DIVE BEHAVIOUR AND DAILY ENERGY EXPENDITURE IN THICK-BILLED MURRES *URIA LOMVIA* AFTER LEAVING THE BREEDING COLONY

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Received 12 July 2014, accepted 8 September 2014

SUMMARY

ELLIOTT, K.H & GASTON, A.J. 2014. Dive behaviour and daily energy expenditure in Thick-billed Murres *Uria lomvia* after leaving the breeding colony. *Marine Ornithology* 42: 183–189.

In Thick-billed Murres *Uria lomvia* and other members of the tribe Alcini, chicks are reared at sea by their male parent after they leave their colony. It has been suggested that murre fathers increase time spent self-feeding and reduce time feeding their chick during the final week that the chick is at the colony because of the energy cost of provisioning for the chick post-departure ("energy constraint hypothesis"). To examine the post-breeding foraging behaviour of Thick-billed Murres and to provide information bearing on the energy constraint hypothesis we attached time-depth-temperature recorders to Thick-billed Murres to measure diving behaviour and estimate daily energy expenditure. We were able to retrieve the recorders and access data for six (four females and two males). We compared those values to values from a larger sample of birds from both sexes measured during the breeding season (July–August). One male soon returned to the colony without a chick and thereafter its dive behaviour and daily energy expenditure resembled those of the females. The other male, which apparently successfully reared a chick, had a high dive rate and foraged at low-quality patches. Daily energy expenditure from July to December peaked when chicks were being raised at the colony, especially for males before chicks departed the colony, and we argue that the high daily energy expenditure at that time is associated with increasing energy reserves to overcome poor foraging opportunities for males post-fledging, in support of the energy constraint hypothesis. Very high energy expenditure prior to chick departure may explain why murres and other members of Alcini conduct late chick-rearing at sea rather than at the colony.

Key words: *Uria lomvia*, sex-specific behaviour, colony departure, moult, migration, winter, diving

INTRODUCTION

Sex-specific differences in breeding behaviour are common among animals, and sex-specific constraints on energy demands at bottlenecks may cause sex-specific differences in behaviour at other periods of the annual cycle (the energy constraint hypothesis: Thaxter *et al.* 2009, Elliott *et al.* 2010, Pinet *et al*. 2012). Male, but not female, Thick-billed Murres *Uria lomvia* accompany and feed their single offspring for several weeks after the chick leaves the breeding site. In the last week of biparental offspring care at the colony, females increase provisioning rates to their offspring at a cost to their own condition, whereas males reduce provisioning rates, maintain condition and increase time spent submerged (Paredes *et al.* 2006; Thaxter *et al*. 2009, Elliott *et al*. 2010). It has been suggested (Thaxter *et al*. 2009, Elliott *et al*. 2010) that murre fathers increase time spent self-feeding and reduce time feeding their chick during the final week that the chick is at the colony because of the energy cost of provisioning for the chick post-departure ("energy constraint hypothesis"). That cost could be incurred owing to either reduced energy intake or increased energy expenditure.

During the post-colony period, both male and female murres moult all of their flight feathers sequentially (i.e. there is no period when all feathers are missing), resulting in a period of flightlessness associated with reduced dive capabilities (Bridge 2004). Such a period would presumably handicap males and females equally but may cause an additional burden on males feeding their offspring at that time. Furthermore, common murres *Uria aalge* congregate loosely in nursery areas where they apparently feed on invertebrates during the flightless period, rather than foraging on fish at denser patches, as they predominantly do during the breeding season (Davoren *et al*. 2002); in some cases, murres with chicks avoid high-quality patches for lower-quality, offshore patches with lower predation risk (Camphuysen 2002). The period of flightlessness in murres has never previously been examined on an individual basis, and one purpose of the current study is to describe that period in more detail.

To investigate the role of post-departure care in murres, we equipped six Thick-billed Murres with time-depth-temperature recorders to record diving behaviour and estimate daily energy expenditure during the transition from breeding to non-breeding. In support of the energy constraint hypothesis, we expected that daily energy expenditure for adult males would peak prior to the departure of the offspring from the colony and that foraging efficiency (rate of energy intake) would be low when males are constrained to forage with their offspring. We compare post-departure dive and flight behaviour, as well as daily energy expenditure, with behaviour during chick-rearing at the colony. A significant advantage of our study site was the large dataset of activity budgets and daily energy expenditure measurements of Thick-billed Murres previously collected during the breeding season (Elliott *et al.* 2008, 2013a,b), which could be drawn on for comparison. Due to our sample size of a single male presumed to have a chick, our results are necessarily preliminary and require further study.

