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Energetic consequences of time-activity budgets for a breeding seabird

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21 ABSTRACT

22 How animals allocate their time to different behaviours has important consequences for their overall
23 energy budget and reflects how they function in their environment. This potentially affects their
24 ability to successfully reproduce, thereby impacting their fitness. We used accelerometers to record
25 time-activity budgets of 21 incubating and chick-rearing kittiwakes on Puffin Island, UK. These
26 budgets were examined on a per day and per foraging trip basis. We applied activity-specific
27 estimates of energy expenditure to the kittiwakes' time-activity budgets in order to identify the
28 costs of variation in their allocation of time to different behaviours. Estimates of daily energy
29 expenditure for incubating kittiwakes averaged 494 ± 20 kJ d⁻¹ while chick-rearing birds averaged
30 559 ± 11 kJ d⁻¹. Time-activity budgets highlighted that kittiwakes did not spend a large proportion of
31 their time flying during longer foraging trips, or during any given 24-hour period. With time spent
32 flying highlighted as the driving factor behind elevated energy budgets, this suggests behavioural
33 compensation resulting in a possible energetic ceiling to their activities. We also identified that
34 kittiwakes were highly variable in the proportion of time they spent either flying or on the water
35 during foraging trips. Such variation meant that using forage trip duration alone to predict energy
36 expenditure gave a mean error of 19% when compared to estimates incorporating the proportion of
37 a foraging trip spent flying. We have therefore highlighted that trip duration alone is not an accurate
38 indicator of energy expenditure.

39 INTRODUCTION

40 During their breeding periods, many animals must increase their foraging effort in an attempt to
41 provide enough food not only for their own survival but also for the survival and growth of their
42 offspring (Grémillet, 1997). As movement accounts for a large proportion of energy expenditure in
43 many free-ranging animals (Brit-Friesen *et al.*, 1989), this elevated foraging effort impacts the energy
44 budgets of individuals. Thus how animals allocate their time to different behaviours during the
45 breeding period can be a key component to their eventual reproductive success and fitness
46 (Gittleman & Thompson, 1988).

47

48 Understanding the interactions between behaviour, energetics, and fitness is a key consideration for
49 comprehending the roles of organisms in their ecosystems (Tomlinson *et al.*, 2014). However, free-
50 ranging animals are often difficult to observe over long periods of time without interruption.
51 Seabirds exemplify this difficulty, with individuals often foraging far out at sea, where directly
52 observing their behaviour is highly impractical. Conventionally, presence or absence of individuals at
53 their nest has been used to indicate how they allocate their time during the breeding season
54 (Granadeiro *et al.*, 1998; Lewis *et al.*, 2001), yet this approach lacks detailed information regarding
55 activity when away from the nest. As time away from the nest comprises of a variable combination
56 of time spent in either active behaviours (such as flight or foraging) or resting, allocation of time to
57 activity within this period is likely to be of major energetic importance. Using animal-borne data
58 loggers such as accelerometers, which measure an animal's body acceleration continuously, it is
59 now possible to collect continuous measurements of the behaviour of individuals to generate
60 detailed time-activity budgets regardless of location (e.g. Shepard *et al.*, 2008; Halsey *et al.*, 2009b).

61

62 While the biological implications of variation in time-activity budgets are informative alone, it is even
63 more informative to estimate how differences in time allocation to behaviour relate to energy
64 expenditure. Currently the most prominent approaches for estimating energy expenditure *in-situ* are
65 the doubly-labelled water (DLW) method and the heart rate method. Although these techniques
66 have greatly enhanced our understanding of energy expenditure in wild animals, they do have
67 limitations, notably the DLW method has poor temporal resolution (Butler *et al.*, 2004; Shaffer,
68 2011) and the heart rate method generally requires surgical implantation of a data logger (Butler *et*
69 *al.*, 2004). Alternatively, by combining time-activity budgets with either laboratory or model derived
70 estimates of activity-specific energy expenditure, time-energy budgets can be constructed
71 (Goldstein, 1988). Such an approach is not novel in principle, yet the inclusion of accelerometry
72 derived time-activity budgets now allows for this approach to be applied to continuous, high-
73 resolution behavioural information from highly mobile animals (Shamoun-Baranes *et al.*, 2012). This
74 alternative approach then allows estimation of energy expenditure of free-ranging animals at a finer
75 temporal scale than the DLW method, and in a less invasive manner than the heart-rate method.

