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Age-related variation in energy expenditure in a long-lived bird within the envelope of an energy ceiling

Kyle H. Elliott[1]*, Maryline Le Vaillant[2,3,4], Akiko Kato[2,3], Anthony J. Gaston[5], Yan Ropert-Coudert[2,3], James F. Hare[1], John R. Speakman[6,7] and Donald Croll[8]

[1]*Department of Biological Sciences, University of Manitoba, Winnipeg, MB R3T 2N2, Canada;* [2]*Université de Strasbourg, IPHC, 23 rue Becquerel, 67087 Strasbourg, France;* [3]*CNRS, UMR7178, 67037 Strasbourg, France;* [4]*Department of Zoology, Stockholm University, SE-106 91 Stockholm, Sweden;* [5]*Science & Technology Branch, Environment Canada, Ottawa, ON K1A 0H3, Canada;* [6]*Institute of Environmental and Biological Sciences, University of Aberdeen, Tillydrone Ave, Aberdeen, AB24 2TZ, UK;* [7]*Key State Laboratory of Molecular Developmental Biology, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, 1 West Beichen Road, Chaoyang, 100101, Beijing, China; and* [8]*Department of Ecology & Evolutionary Biology, University of Santa Cruz, 100 Shaffer Road, Santa Cruz, CA 95060, USA*

Summary

1. Energy expenditure in wild animals can be limited (i) intrinsically by physiological processes that constrain an animal's capacity to use energy, (ii) extrinsically by energy availability in the environment and/or (iii) strategically based on trade-offs between elevated metabolism and survival. Although these factors apply to all individuals within a population, some individuals expend more or less energy than other individuals.

2. To examine the role of an energy ceiling in a species with a high and individually repeatable metabolic rate, we compared energy expenditure of thick-billed murres (*Uria lomvia*) with and without handicaps during a period of peak energy demand (chick-rearing, $N = 16$). We also compared energy expenditure of unencumbered birds ($N = 260$) across 8 years exhibiting contrasting environmental conditions and correlated energy expenditure with fitness (reproductive success and survival).

3. Murres experienced an energy ceiling mediated through behavioural adjustments. Handicapped birds decreased time spent flying/diving and chick-provisioning rates such that overall daily energy expenditure remained unchanged across the two treatments. The energy ceiling did not reflect energy availability or trade-offs with fitness, as energy expenditure was similar across contrasting foraging conditions and was not associated with reduced survival or increased reproductive success.

4. We found partial support for the trade-off hypothesis as older murres, where prospects for future reproduction would be relatively limited, did overcome an energy ceiling to invest more in offspring following handicapping by reducing their own energy reserves. The ceiling therefore appeared to operate at the level of intake (i.e. digestion) rather than expenditure (i.e. thermal constraint, oxidative stress).

5. A meta-analysis comparing responses of breeding animals to handicapping suggests that our results are typical: animals either reduced investment in themselves or in their offspring to remain below an energy ceiling. Across species, whether a handicapped individual invested in its own energy stores or its offspring's growth was not explained by life history (future vs. current reproductive potential). Many breeding animals apparently experience an intrinsic energy ceiling, and increased energy costs lead to a decline in self-maintenance and/or offspring provisioning.

Key-words: device effects, doubly labelled water, energy ceiling, extrinsic limitation, intrinsic limitation, repeatability, thick-billed murre, *Uria lomvia*

*Correspondence author. E-mail: urialomvia@gmail.com

Introduction

Even under conditions of unlimited energy availability, energy expenditure in wild animals is limited (Drent & Daan 1980; Peterson, Nagy & Diamond 1990; Hammond & Diamond 1997). Expenditure may be limited by 'decisions' linked to individual fitness, such as trade-offs between expenditure and survival or intrinsically by the animal's ability to process energy (Speakman *et al*. 2003; Green *et al*. 2009; Welcker *et al*. 2010). For instance, digestive efficiency may limit energy intake per unit time while thermal or metabolic constraints may limit energy expenditure per unit time (Hammond & Diamond 1997; Heath, Gilchrist & Ydenberg 2010; Speakman & Król 2010). Consequently, internal constraints on energy processing may impose an 'energy ceiling' – a maximum limit to energy expenditure averaged over a long enough period for expenditure to be balanced by intake. The existence of such a limit has been supported in some studies of wild animals (Drent & Daan 1980; Moreno *et al*. 1999; Tinbergen & Verhulst 2000; Table 1), and interspecific comparisons support the idea of an intrinsic constraint as animals seldom exceed a long-term energy ceiling of 7× basal metabolic rate (Ricklefs, Konarzewski & Daan 1996; Hammond & Diamond 1997; Speakman 2000).