METHODS

We attached nine LAT 1500 time-depth-temperature recorders (TDRs; Lotek Wireless, St. John's NL, Canada; 3.2 g, accuracy ±2 m) to the leg bands of breeding Thick-billed Murres at Coats Island, Nunavut, on 13–15 August 2009 (Table 1). We retrieved seven recorders the following year and were able to download data from six (two males and four females). We only report data from two males and two females. All TDRs logged temperature every 2 min. The duration recorded depended upon the amount of memory devoted to the temperature log, with birds' data recorded to March 15, June 23, June 25 and June 26, 2010, respectively. As we did not know the likely diving behaviour, we tried two different strategies for the pressure log (Table 1). The duration recorded depended upon the amount of memory devoted to the pressure log and the amount of diving by a particular bird. On 11 August 2010, we deployed another four TDRs. Of those, we were able to retrieve two. As reproduction at those sites was prevented by a polar bear *Ursus maritimus* in 2011 (Gaston & Elliott 2013), and the colony was not visited in 2012, these TDRs were retrieved in 2013. For this sample we attempted to record dive data in more detail by logging dive depth every 4 s when depth was greater than 5 m, but only a single dive log was uncorrupted, and that log ceased on 3 September 2010. The temperature logs recorded until 1 April 2011 and 22 June 2011, respectively. Bird sex was determined by partnership history, copulation behaviour or genetic analysis (Elliott *et al.* 2010). All time-depth-temperature data are presented in Appendix 1 (online only).

We calculated dive depth and an index of patch quality for each dive (Mori *et al*. 2002, Elliott *et al*. 2008). The index of patch quality is based on a theoretical model of optimal diving behaviour for defined relationships between dive depth, dive duration and surface interval duration (Mori *et al.* 2002). The index of patch quality increases with bottom time for a given dive depth, under the assumption that bottom time will be extended only if patch quality is high; otherwise, increasing bottom time will decrease dive efficiency by extending the duration of surface intervals. For each dive, we calculated the index of patch quality as:

$$IPQ = Ln\left[\frac{(1+3.18*0.0191e^{0.0191*Duration})(u-1.321*Depth)}{3.18e^{0.0191*Duration}+Duration}\right],$$

where Duration is dive duration and Depth is dive depth. The index of patch quality (IPQ in equation) correlates positively with energy delivered to the offspring by murres (Elliott *et al.* 2008) and prey encounter rates in seals equipped with cameras (Mori *et al.* 2005; Heaslip *et al.* 2014). We averaged dive depth, maximum dive depth per day, number of dives per day and patch quality across three day bins. For the TDR (attached to a female) that recorded dives >5 m, we excluded dives between 5 m and 10 m in depth. For the three TDRs that recorded dive depth to >10 m, we recalculated those same values, averaged across three days, including only dives >23 m. We used the regression between the two measurements ($R^2 > 0.82$), along with the measured average dive depth, maximum depth, patch quality and number of dives, to estimate the values between 10 m and 23 m for the TDR that recorded only dives >23 m (attached to a female). Thus, we had depth estimates for all dives >10 m from five TDRs.

We used the temperature log to determine sea surface temperature, time spent flying and time spent diving (Elliott *et al*. 2008, Linnebjerg *et al*. 2014). We used the formula presented by Daunt *et al*. (2003) to calculate ambient temperature and the depth log to calculate depth histograms, which we extrapolated using a Poisson distribution to determine total time spent diving in the day during the simultaneous deployment of depth and temperature logs. We used that relationship to calculate time spent diving from the temperature logs in the absence of depth information. Principally at night, birds tuck one leg into their body (Robertson *et al*. 2012, Linnebjerg *et al*. 2014). During leg tucks, the temperature recorder records high temperatures (Robertson *et al*. 2012), and we considered a leg tuck to have occurred when the ambient temperature (calculated with Daunt *et al*. 2003) was 2 °C above the average maximum weekly air temperature for that date at the Coral Harbour weather station. In practice, this meant that leg tucks were assumed to have occurred when the temperature was above ~9 °C; most leg tuck events were much warmer (Fig. 1).