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77 In this study, we combine accelerometer-derived time-activity budgets with published values of
78 activity-specific metabolic costs to estimate the energy expenditure of free-ranging black-legged
79 kittiwakes (*Rissa tridactyla*). Kittiwakes are a suitable species on which to apply this approach as they
80 have a relatively simple repertoire of coarse-scale behaviours, consisting of flight, being on water,
81 and attending the nest; these behaviours are readily identifiable from accelerometry traces (Collins
82 *et al.*, 2015). To date, energy expenditure of kittiwakes has been estimated numerous times with the
83 DLW method (Gabrielsen, Mehlum & Nagy, 1987; Thomson, Furness & Monaghan, 1998; Golet, Irons
84 & Costa, 2000; Jodice *et al.*, 2002, 2003; Welcker *et al.*, 2009, 2014; Schultner *et al.*, 2010),
85 highlighting variation within and between individuals and populations, as well as showing that time
86 away from the colony is an important component of total daily energy expenditure (DEE) (Fyhn *et*

87 *al.*, 2001). Furthermore, in a study by Welcker et al. (2010) which employed the DLW method,
88 kittiwakes exhibited remarkably similar DEE across years with different prey availability. They
89 therefore posited that kittiwakes were operating at an intrinsic energy ceiling, whereby individuals
90 apparently had a limit to the amount of energy they expend (Drent & Daan, 1980). It is likely that
91 kittiwakes exhibit behavioural compensation, whereby they adjust time spent in more energetically
92 demanding activities to limit energy expenditure (Elliott *et al.*, 2014a), however, the poor temporal
93 resolution of the DLW method coupled with a lack of continuous behavioural data has largely
94 inhibited the possibility of identifying evidence for this. In this study, by deploying accelerometers on
95 both incubating and chick-rearing kittiwakes, we quantify how kittiwakes allocate their time, and
96 what the energetic consequences of variation in time allocation are. By linking behaviour to energy
97 expenditure we set out to identify if there is evidence for behavioural compensation.

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109 **METHODS**

110 **Data collection**

111 Tri-axial accelerometers (X8m-3 Gulf Coast Data Concepts, LLC; recording range ± 8 g, resolution:
112 0.001 g, weight: 14 g), set to record at 25 Hz, were deployed on 50 kittiwakes over three breeding
113 seasons. Accelerometers were attached to feathers on the centre of the backs of individuals using
114 clothed black Tesa® tape. The placement of the accelerometer was kept as consistent as possible
115 across all birds. Mean body mass was 365 ± 31 g (mean \pm SD), ranging from 310 – 435 g, with data
116 loggers weighing on average $3.8 \pm 0.3\%$ of body mass. 28 accelerometers were retrieved, of which 21
117 were functioning correctly. Of these 21 accelerometers, 17 were from individuals during the early
118 chick-rearing stage (chicks less than 10 days old), and 4 were from adults at the late incubation
119 stage. Accelerometers were deployed on birds at a similar point within the incubation or chick-
120 rearing process as energy expenditure changes dependent on time into these stages (Fyhn *et al.*,
121 2001). Accelerometers that were not retrieved were either deployed on individuals which evaded
122 recapture, or had fallen off before retrieval was attempted. Accelerometers not removed would
123 have fallen off within two weeks. Deployment time for recaptured birds averaged 58 ± 22 h and
124 ranged from 23 – 114 h, during which time birds exhibited apparently normal breeding behaviour,
125 including nest attendance (comprising of care of eggs or chicks) or absence from the nest (most
126 likely on foraging trips). Fieldwork was carried out on Puffin Island, North Wales in July 2012, July
127 2013 and July 2014. All work was carried out under Countryside Council for Wales permit numbers
128 (37727:OTH:SB:2012, 44043:OTH:SB:2013, 53628:OTH:SB:2014).