Whether an individual operates near its energy ceiling will depend partly on the costs and benefits of energy expenditure. For example, animals may exist below their ceiling and increase energy expenditure when energy availability or demand increases (flexible investment strategy: Speakman *et al*. 2003; Jodice *et al*. 2006; Welcker *et al*. 2009; Harding *et al*. 2009). Alternatively, animals may

Table 1. None of the studies that examined daily energy expenditure with and without handicapping showed statistical significance at the sequential Bonferroni-corrected α-value of 0·004. The overall effect size across all 13 studies is −0·01 (SE = 0·33, z-test $P = 0·51$). In contrast, five of six studies that examined locomotory costs for similar-sized handicaps revealed statistical significance at the sequential Bonferroni-corrected α-value of 0·017

Species (L = Laboratory study; **Non-flyers in bold**)	Handicap (as a percentage of body mass)	Energy expenditure ± SD		P	Source
		Handicapped (N)	Non-handicapped (N)		
Daily energy expenditure (kJ per day)					
Thick-billed murre[a]	Accelerometer (1·7%)	1926 ± 405 (16)	2036 ± 552 (16)	0·25[c]	Our study (2009 only)
White-tailed tropicbird[a]	Radiotransmitter (2·2%)	1693 ± 803 (5)	778 ± 244 (5)	0·04	Pennycuick *et al*. (1990)
Brant (L)	Dummy radio (2·9%)	550 ± 137 (4)	594 ± 103 (4)	0·62	Sedinger, White & Hauer (1990)
Northern bobwhite (L)	Radiotransmitter (3·1%)	157 ± 23 (5)	150 ± 6 (5)	0·77	Hernández *et al*. (2004)
Common tern[a]	Radiotransmitter (6·2%)	368 ± 58 (6)	343 ± 37 (7)	0·45	Klaassen, Becker & Wagener (1992)
Zebra finch (L)	Backpacks (27%)	48·1 ± 7·9 (9)	53·4 ± 6·6 (7)	0·34	Nudds & Bryant (2002)
House wren[a]	Wings clipped by 4·2%	43·0 ± 3·1 (16)	40·5 ± 2·6 (16)	0·18	Tieleman *et al*. (2008)
Pied flycatcher[a]	Removed two primaries	64·2 ± 5·4 (9)	61·2 ± 5 (13)	0·37	Moreno *et al*. (1999)
African penguin[a]	Swim speed logger (0·6%)	2007 ± 405 (5)	2433 ± 796 (10)	0·29	Nagy, Siegfried & Wilson (1984)[d]
Adélie penguin[a]	Dummy (0·8%)	5323 ± 1115 (4)	5790 ± 1115 (4)	0·71	Culik & Wilson (1992)
Little blue penguin[a]	Activity logger (5·5%)	1349 ± 112 (6)	1671 ± 130 (4)	0·04	Gales, Williams & Ritz (1990)
Takahe[b]	Radiotransmitter (1·9%)	1274 ± 42 (6)	1174 ± 42 (6)	0·03[c]	Godfrey, Bryant & Williams (2003)
Meadow vole (L)	Radiotransmitter (7·9%)	92 ± 16 (10)	91 ± 17 (10)	0·45	Berteaux *et al*. (1996b)
Locomotory (flying or swimming) costs (kJ per hour) associated with attaching a device that primarily increased body drag rather than load					
Thick-billed murre[a,g]	Accelerometer (1·7%)	631 ± 111 (16)	505 ± 114 (16)	0·0005	Our study (flight)
Rock pigeon	Dummy (2·5–5%)	292 ± 45 (8)	158 ± 22 (8)	<0·0001[c]	Gessaman & Nagy (1988)
Rose-coloured starling (L)[f]	Box + antennae (2·6%)	0·225 ± 0·064 (3)[e]	0·116 ± 0·040 (3)[e]	<0·0001	Pennycuick *et al*. (2012)
Adélie penguin (L)[f]	Dummy (0·8%)	435 ± 30 (5)	334 ± 7 (4)	0·0003	Culik & Wilson (1991)
Atlantic cod (L)[f]	Dummy (3·1%)	146 ± 14 (7)	127 ± 5 (7)	0·01	Steinhausen, Andersen & Steffensen (2006)
European eel (L)[f]	Dummy (1·6%)	27·4 ± 8·6 (9)	25·4 ± 6·9 (9)	0·60	Methling *et al*. (2011)