We assumed that leg tucks represented resting or sleeping posture and that time spent resting on the water surface was equal to the time spent tucking the leg (twice the time recorded by the recorder, assuming that both legs were tucked equally). There was no relationship between sea surface temperature and percentage of the day spent tucking legs ($R^2 = 0.00$; $t_{321} = 0.05$, $P = 0.96$), supporting our assumption that leg tucks were associated with resting and not thermoregulation. Leg tucking occurred primarily at night, as was the case in a recent study by Robertson *et al*. (2012), although in our dataset a particular leg was tucked ~30% of the time at night compared with ~5% of the time at midday (Fig. 2a). We assumed that flights occurred only during daylight hours (Robertson *et al*. 2012, Fig. 2b).

TABLE 1
Tag deployments on six Thick-billed Murres[a]

Bird (band number)	Sex	Pressure log setting	Log started	Last day on colony	Flightlessness began	Flightlessness ended	Pressure log ended
99687028	M	6 s if >9 m	13 August 2009	31 August 2009[b]	1 Sept 2009	11 Nov 2009	6 Dec 2009
118600011	M	6 s if >9 m	15 August 2009	16 August 2009	20 August 2009	10 Nov 2009	11 Nov 2009
99685502	F	6 s if >9 m	14 August 2009	27 August 2009	28 August 2009	31 Oct 2009	26 Dec 2009
99671531	F	4 s if >23 m	15 August 2009	28 August 2009	29 August 2009	31 Oct 2009	15 Nov 2009
99689065	F	4 s if >5 m	11 August 2010	25 August 2010	26 August 2010	8 Nov 2010	3 Sept 2010
99656976	F	None	11 August 2010	22 August 2010	23 August 2010	6 Nov 2010	None

[a] All temperature logs lasted from the start of the pressure log to the end of the calendar year.
[b] Absent from colony 13 August 2009 to 15 August 2009.

Daily energy expenditure (DEE in equation) was estimated using the method of Elliott *et al*. (2013a). Their Table 1 gave daily energy expenditure in kilojoules per day as:

$$\mathrm{DEE} = 508\ T_f + 33\ T_c + 1.01\ \Sigma[1\text{-}e^{(\text{-Duration}/1.23)}] + 94\ T_w,$$

where T_f is hours per day spent flying, T_c is hours per day at the colony, Duration is dive duration in minutes (with the summation taken over all dives in each day) and T_w is hours per day spent at the water surface. There is no difference in the metabolic rate between murres resting on the water and in the air (Croll & McLaren 1992), and the relationship between metabolic rate and activity is the same in both media (Elliott *et al*. 2013b). Thus, the measured difference in metabolic rate between birds at the water surface and birds at the colony (Elliott *et al*. 2013a) likely arises because of differences in activity and thermoregulation. We subdivided time spent on the water into T_r, hours spent resting at the water surface with leg tucked, and T_s, hours spent active at the water surface. As we could account for the effect of thermoregulation (Croll & McLaren 1992; see below), we attributed all of the residual variation to differences in activity. Our equation for DEE assumed that the metabolic rate of birds resting on the water surface was similar to that of birds resting at the colony (i.e. that the coefficient for T_c and T_r is the same for a constant temperature):

$$\mathrm{DEE} = 508\ T_f + 33\ (T_c + T_r) + 1.01\ \Sigma[1\text{-}e^{(\text{-Duration}/1.23)}] + 94\ T_s$$

Elliott *et al*. (2013a) found no effect of temperature on daily energy expenditure using a narrow range of temperatures experienced during each activity; therefore, we estimated the effect of temperature on metabolic rate using information in Croll & McLaren (1992), who measured metabolic rate relative to temperature for murres in water. The equation was altered so that at T = 7 °C (average sea surface temperature at the colony) the average metabolic rate for murres at the water surface was 94 kJ/h, the same as measured by Elliott *et al*. (2013a) in that context. Thus, further, at T = 15 °C (average air temperature at the colony) the average metabolic rate when resting at the water surface was 33 kJ/h, the same as that measured by Elliott *et al*. (2013a) when birds were at the colony:

$$\mathrm{DEE} = 508\ T_f + 33\ T_c + 1.01\ \Sigma[1\text{-}e^{(\text{-Duration}/1.23)}] + (113\text{-}2.75T)\ T_w + (72\text{-}2.75T)\ T_s$$

where T = sea surface temperature.