129

130 **Behavioural assignments**

131 To generate time-activity budgets, acceleration data were assigned to three coarse-scale behaviours:
132 “nest attendance”, “on water”, and “flying”. Although finer-scale behaviours such as foraging,

133 preening, and courtship are exhibited by kittiwakes, the amount of time these behaviours take up is
134 relatively little (Jodice *et al.*, 2003). As per Collins *et al.* (2015), behaviours were assigned using a
135 simple method that categorises different activity types based on readily calculable metrics indicating
136 body orientation or amount of movement. This method has been shown to give high accuracy
137 (>95%) of coarse-scale behaviour assignments in kittiwakes (Collins *et al.*, 2015). Behaviours of “nest
138 attendance” and “on water” were assigned depending on the body angle of the bird; periods when
139 the bird was at a lower angle were assigned as “on water”, and periods at which the bird was at a
140 higher body angle were identified as being on land. The body angle thresholds at which these
141 behaviours were separated were specific to each individual. When classified as on land, based on
142 observations of their behaviours, the birds were assumed to be attending their nest, and were thus
143 assigned the behaviour “nest attendance”. Flight was assigned based on the standard deviation of
144 acceleration values in the heave axis, with higher values indicating movement in this channel relating
145 to flight. Flight was not separated into flapping or gliding, although inspection of acceleration traces
146 suggested that the kittiwakes flapped much more than glide.

147

148 **Time-activity budgets**

149 We constructed time-activity budgets at two scales of interest; daily and complete foraging trips. For
150 each day and each foraging trip we determined the amount and proportion of time spent on the
151 three coarse-scale behaviours. For daily time-activity budgets, only records consisting of 24 hours of
152 continuous data starting at midnight were used. The sample size for incubating birds was 3 days’
153 worth of data from 3 individuals, and that for chick-rearing birds was 25 days’ worth of data from 17
154 individuals. Foraging trips were defined as a period in which the bird flew from the land, spent time
155 on water, and then returned to the land, with trips varying in duration. Only trips over 30 minutes
156 were used, to exclude periods when birds might have left the land for reasons other than foraging
157 (such as researcher disturbance, or predator avoidance (Collins *et al.*, 2014)). In total 146 trips were

158 identified and analysed. Trips were further separated into two types; those which started one day
159 and finished the next were assigned as overnight trips (n=18), while those starting and finishing on
160 the same day were assigned as day trips (n=128).

161

162 **Time-energy budgets**

163 To estimate the energy expenditure for the behaviours “nest attendance” and “on water” we used
164 the intraspecific allometric equations for resting metabolic rates of these behaviours reported in
165 Humphreys et al. (2007). For estimating the energy cost of flight we used the modelling software
166 Flight 1.25 (<http://www.bristol.ac.uk/biology/people/colin-j-pennycuick/index.html>, Pennycuick
167 (2008)). We used the default values for a kittiwake wingspan (0.947 m) and aspect ratio (9.44 m²)
168 and input mass per bird from our data. We included a payload of 14g to account for the
169 accelerometer and set altitude at 10m above sea level. Standard errors of energy cost estimates
170 were calculated through 10 000 iterations of bootstrapping with replacement from the distribution
171 of the activity-specific energy costs (n=21).