[a]Measured while rearing offspring.
[b]Flightless runner; change in energy costs thought to reflect changes in thermoregulation.
[c]Pairwise comparisons of the same individuals with and without handicaps.
[d]Recalculated from values presented in their Tables 1 and 2 during the period away from the colony.
[e]Drag coefficient; we only reported on experiments with live animals as coefficients on frozen specimens are unrealistic (Pennycuick *et al*. 2012).
[f]Studies used respirometry (all other studies used doubly labelled water).
[g]General linear model output including all four activities (see Methods) had $R^2 = 0·72$.

exist at a ceiling and hold energy investment constant in spite of increased energy availability or demand, as occurs when parents maintain investment in reproduction when energy costs are increased via a handicap experiment (fixed investment strategy: Tinbergen & Verhulst 2000; Paredes, Jones & Boness 2005; Leclaire *et al.* 2011). However, behavioural adjustments to handicapping may not reflect an underlying energy ceiling because those behaviours may cause individuals to increase or decrease daily energy expenditure, because changes in behaviours may reflect reduced foraging efficiency without any change in energy costs or because changes in maintenance costs may counteract the effect of changes in activity budgets (Drent & Daan 1980; Green *et al.* 2009). In support of the last possibility, hunter-gatherers have the same daily energy expenditure as Westerners despite having higher activity levels presumably due to reductions in other energy costs among hunter-gatherers (Pontzer *et al.* 2012). In support of an energy ceiling, animals that are handicapped with increased locomotory costs exhibit no change in daily energy expenditure (Table 1).

Although average energy expenditure is often remarkably constant across environmental conditions, there can be considerable individual variation in energy expenditure (Speakman 2000; Speakman 2008; Welcker *et al.* 2010). If energy is limited intrinsically how can some individuals expend more energy than other individuals? Why aren't all individuals limited by the ceiling? One possibility is that the variation represents error associated with short-term measurements; energy budgets may be balanced over longer time-scales. Although daily energy expenditure is limited at about 7× basal metabolic rate (Peterson *et al.* 1990; Hammond & Diamond 1997), short-term activity costs can exceed 30× basal metabolic rate (Elliott *et al.* 2013b), and variation in activity budgets can cause variation in apparent daily energy expenditure over short time-scales. If the variation is due to measurement error, daily energy expenditure would not be expected to be repeatable across time. Another possibility is that variation in internal constraints, such as thermal properties or digestive abilities, may limit all individuals but that there is nonetheless variation in the internal morphology that causes individual variation in energy expenditure. In that case, one would expect energy expenditure to be repeatable across time. Alternatively, some individuals may invest more heavily in offspring by feeding them more often, possibly at the cost of their future survival. In that case, energy expenditure may be repeatable but also positively correlated with feeding rates and negatively correlated with survival at the level of the individual.

Auks are good models for examining the role of energy ceilings because the high activity costs in chick-rearing auks impose high daily energy expenditures and they are therefore likely to be at or near an energy ceiling (Roby & Ricklefs 1986; Elliott *et al.* 2013a,b). Indeed, the high cost of provisioning in some auks (e.g. murres, *Uria* spp.) is partially responsible for their semi-precocial fledging strategy, where the single offspring leaves the breeding site while still unable to fly and completes its growth at sea (Ydenberg 1989; Houston, Thompson & Gaston 1996). Chick-rearing birds in general appear unable to work harder to produce more offspring (Lack's principle; Drent & Daan 1980).