We report previously collected dive data (n = 105 females and 131 males) at Coats Island to provide average diving behaviour during the colony period (Elliott *et al*. 2008, 2010). We also report previously collected daily energy expenditures derived from doubly labelled water (Elliott *et al*. 2013a,b) to provide daily energy expenditure during the colony period. For four three-day periods during incubation during which we lacked daily energy expenditure data from doubly labelled water, we calculated values using the equation for DEE provided in the previous paragraph. Thus, when possible, we used direct measurement of DEE from doubly labelled water. Otherwise, we used the final equation above to calculate DEE from time budgets. Elliott *et al.* (2013a,b) demonstrated that these two techniques are strongly correlated with one another and without systematic bias.

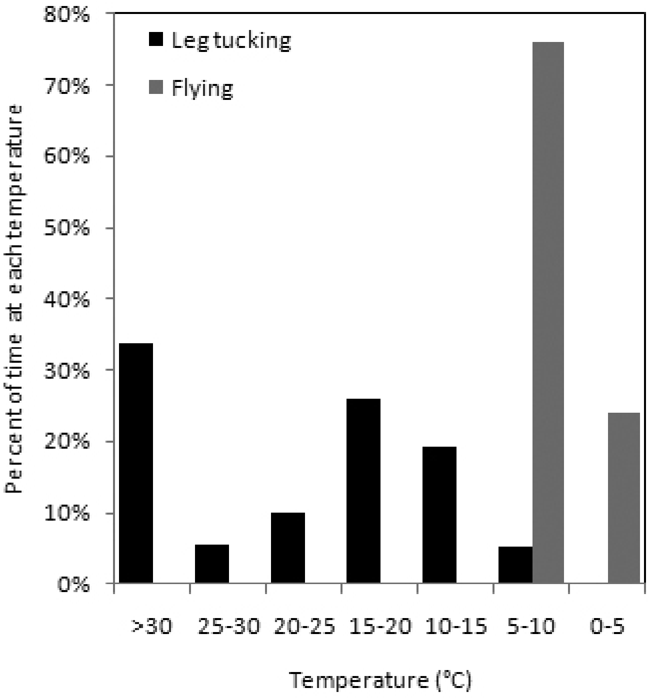

Fig. 1. Temperature records associated with legs tucked into feathers (black bars) or flying (grey) for Thick-billed Murres tagged at Coats Island. Leg tucks were mainly associated with temperatures >10 °C.