172

173 To estimate the most accurate total DEE possible for each bird we input individual kittiwake mass
174 into our equations for activity-specific energy expenditure and combined these activity-specific costs
175 with each individual’s time-activity budget. These values are used to report estimates of DEE for the
176 population for the incubation and chick-rearing periods overall. To get an estimate of DEE which
177 indicates how time spent in each behaviour alone influences energy expenditure, we estimated
178 activity-specific energy costs based on the mean kittiwake mass of 365g and combined these with
179 each individual’s time-activity budget. This method was also used to estimate foraging trip energy
180 expenditure. For estimates using mean mass, energy expenditure while attending the nest was
181 calculated to be $13.6 \pm 1.2 \text{ kJ h}^{-1}$, energy expenditure while on water was $18.8 \pm 3.0 \text{ kJ h}^{-1}$, and energy

182 expenditure for flying was $48.24 \pm 5 \text{ kJ h}^{-1}$. Estimating energy expenditure for these behaviours based
183 on mean mass is justified as preliminary analysis showed no relationship between body mass and
184 time-activity budgets.

185

186 **Statistical analysis**

187 A Welch's t-test (used due to unequal variances) was applied to test for differences in DEE between
188 the three study years. As DEE did not significantly differ between years ($t_{13,191} = -0.494$, $p = 0.6297$) we
189 pooled all data for analysis. A Welch's t-test was also used to test for differences in DEE between
190 incubating and chick-rearing birds. To analyse differences in foraging trip durations and proportion
191 of trips spent in flight between breeding stages and trip type, generalised linear mixed models
192 (GLMMs) including these variables and the interaction between them were constructed. A GLMM
193 was also constructed to analyse the effect of forage trip duration on the proportion of trip spent in
194 flight. Due to each kittiwake undertaking numerous foraging trips, in all GLMMs individual bird
195 identity was assigned as a random factor. Models with foraging trip duration as the response
196 variable were constructed using a Gaussian family with a log link due to the response variable
197 conforming to assumptions of normality, while models with proportion of trip spent in flight as the
198 response variable used a binomial family with logit link, as this response variable did not conform to
199 assumptions of normality. To assess the accuracy of using foraging trip duration alone to predict
200 energy expenditure, the difference between estimated energy expenditure for each foraging trip to
201 that predicted by a general linear model between forage trip duration and energy expenditure was
202 calculated.

203 P-values below 0.05 were deemed to be significant, although our analysis places a greater emphasis
204 on graphical representation of the data due to the imprecise nature of P-values (Halsey *et al.*, 2015)
205 and low sample sizes in some aspects of the study. All means are presented ± 1 standard error unless

206 otherwise stated. All data analysis was conducted in R statistical software version R 3.2.1 (R
207 Development Core Team, 2015) using 'glmmPQL' from the 'MASS' package.

208

209 RESULTS

210 **Time-activity budgets**

211 Over a 24-hour period, incubating and chick-rearing kittiwakes differed in how they allocated their
212 time to the three behaviours (Fig. 1.). Incubating kittiwakes spent a similar percentage of their time
213 attending their nest as they spent on water (41.7 ± 18.4 and $43.8\pm 20.3\%$, respectively), and
214 proportionally less of their time in flight ($14.5\pm 3.3\%$). Chick-rearing kittiwakes spent more of their
215 time attending their nest ($58.9\pm 2.4\%$), with time spent on water taking up the least amount of their
216 daily time budget ($13.5\pm 5.8\%$). Chick-rearing kittiwakes spent almost twice as much of their day in
217 flight than incubating kittiwakes did ($27.6\pm 2.1\%$).

218

219 Time spent on foraging trips, and the proportion of time spent either flying or on water within these
220 trips, varied considerably both within and between birds. Duration of foraging trips was highly
221 variable for all kittiwakes (Fig. 2a); mean duration of foraging trips for incubating kittiwakes was
222 3.10 ± 0.73 h, ranging from 0.53–9.22 h ($n=17$), while the mean foraging trip duration for chick-
223 rearing kittiwakes was 2.70 ± 0.20 h, ranging from 0.50–10.83 h ($n=129$). These differences were not
224 significant, however ($t_{19} = 1.14$, $p=0.267$). Trip duration was significantly longer for overnight trips
225 compared to trips starting and ending on the same day (Fig. 2b) ($t_{19} = 13.48$, $p<0.001$), with daytrips
226 averaging 2.07 ± 0.15 h (range 0.50–7.88 h, $n=128$) and overnight trips averaging 7.60 ± 0.47 h (range
227 3.67–10.83 h, $n=18$). There was no significant interaction between breeding stage and trip type in
228 relation to trip duration ($t_{123} = -0.60$ $p=0.552$).