We measured daily energy expenditure and activity budgets of a diving auk, the thick-billed murre (*Uria lomvia*), to test for evidence of an energy ceiling and the expression of either a flexible or fixed investment strategy in the presence and absence of handicaps and across years of differing prey availability. We examined mechanisms underlying a potential energy ceiling, such as whether energy was adjusted by altering behaviour (rather than maintenance costs, for example, which account for *c.* 30% of murre daily energy expenditure during chick-rearing; Elliott *et al.* 2013b), and whether energy was limited at the level of energy intake (e.g. digestive bottleneck) or expenditure (e.g. thermal constraint). First, we tested whether (i) daily energy expenditure was a repeatable trait of the individual. Demonstrating that daily energy expenditure was an inherent trait of the individual was essential prior to asking whether there could be fitness consequences to energy expenditure. Next, we tested the ideas that energy expenditure was limited by (ii) energy availability (environmental conditions that varied between handicapping treatments and among years), (iii) an intrinsic ceiling, or (iv) survival costs such that birds with high expenditure experienced increased reproductive investment but also greater mortality (Table 2).

Materials and methods

We used four separate methods: (i) we attached handicaps and examined energy expenditure, activity costs, survival and adult investment in energy for its own reserves (body mass change) and offspring (energy delivered to offspring) with and without handicaps; (ii) we measured energy expenditure in years of contrasting food availability; (iii) we correlated energy expenditure against fitness (survival and reproduction); and (iv) we conducted a meta-analysis to place our results within the broader life-history continuum (Table 2). We measured the energy expenditure of chick-rearing murres across 8 years, incubating murres across 4 years and murre chicks in 2 years. Across all 8 years, we recorded two accurate indicators of feeding conditions: 14-day old chick mass and change in adult energy reserves between incubation and chick-rearing (Gaston & Hipfner 2006). Methods are described in greater detail in the 'Detailed Methods'.

DAILY ENERGY EXPENDITURE: DOUBLY LABELLED WATER AND TIME BUDGET ANALYSES

We injected murres intramuscularly (1987–1988) or in the brood patch (2006, 2009) with doubly labelled water. The optimal method for measuring equilibrium isotopic values in murres is the plateau method at 90–120 min using the ^{18}O equilibrium value (Jacobs *et al.* 2012). We obtained equilibrium blood

Table 2. Predictions derived from the five hypotheses tested in our study

Hypothesis	Prediction	Method	Supported?
1. Repeatability	Energy expenditure for a given individual would be repeatable across time	Measure energy expenditure for the same individual within and across years	Yes
2. Energy availability[a]	Energy expenditure would vary across environmental conditions	Measure energy expenditure across years and handicapping treatments.	No
3. Ceiling	Energy expenditure would not vary across environmental conditions or be associated with fitness	Same as for (2) and (4)	Yes
4. Trade-offs[a]	(i) Energy expenditure would be associated with fitness trade-offs: birds that fed their offspring more often would be more active (higher energy expenditure) but have lower survival. (ii) Regardless of what limits energy expenditure, increased investment in energy for adult energy stores (self-feeding) when environmental conditions deteriorate would mean decreased energy available to feed offspring. However, older birds and short-lived bird species, both with lower future reproductive potential, would expend more energy feeding offspring when environmental conditions deteriorate because their current brood value is higher	(i) Correlate reproductive success and survival with energy expenditure. (ii) Measure adult mass loss (an indication of self-feeding), chick provisioning rate and energy expenditure with and without handicaps	Partially (i) No (ii) Yes, except short-lived birds did not invest more in offspring and less in themselves than long-lived birds

[a]Meta-analysis used to examine whether results held across broader taxonomic groups.

