS: A package for running WinBUGS from R. *Journal of Statistical Software* 12:1–16.
- Thackeray, S. J., et al. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology* 16:3304–3313.
- Thaxter, C. B., F. Daunt, D. Grémillet, M. P. Harris, S. Benvenuti, Y. Watanuki, K. C. Hamer, and S. Wanless. 2013. Modelling the effects of prey size and distribution on prey capture rates of two sympatric marine predators. *PLoS ONE* 8:e79915.
- Thomas, D. W., J. Blondel, P. Perret, M. M. Lambrechts, and J. R. Speakman. 2001. Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science* 291:2598–600.
- Tremblay, Y., Y. Cherel, M. Oremus, T. Tveraa, and O. Chastel. 2003. Unconventional ventral attachment of time-depth recorders as a new method for investigating time budget and diving behaviour of seabirds. *Journal of Experimental Biology* 206:1929–1940.
- Uttley, J. D., P. Walton, P. Monaghan, and G. Austin. 1994. The effects of food abundance on breeding performance and adult time budgets of guillemots *Uria aalge*. *Ibis* 136:205–213.
- Vatka, E., M. Orell, and S. Rytönen. 2011. Warming climate advances breeding and improves synchrony of food demand and food availability in a boreal passerine. *Global Change Biology* 17:3002–3009.
- Visser, M. E., L. te Marvelde, and M. E. Lof. 2011. Adaptive phenological mismatches of birds and their food in a warming world. *Journal of Ornithology* 153:75–84.
- Visser, M. E., A. J. V. Noordwijk, J. M. Tinbergen, and C. M. Lessells. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society B* 265:1867–1870.
- Watanuki, Y., M. Ito, T. Deguchi, and S. Minobe. 2009. Climate-forced seasonal mismatch between the hatching of rhinoceros auklets and the availability of anchovy. *Marine Ecology Progress Series* 393:259–271.
- Weimerskirch, H. 1998. How can a pelagic seabird provision its chick when relying on a distant food resource? Cyclic attendance at the colony, foraging decision and body condition in sooty shearwaters. *Journal of Animal Ecology* 67:99–109.
- Weiner, J. 1992. Physiological limits to sustainable energy budgets in birds and mammals: Ecological implications. *Trends in Ecology & Evolution* 7:384–388.
- Wilhelm, S. I., G. J. Robertson, P. A. Taylor, S. G. Gilliland, and D. L. Pinsent. 2003. Stomach contents of breeding common murrelets caught in gillnets off Newfoundland. *Waterbirds* 26:376–378.
- Wilhelm, S. I., C. J. Walsh, and A. E. Storey. 2008. Time budgets of common murrelets vary in relation to changes in inshore capelin availability. *Condor* 110:316–324.