229

230 The proportion of time spent flying during each trip also varied considerably between trips (Figs. 2c
231 & 2d). For incubating kittiwakes the mean proportion of foraging trips spent flying was $53\pm 9\%$
232 (ranging from 24–99%, $n=17$) while for chick-rearing kittiwakes the mean was $69\pm 2\%$ (ranging from

233 47-99%, n=129). As with foraging trip duration, percentage of foraging trip spent flying did not differ
234 significantly between breeding stages ($t_{19} = -1.55$, $p=0.137$). Trip type (day trip or overnight trip) had
235 a significant effect on the proportion of time spent flying over the foraging trip, with the proportion
236 of time spent flying during daytrips (mean= $72\pm 2\%$, ranging from 2-99%, n=128) being significantly
237 greater ($t_{123} = -6.78$ $p<0.001$), than proportion of time spent flying during overnight trips (mean =
238 $31\pm 4\%$, ranging from 30-74%, n=18). There was no significant interaction between breeding stage
239 and trip type in relation to proportion of time spent flying ($t_{123} = -0.35$ $p=0.725$).

240

241 **Energy expenditure**

242 Estimated individual DEE averaged 552 ± 12 kJ d⁻¹ (n=28). The average for incubating kittiwakes was
243 494 ± 20 kJ d⁻¹ (n=3), which was 13% lower than chick-rearing kittiwakes which averaged 559 ± 11 kJ d⁻¹
244 (n=25) however these estimates did not differ significantly ($t_5=2.0$, $p=0.10$). Individual DEE values
245 (range 358 ± 31 - 745 ± 67 kJ d⁻¹) as well as mass and time spent in each behaviour are presented in
246 Appendix S1.

247

248 Using estimates of energy expenditure based on average mass, due to the higher energy cost per
249 unit time of flight, kittiwakes that spent a greater proportion of the day flying had higher DEE (Fig.
250 3.). As a result, high variation in the proportion of time individuals spent flying across the day drove
251 the variability in estimated DEE (Fig. 3.).

252

253 As foraging trips were highly variable in both duration and allocation of time to either flying or
254 resting on water, the estimated energy expenditure across those trips also varied widely, from 14 ± 1
255 kJ to 368 ± 19 kJ, averaging 103.1 ± 7 kJ (n=153) (Fig. 4.). Expressed as rate of energy expenditure, on

256 foraging trips kittiwakes expended between 19.5 ± 1.4 and 48.2 ± 2.2 kJ h⁻¹, averaging 38.2 ± 1.9 kJ h⁻¹.
257 Of all 153 foraging trips measured, 62% of them cost less than 100 kJ of energy, with 84% costing
258 less than 200 kJ. Shorter foraging trips were highly variable in time spent flying, but had the highest
259 recorded percentage of time spent flying across foraging trips (Fig. 4.). Overall, proportion of time
260 spent in flight decreased significantly with duration ($t_{124} = -5.52$, $p < 0.001$). As foraging trips which
261 lasted longer tended to have a lower proportion of time spent in flight, the hourly rate of energy
262 expenditure for such trips was lower than for shorter trips. No kittiwakes exhibited extremely high
263 percentages of time spent in flight during foraging trips of longer duration, with the maximum
264 estimated energy expenditure of 368 ± 19 kJ corresponding to a trip lasting 10.29 h, of which 57.6%
265 (5.92 h) was spent flying.