samples at 120 min (1987–88) or 90 min (2006–2009). We recaptured the birds and obtained a second blood sample from the brachial vein 24–72 h later. Samples were timed as close to multiples of 24 h as possible to avoid circadian effects (Speakman & Racey 1988). As longer sampling periods reduce the error due to day-to-day variance in daily energy expenditure (Speakman & Racey 1988), we calculated daily energy expenditure over the extended time period for individuals that were recaptured more than once for second blood samples. All samples were run blind to the identity of the bird and converted to values of daily energy expenditure using a single pool model with a fixed 25% evaporative water flux (equation 7·17: Speakman 1997) and a respiratory quotient of 0·81. Using this equation, estimates for energy expenditure based on doubly labelled water in auks are accurate within 2–18% relative to respirometry values from the same individual and within 3% relative to the average respirometry value across the group (Shirai *et al.* 2012). Analytical errors in individual DLW measurements were generated by iterating the replicate data at each position in the equation to generate a distribution of estimates. Using different equations for calculating daily energy expenditure results in different absolute values for energy expenditure (Speakman & Krol 2005; Shaffer 2011), but within our data set those differences had no effect on the hypotheses we tested because we examined only relative differences and we used the same equation for all analyses. For those years when we did not measure daily energy expenditure using doubly labelled water, we estimated daily energy expenditure from time budgets. To convert time budgets into daily energy expenditure, we used activity-specific metabolic rates that explained 72% of the variation in daily energy expenditure (from Table 1 in Elliott *et al.* 2013b). We also calculated activity-specific metabolic rate with and without handicaps.

HANDICAPPING

In 2006 and 2009, we equipped all individuals (including handicapped birds) with time-depth-temperature recorders (3–5 g, Lotek Wireless, Canada) that allowed us to determine time spent flying, diving, resting on water and resting on land (Elliott *et al.* 2009). The small recorders were attached to the leg and had no measurable impact on behaviour (Elliott, Davoren & Gaston 2007; see also Ropert-Coudert *et al.* 2009). In 1999, 2009 and 2010 we used Tesa tape to attach handicaps (1·7–2·8% of murre body mass) to the lower back of murres. In 2009, we measured energy expenditure over 48 h using doubly labelled water for 16 individuals with and without handicaps. We sampled the same individuals twice (24 and 48 h); we measured energy expenditure during 24 h with the handicap and 24 h without the handicap for each individual.

SURVIVAL AND REPRODUCTIVE FITNESS: ADULT SURVIVAL, MASS LOSS AND ENERGY DELIVERED TO OFFSPRING

Our project is part of a long-term study (1981–2011) and all birds were marked, often in the year they hatched, with a unique metal leg band. To determine survival, we resighted handicapped and *c.* 100 unhandicapped individuals in the year following handicapping. We also examined survival in relation to non-handicapped energy expenditure in 2004–2009 (we have no information from the 1980s, when experiments occurred away from the main study area). Estimates of apparent survival were robust as we resighted upwards of 80% of unequipped birds, except in 2011 when polar bear *Ursus maritimus* disturbance reduced resighting probabilities (Gaston & Elliott 2012). We used energy delivered to the offspring as a proxy for reproductive fitness, as energy delivered

to the offspring is closely linked to offspring energy reserves at fledging and post-fledging reproductive success (see model in Elliott, Crump & Gaston 2010). Using mass–length relationships and energy densities derived from prey collected at our study site, we converted feeding watch data into energy delivered per day (Elliott, Davoren & Gaston, 2008). We measured adult body mass before and after handicapping and for a separate group of control (unhandicapped) birds.

META-ANALYSIS AND STATISTICAL ANALYSES

To provide a taxonomic context for our results, we searched the literature for studies that added loads, clipped wings or attached recorders and reported both changes in chick-provisioning rates (or chick growth rates), adult body mass or daily energy expenditure relative to controls. Because there were relatively few studies that reported daily energy expenditure, we simply compared the effect size (the difference in average values divided by root mean square of their standard deviations) of energy expenditure among the different studies. For the larger sample of studies that reported adult body mass and chick-provisioning/growth rates in birds, we report values as residuals after accounting for degree of handicapping (per cent wing area reduction for wing clipping, per cent mass increase for added load and per cent cross-sectional area increase for back-mounted devices). Brood value for interspecific studies was calculated following Bókony *et al.* (2009) and incorporating phylogenetically independent contrasts. To compare our own individual murre values, we calculated brood value for individual murres as the most-probable number of subsequent clutches an individual is likely to produce for its age based on age-specific survival at our colony. We used R 2.10.1 for all statistical analyses, with an $\alpha = 0{\cdot}05$ and report all values as means ± SD. We used a general linear model including all interactions to describe daily energy expenditure during chick-rearing with sex, ambient temperature, body mass, body mass change, time to recapture and chick age as independent variables.