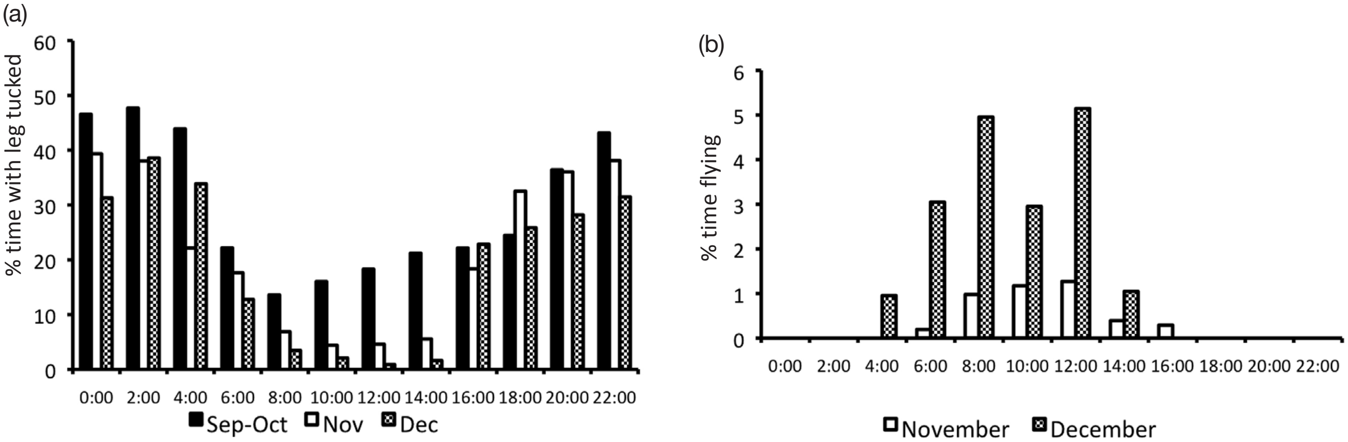

Fig. 2. Proportion of time spent with leg tucked (a) and flying (b) in relation to time of day for Thick-billed Murres tagged at Coats Island. None of the birds registered any flying during September–October.

We used *z*-tests to compare the distribution of average values measured during post-departure for all other individuals to the value recorded for the single individual male presumed to be with a chick.

RESULTS

The male presumed to have departed with a chick that survived (hereafter "the male with chick") left the colony on 16 August and began the flightless period, which lasted 82 days, on 20 August. The other five birds left between 22 August and 31 August and began the flightless period between 23 August and 1 September (Table 1). Flightlessness lasted 63–75 days (mean 69.4 SD 5.6 days). Hence, the male with chick had a slightly longer flightless period than the 95% interval for the other five birds (81.1 days, $z = 2.32$, one-tailed $P = 0.04$). During the period from mid-August to the end of September the male with chick made many more dives per day (rising from ~120/day in August to ~200/day in late September, Fig. 3) than the other study birds (~50/day, $z = 30.6$, one-tailed $P < 0.0001$). At the same time, the patch quality for the male with chick declined from -0.8 to -1.2, and tended to be lower than for the other study birds (Fig. 4, $z = 2.06$, one-tailed $P = 0.05$). The mean and maximum dive depth of this bird in the second half of September tended to be greater than those recorded for other individuals (mean depth $z = 3.23$, one-tailed $P = 0.03$), although this was mostly because the male with chick tended to dive more in the day than at twilight, Fig. 3. In late September its behaviour, in terms of dive frequency, changed abruptly and from then onwards became similar to the behaviour of the other birds. We assume that this abrupt change in behaviour coincided with the independence or death of its chick.

During October and November, by which time we assume that all individuals were foraging only for themselves, there was no clear difference in behaviour between males and females. However, the dive frequency of females decreased and dive depth increased after late November (Fig. 4). The deepest dive was 155.5 m and occurred on 15 December.

As expected, energy expenditure peaked in the late chick-rearing period, especially for males (Fig. 5). It then fell abruptly, presumably coincident with the cessation of chick feeding on the colony, remained fairly low until late October and then increased gradually, perhaps in response to decreasing temperature and increased time spent flying during migration. Daily energy expenditure was not obviously different for the male with chick than for the other study birds.

DISCUSSION

In comparison to the four female murres, one male murre spent the period after departure from the colony foraging intensively (many dives per day) at low-quality foraging patches. Likewise, the other male murre, which returned to the colony after only three days at sea post-departure, dived many times per day at low-quality foraging patches during that three-day period. From these preliminary data, it appears that male and female behaviour differs more during the post-departure period than during any other period in the latter half of the annual cycle. During this period, males appear to be constrained to forage at low-quality patches by the need to remain with the chick, supporting the energy constraint hypothesis. It appears that the energy constraint was created by reduced energy intake rates (lower patch quality), rather than by increased energy expenditure. In contrast, females and the male without a chick spent one day at sea while still able to fly prior to the cessation of flights and presumed onset of flightlessness (Table 1). During that day (or via sampling during extended visits away from the colony prior to their final departure), individuals can gain altitude to search out foraging flocks and sample multiple patches to choose an optimal area to remain during the post-breeding period. This, coupled with the extended period at the colony after the chick's departure, would allow females to quickly regain the condition lost during the latter part of the chick-rearing period.

Since Lack's (1968) time, it has been assumed that chick-rearing is the most costly period for birds (Drent & Daan 1980, Gaston 1985).