266

267 Foraging trip duration alone was a poor predictor of estimated foraging expenditure. Although the
268 R² value of the linear fit between foraging trip duration and total energy expenditure (Fig. 5a) was
269 high at 0.88, estimated energy expenditure differed from that predicted by this relationship by an
270 average of 19.8%, ranging from 0.1 to 60.1% (Fig. 5b). This translates to a mean difference in energy
271 expenditure of 20.1 kJ (range 0.1 – 95.7) over the foraging trip.

272

273 DISCUSSION

274 **Activity and energy expenditure over 24 hours**

275 Across the 24-hour day, individual kittiwakes spent the majority of time exhibiting the less
276 energetically expensive behaviours of either attending their nest or being on the water. A greater
277 percentage of time allocated to less energetically expensive behaviours could be due to intrinsic or
278 extrinsic limiting factors (Humphreys, Wanless & Bryant, 2006; Welcker *et al.*, 2009, 2010). For time
279 spent flying to be limited intrinsically would suggest that there is a physiological reason preventing
280 kittiwakes from flying for more of the day, whereas extrinsic limiting factors would suggest that their
281 behaviour was determined by an external feature such as prey availability. Both intrinsic and
282 extrinsic factors could, and are likely to be, influencing the patterns in behaviours we recorded
283 (Humphreys *et al.*, 2006). To elucidate the causes of the potential limitations to daily activity
284 presented, it would be ideal to combine measurements of time spent flying with indicators of rates
285 of prey acquisition and measures of body condition. This has been achieved in two studies on chick-
286 rearing murres, which found both an energetic ceiling determined by the ability of individuals to
287 digest food (Elliott *et al.*, 2014b), and behavioural compensation limiting DEE (Elliott *et al.*, 2014a).

288

289 It is clear from our results that chick-rearing birds spend a greater proportion of time flying than do
290 incubating birds (Fig. 1). This increased amount of time spent flying is likely to be a result of adults
291 needing to make regular foraging trips to provision chicks (Rishworth & Pistorius, 2015). In contrast,
292 during incubation foraging trips are less frequent due to the need for adult kittiwakes only to meet
293 their own energy requirements (Ponchon *et al.*, 2014). With flight being energetically expensive
294 (Jodice *et al.*, 2003), it stands to reason that incubating birds are more capable than chick-rearing
295 birds of mediating their energy expenditure by flying less. Indeed, an increase in time spent flying is
296 likely to be the most important factor in the greater DEE recorded during chick-rearing in

297 comparison to incubation identified in many bird species (e.g. Humphreys *et al.*, 2006; Rishworth,
298 Tremblay & Green, 2014). For kittiwakes, such an increase in energetic expenditure during this
299 period is a likely contributor towards them having a poorer body condition, greater levels of stress,
300 and a greater likelihood of breeding failure while chick-rearing than when incubating their eggs
301 (Kitaysky, Wingfield & Piatt, 1999; Ponchon *et al.*, 2014). It should be noted, however, that the
302 sample size for incubating birds in this study was much lower than that for chick-rearing birds, thus
303 for incubating birds the time and energy estimates must be considered with caution.

304

305 **Activity and energy expenditure over foraging trips**

306 By examining time-activity and time-energy budgets at the level of the foraging trip we have
307 provided a more detailed level of behavioural information than has been previously available for
308 kittiwakes. We have highlighted a large degree of variation in the relationship between trip duration
309 and proportion of time spent flying. Although foraging trip duration correlated positively with total
310 energy expenditure (Fig. 5), the variation around a positive linear relationship between trip duration
311 and energy expenditure had an average error of 19% when compared to estimates of energy
312 expenditure which took proportion of trip spent flying into account (Fig. 5). Notably, when looking at
313 proportion of time spent flying plotted against duration of foraging trip (Fig. 4) there is an absence of
314 data points in the top right hand corner where energy costs are highest. This provides some
315 evidence towards the presence of behavioural compensation, whereby individuals limit total energy
316 expenditure on longer trips by spending a lower proportion of time flying. This could also be seen as
317 providing support for the idea of an energetic ceiling, whereby individuals are constrained in their
318 total energy expenditure at this scale (Welcker *et al.*, 2010; Elliott *et al.*, 2014b). This finding also
319 highlights the inadequacy of using foraging trip duration alone as a proxy for energy expenditure.
320 Foraging trip duration is often used as a direct indication of energy expended when away from the
321 nest (Welcker *et al.*, 2010; Rishworth *et al.*, 2014), as well as an indication of foraging conditions and