Results

INTERYEAR VARIATION

For those individuals where daily energy expenditure was measured in multiple years, energy expenditure in 1 year ('years') was strongly linked with energy expenditure in another year (year 1 = 2060 ± 335 kJ per day; year 2 = 2073 ± 411 kJ per day; Fig. 1b). Likewise, energy expenditure measured via doubly labelled water over 48 h ('days') was correlated with energy expenditure in the subsequent 48 h (period 1 = 2048 ± 609 kJ per day; period 2 = 2080 ± 592 kJ per day; Fig. 1b). Across all 8 years, energy expenditure did not vary with sex, ambient temperature, body mass, body mass change, time to recapture, or chick age (all $P > 0{\cdot}2$). In particular, energy expenditure did not vary among years (Fig. 1c). A power analysis demonstrated that we had an 87% probability of detecting a significant difference at $\alpha = 0{\cdot}05$, given our sample size and an effect size of 10%. Adult body mass ($F_{7,122} = 3{\cdot}81$, $P < 0{\cdot}001$), 14-day chick mass ($F_{7,275} = 8{\cdot}37$, $P < 0{\cdot}001$) and incubation daily energy expenditure (average = 1327 ± 400 kJ per day; Fig. 1c) also varied among

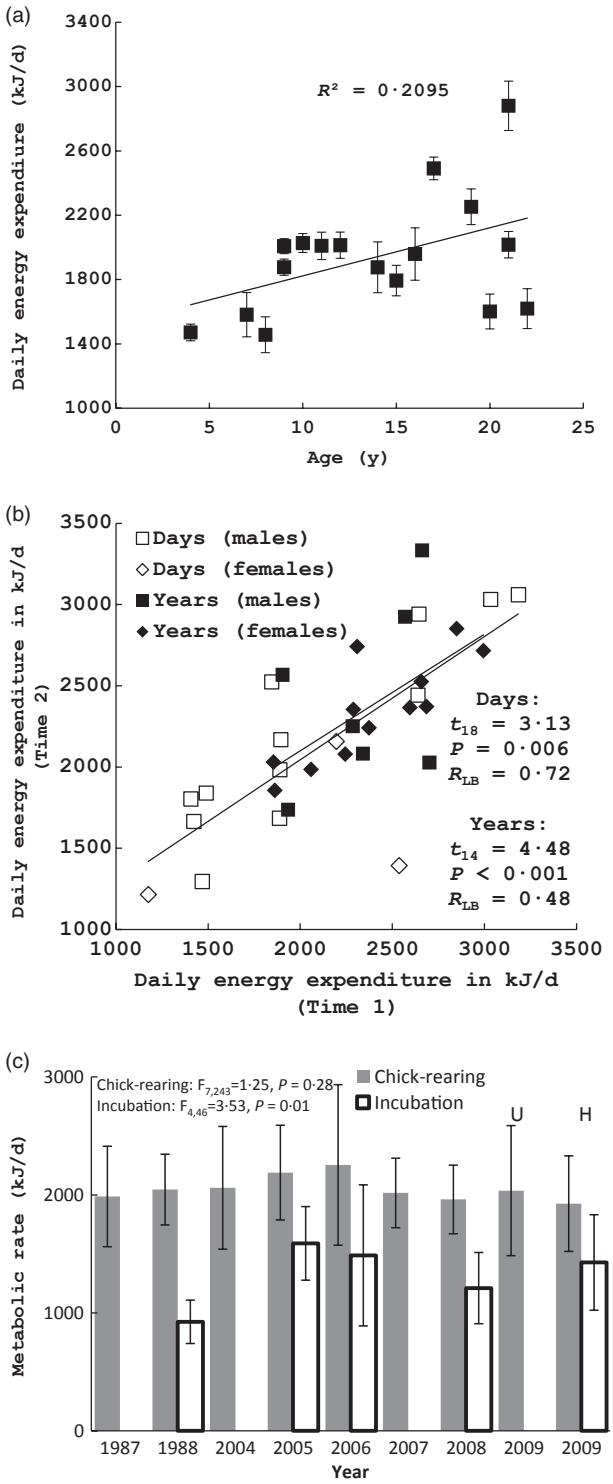

Fig. 1. (a) Daily energy expenditure for handicapped birds changes with age in chick-rearing thick-billed murres. Uncertainty in doubly labelled water measurements were calculated using a jackknife approach. Calculations were made using the mean at each point and systematically omitting individual data points. Multiplying the standard deviation of the resulting confidence interval by 1·96 created the estimated uncertainty. (b) Daily energy expenditure for unhandicapped birds is repeatable across time. Lessells & Boag (1987) repeatabilities are shown. (c) Average ± SD energy expenditure during reproduction across eight years (U = non-handicapped, H = handicapped for 2009).

years. The effect sizes were 68% for adult body mass, 72% for chick growth rates and 52% for incubation energy expenditure. Chick energy expenditure was 289 ± 129 kJ per day pooled across both years.