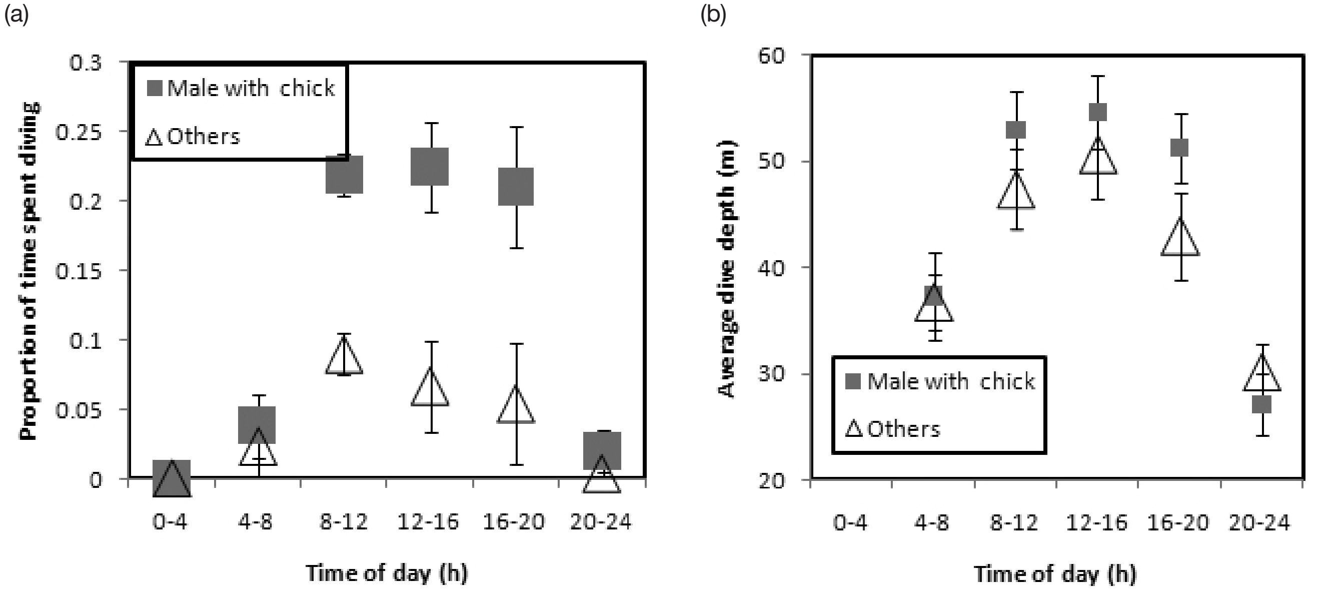

Fig. 3. Proportion of time spent diving (a) and average dive depth (b) for 4 h blocks over the course of the day for the flightless period for Thick-billed Murres tagged at Coats Island. Only dives >10 m in depth were included; the individual whose logger was set to record >23 m was not included in these analyses. We could not analyze similar data for the migratory period because most loggers ceased deploying prior to December.

Our results confirm this assumption, at least for a species with exceptionally high flight costs in which the semi-precocial fledging strategy is likely linked to those high costs (Elliott *et al*. 2014). Other studies have also found that energy expenditure peaks during chick-rearing (Bryant & Tatner 1988, Masman *et al*. 1988, Gales & Green 1990, Green *et al*. 2009). The very high flight costs in late chick-rearing likely explain why murres are unable to continue to rear their chick at the breeding site and why the chick departs the colony at one-third of adult size (Gaston 1985, Houston *et al*. 1996, Elliott *et al*. 2014).

Our estimates of the flightless period, presumably indicative of primary moult, are the first published for Thick-billed Murres and suggest that females and males unaccompanied by chicks