322 food availability (Kitaysky *et al.*, 1999). However, we suggest that both trip duration and time spent
323 flying should be considered together before making inferences relating to energy expenditure.
324 Indeed, to further improve estimates of energy expenditure when away from the colony, wind
325 conditions and time spent in either flapping or gliding flight could be taken into account.

326

327 **Estimates of energy expenditure**

328 The absolute DEE values we estimated for breeding kittiwakes are lower than existing published
329 studies (Table 1). Reports of energy expenditure differ between kittiwake colonies (Table 1) and as
330 such it may be that kittiwakes on Puffin Island are less active and expend less energy than those
331 from other colonies. There are many possible explanations for this. For example, low intraspecific
332 competition due to low breeding density of kittiwakes on Puffin Island could have reduced the
333 amount of energy they needed to expend to successfully forage (Ballance *et al.*, 2009), relatively
334 short day lengths at Puffin Island compared to higher latitude colonies could limit time spent
335 foraging, and/or the presence of the accelerometer itself may have decreased the amount of time
336 kittiwakes spent flying (Chivers, Hatch & Elliott, 2016).

337 Methodological considerations may also explain our comparatively low estimates of energy
338 expenditure. The flight model we used to estimate flight costs has been shown to sometimes
339 misestimate energy expenditure in comparison to empirical estimates (McWilliams *et al.*, 2004;
340 Schmidt-Wellenburg *et al.*, 2007). The only other study providing activity-specific estimates of
341 energy expenditure for kittiwakes, Jodice *et al.* (2003), suggests that flight is 5.6 times more
342 expensive than nest attendance, whereas our approach estimates it to be 3.5 times more expensive.
343 By following Jodice *et al.* (2003) and multiplying basal metabolic rate by activity-specific factors, our
344 estimates of DEE increase to $833 \pm 23 \text{ kJ d}^{-1}$ (detailed in Appendix S1). Although the suitability of
345 multiplying basal metabolic rates to estimate energy expenditure during activity is contested

346 (Pennycuik, 2008), this does indicate that low flight costs are likely driving our low energy
347 expenditure estimates. Furthermore, the estimates of DEE we have presented have a strong linear
348 correlation ($r^2 = 0.97$, Appendix S1) with those we achieved by following the method in Jodice et al.
349 (2003). This indicates that between these methods it is only the absolute values of energy
350 expenditure that differ, rather than the key biological findings.

351 Our approach also does not take into account variation in energy expenditure relating to varying
352 degrees of movement during behaviours. Energetic variation during behaviours may arise from
353 sources such as switching between flapping and gliding flight, or from take-offs and landings (Shaffer
354 et al. 2001). Amount of body movement can be quantified from acceleration data as dynamic body
355 acceleration (DBA). DBA can be calibrated with energy expenditure either through oxygen
356 consumption measurements in the laboratory (Halsey et al. 2009a) or with estimates from the DLW
357 technique (Elliott *et al.*, 2013). This has been attempted for kittiwakes by Kristiansen (2014), who
358 regressed DBA against energy expenditure as measured through the DLW technique for five birds,
359 having discarded measurements from a sixth bird due to it being a heavy outlier. By applying the
360 equation from their linear regression to calculations of DBA from our study birds, we estimate DEE
361 to be $1130 \pm 28 \text{ kJ d}^{-1}$ (Appendix S1). Estimates of individual DEE we achieve by following this
362 approach have a positive linear relationship with an r^2 value of 0.70 when correlated with the
363 estimates we have presented (Appendix S1). This indicates that the overall trends found using these
364 two methods do correspond, however at the individual level, estimates of energy expenditure are
365 variable depending on the method used. There are some serious limitations with this approach
366 however. Firstly, a number of previous studies using DLW on seabirds have shown that estimate
367 errors on an individual basis tend to be very large (Shaffer, 2011) and as such they should not be
368 relied upon (Butler *et al.*, 2004), and in addition to this, the small sample size of the study severely
369 limits the confidence we can have in the reported linear relationship. Furthermore, the relationship
370 between rate of energy expenditure and DBA is not always constant across different behaviours and