HANDICAPPING

Overall energy expenditure did not differ significantly between handicapped and non-handicapped birds (pairwise difference = 172 kJ per day ± 572 kJ per day; pairwise $t_{15} = 1{\cdot}20$, $P = 0{\cdot}25$, Table 2). Birds equipped with accelerometers reduced time spent flying (handicapped: 11·6 ± 6·2% of time away from the colony; non-handicapped: 18·5 ± 7·5% of time at sea; pairwise $t_{15} = -3{\cdot}43$, $P = 0{\cdot}004$), time spent diving (handicapped: 26·2 ± 8·1% of time at sea; non-handicapped: 30·0 ± 6·0% of time at sea; pairwise $t_{15} = -2{\cdot}89$, $P = 0{\cdot}01$) and provisioning rates (pooled 2009 and 2010: pairwise $t_{35} = 2{\cdot}12$, $P = 0{\cdot}04$) while increasing time resting on the surface (handicapped: 62·3 ± 11·3% of time at sea; non-handicapped: 51·5 ± 9·2% of time at sea; pairwise $t_{15} = 3{\cdot}42$, $P = 0{\cdot}004$). Body mass loss did not differ between groups (pooled 2009–10: pairwise $t_{35} = 1{\cdot}17$, $P = 0{\cdot}25$). In 2009, daily energy expenditure of handicapped birds increased with age and became more variable (Fig. 1a), but was independent of age in non-handicapped birds ($t_{15} = 1{\cdot}05$, $P = 0{\cdot}31$, $R^2 = 0{\cdot}07$). Likewise, investment in the chick (provisioning rate) increased with age of the adult (brood value; Fig. 1), but mass loss declined with murre age (brood value; $t_{15} = -2{\cdot}07$, $P = 0{\cdot}04$). Whereas murres averaged 7·0 ± 1·2 h per day at the water surface, we estimated that 8·3 h per day were required to assimilate all energy obtained (see Detailed Methods).

FITNESS CONSEQUENCES

Birds not resighted the following season had lower daily energy expenditure than those resighted in all 6 years where we resighted individuals in the subsequent year, and that relationship was significant for the pooled data set (resighted: 2151 ± 1109 kJ per day; not resighted: 1777 ± 624 kJ per day; $t_{228} = 3{\cdot}91$, $P < 0{\cdot}001$). Handicapped birds were as likely to be resighted as controls in 1999–2000 (14/15 or 93% handicapped vs. 54/63 or 86% controls), 2009–2010 (15/19 or 79% handicapped vs. 49/56 or 88% controls), and 2010–2011 (12/21 or 57% handicapped vs 29/47 or 62% controls). Energy delivered to the offspring (kJ per day) was not correlated with daily energy expenditure for those birds we observed simultaneously ($t_{101} = 1{\cdot}55$, $P = 0{\cdot}12$, $R^2 = 0{\cdot}04$).

META-ANALYSIS

Across 25 handicapping studies, investment in self (body mass) decreased with increasing investment in the chick (provisioning rate or chick growth rate, Fig. 2a; phylogenetic contrasts: $t_{25} = 3{\cdot}45$, $P = 0{\cdot}002$). Chick growth/provisioning rate tended to increase with brood value (Fig. 2b), whereas investment in adult's energy stores was independent of brood value across species ($t_{25} = -0{\cdot}17$, $P = 0{\cdot}87$; phylogenetic contrasts: $t_{25} = -0{\cdot}12$, $P = 0{\cdot}91$).