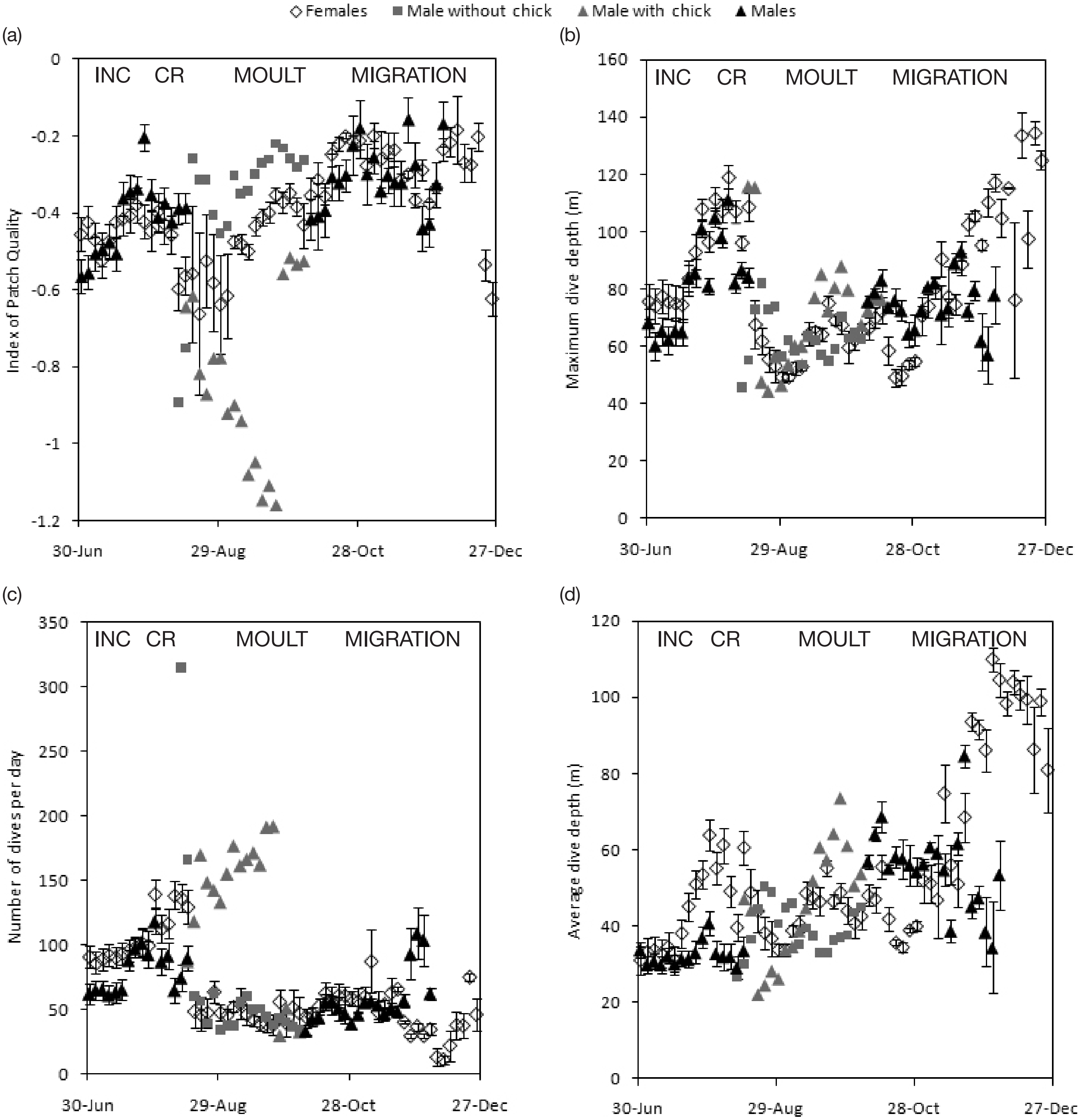

Fig. 4. (a) Index of patch quality for dives >10 m, (b) maximum dive depth, (c) number of dives >10 m per day and (d) average dive depth for dives >10 m for Thick-billed Murres tagged at Coats Island. Shown are average values for females, average values for males prior to tagging and post-chick (after 5 October), and the values for one male that departed successfully with a chick and one male that apparently lost a chick soon after leaving the colony. Also shown are the approximate time periods of different components of the breeding cycle. INC = Incubation, CR = Chick rearing

are flightless for 9–10 weeks. The male accompanied by a chick seems to have taken longer to moult (12 weeks), perhaps because of the energy constraint already identified, but the difference, although suggestive, is only marginally significant. Alternatively, the father may delay moulting until after the chick achieves independence. A delay in the completion of moult, possibly postponing migration, could have fitness consequences for successful fathers.