371 as such different equations for different behaviours are required to accurately estimate metabolic
372 rate (Green *et al.*, 2009; Elliott *et al.*, 2013).

373 Estimates of energy expenditure from the current study, Jodice *et al.* (2003) and Kristiansen (2014)
374 vary substantially in absolute estimates of energy expenditure, although they do all positively
375 correlate (Appendix S1), thus indicating that our overall biological findings, if not the exact estimates
376 of energy expenditure we produce, are robust regardless of method used. To identify if our low DEE
377 estimates are due to biological or methodological reasons, detailed time-activity information is
378 required from other colonies. The method we employ is essentially an update of traditional
379 observation-based time-activity budgets; it is simple to implement and allows insights into variations
380 in behaviour and their energetic consequences at a range of temporal scales and without the need
381 for logistically demanding proxy calibrations.

382

383 **Conclusion**

384 By constructing time-activity and time-energy budgets through coupling accelerometry data with
385 activity-specific rates of energy expenditure, we have highlighted key features of the behavioural
386 ecology of kittiwakes as well as the deficiency of examining forage trip duration alone when
387 considering energy expenditure in breeding seabirds. In particular, we have provided further
388 evidence for behavioural compensation linked to a limitation in the amount of energy individuals
389 expend. A lack of studies using a similar method to ours has not allowed us to make a detailed
390 comparison of DEE to that of kittiwakes at other colonies, however the relative simplicity of our
391 approach should prompt others to employ it.

392

393

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398

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506

507 FIGURE LEGENDS

508 **Fig. 1.** Mean \pm SE daily percentage of time spent undertaking three recorded coarse-scale behaviours
509 for incubating (n=3) and chick-rearing kittiwakes (n=25). Only days with 24 hours-worth of data were
510 used.

511

512 **Fig. 2.** Duration of foraging trip dependent on breeding stage (a) and trip type (b), and proportion of
513 individual foraging trips spent flying dependent on breeding stage (c) and trip type (d). Black dots
514 indicate individual foraging trips, black lines indicate the median value.

515

516 **Fig. 3.** The daily energy expenditures of kittiwakes of average mass, dependent on allocation of time
517 to nest attendance, being on the water, and flying. Each black symbol represents a full 24-hour
518 period of recorded activity from an individual incubating (triangle) or chick-rearing (circle) kittiwake.
519 Percentage of time spent in each activity should be read parallel to the direction of the tick marks for
520 each axis, respectively.

521

522 **Fig. 4.** Total energy cost (kJ) of foraging trips dependent on percentage of trip spent flying in relation
523 to duration of foraging trip. Black dots indicate values from individual foraging trips from 21
524 kittiwakes.

525

526 **Fig. 5.** a) The relationship between foraging trip duration and total estimated energy expended
527 during each foraging trip. The least squares regression line of best linear fit is shown. b) Difference in
528 total measured energy expenditure as a percentage of total energy expenditure predicted from
529 foraging trip duration using the linear relationship displayed in a).

530

531 **Table 1.** Estimates of mean \pm SD daily energy expenditure and mean body mass of chick-rearing
532 kittiwake adults from studies published to date. All previous studies used the DLW method for
533 estimating energy expenditure.