The deep diving noted for females after the beginning of December coincided with the period when geolocator-tracked birds from northern Hudson Bay moved through Hudson Strait and into Davis Strait (Gaston *et al*. 2011, Tranquilla-McFarlane *et al*. 2013). Despite a dataset of ~25 400 dives from five birds (the sixth bird's depth channel failed), compared with a dataset of over 100 000 dives from hundreds of birds during the breeding period (Croll *et al*. 1992, Elliott *et al.* 2008), the winter observations reported here contain a new depth record for a Coats Island Thick-billed Murre: 155.5 m. Other studies have also shown that murres dive exceptionally deep during mid-winter (Fort *et al*. 2013), when they are foraging primarily in pelagic waters and are not constrained by shallow bathymetry around colonies, although murres that remained near their colony off southwest Greenland showed no seasonal depth variation (Linnebjerg *et al*. 2013). Murres seldom dive deeper than ~140 m around most colonies (Paredes *et al*. 2008, Takahashi *et al*. 2008, Thaxter *et al*. 2009, Evans *et al*. 2013, Linnebjerg *et al*. 2013). It remains a mystery how murres are able to locate pelagic, mobile prey 150 m below the surface during relatively brief dives (<5 min).

We necessarily made several assumptions in our calculations of time budgets: (1) leg tucks were representative of time spent resting; (2) activity costs derived during the breeding season are representative of diving costs at other times of the year despite annual variation in body mass; and (3) there was no significant cost associated with moulting. Accelerometers or heart rate recorders that clearly distinguish flight from other activities would permit refinement of energetic models, especially given the high cost of flight in murres (Elliott *et al*. 2013a). Dynamic body acceleration at the water surface is a strong predictor of energy expenditure (Elliott *et al*. 2013b), and year-round deployment of accelerometers would refine estimates of energy expenditure at the water's surface, eliminating the need for our first assumption. Furthermore, our sample size of a single male presumed to have a chick is clearly inadequate for strong conclusions, as inter-individual variation may have been particularly stark for that individual. These issues clearly require further study with larger samples.

Events occurring at one portion of the annual cycle can impact events occurring at another portion of the annual cycle (Sorenson *et al*. 2012, Betini *et al*. 2013). Specifically, energy constraints during the non-breeding season may impact the timing of migration and behaviour during the breeding season (Crossin *et al*. 2012, Sorenson *et al*. 2012, Schultner *et al*. 2014). Our results suggest that such "carry-over effects" from one stage of the breeding season to a subsequent stage may impact one sex more than the other. Similarly, Green *et al*. (2009) demonstrated that male Macaroni Penguins have high daily energy expenditure during incubation and low daily energy expenditure during brooding, while females show the opposite patterns. Sex-specific carry-over effects may play an important role in determining sex-specific behaviour in a broad range of animals.

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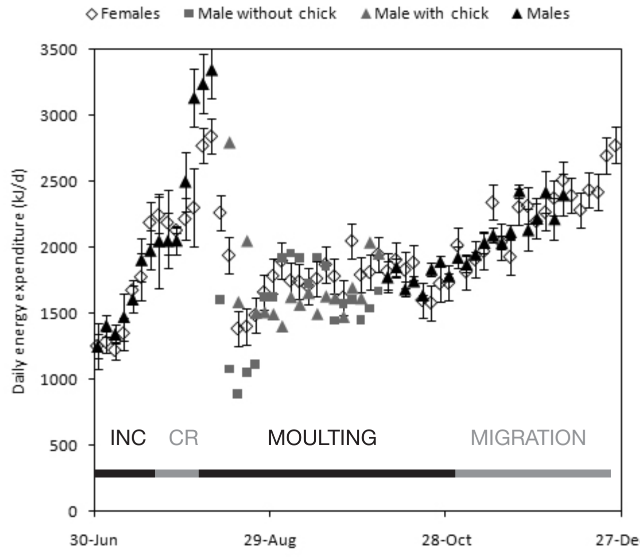

Fig. 5. Daily energy expenditure for Thick-billed Murres tagged at Coats Island. Shown are average values for females, average values for males prior to tagging and post-chick (after 5 October) and the values for one male that departed successfully with a chick and one male that apparently lost its chick. Values during incubation (INC) and chick-rearing (CR) were measured directly using doubly labelled water. Values during moulting and migration were inferred from time budgets.

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