Discussion

Chick-rearing murres – animals with exceptionally high activity costs – experienced an energy ceiling regardless of energy availability. The ceiling was mediated by behavioural adjustment; when handicapped, flight/dive costs increased substantially but daily energy expenditure remained markedly constant because the animals reduced time spent flying/diving. As older birds were able to overcome the energy ceiling over short time-scales by using up their energy reserves, we suggest that the ceiling occurs at the level of intake rather than expenditure. A meta-analysis of data from 25 studies examining the response of breeding animals to handicapping showed that although

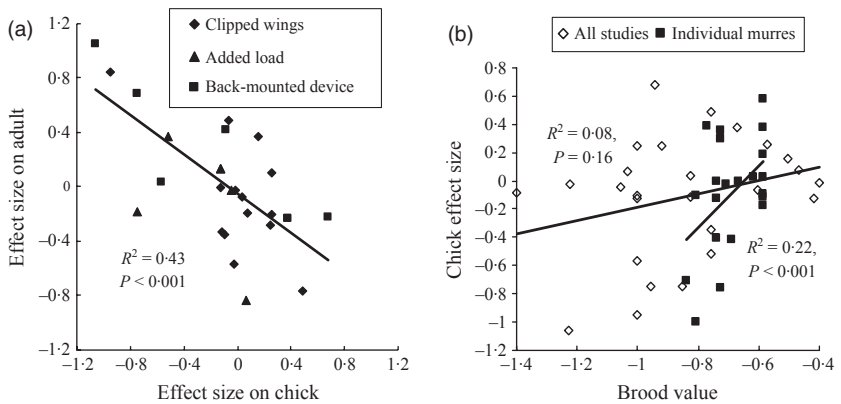

Fig. 2. (a) Meta-analysis of studies ($N = 25$) that handicapped birds (by clipping wings, adding load or mounting a device on the back) and reported both effects on the adult (residual of body mass change on degree of handicapping) and the chick (residual of chick growth rate or provisioning rate on degree of handicapping) relative to controls. (b) Effect size on chick increased with brood value across the same studies as in (a) and for individuals in our study. Effect size = (average for handicapped – Average for control)/(pooled standard deviation). Values and studies used in the meta-analysis appear in the Supplementary Information.

there was strong evidence of an energy ceiling – a reduction in either self-investment or investment in reproduction – the ceiling was largely independent of the slow–fast life-history continuum. Thus, although many breeding animals are apparently limited by an intrinsic energy ceiling and adjust the time spent in behaviours directed towards self-feeding or offspring nourishment to remain within that ceiling – life history did not appear to play a role in explaining differences in what behaviours were adjusted.

DAILY ENERGY EXPENDITURE WAS INDIVIDUALLY REPEATABLE (HYPOTHESIS ONE)

Repeatability in daily energy expenditure was higher over short (days) than long time-scales (years), which is not surprising given the high individual repeatability in foraging location, diet, flight times and dive depths at our location, with no effect on fitness (Woo *et al*. 2008; Elliott, Woo & Gaston 2010). An individual's physiology may be geared towards a particular level of energy expenditure. When pushed beyond that level, there can be consequences for survival and social relationships (e.g. break down of pair bonds), as shown by reduced survival associated with long-term handicapping (Wolf & Schmid-Hempel 1989; Daan, Deerenberg & Dijkstra 1996; Paredes, Jones & Boness 2005). Our handicapping study was too short to observe such effects. Individual murres' physiology may be geared towards a particular level of energy expenditure as murres adjust the size of energy-related organs (heart and muscle) separately from overall body mass (Jacobs *et al*. 2011). Trade-offs between body mass (flight costs), fasting endurance (brooding shifts), thermoregulation (insulation), oxidative stress and digestion mediated via body composition may all influence murres' ability to use energy (Drent & Daan 1980; Hammond & Diamond 1997; Speakman & Król 2010).

THE PRESENCE OF AN ENERGY CEILING REGARDLESS OF ENERGY AVAILABILITY (HYPOTHESES TWO AND THREE)

Across treatments and environmental conditions, average energy expenditure during chick-rearing was remarkably constant despite ample statistical power to detect a difference (87% chance of detecting a 10% difference, whereas incubation energy expenditure, chick body mass and adult body mass all showed >50% difference, Fig. 1c). Chick-rearing murres appeared to operate near a fixed energy ceiling (fixed investment strategy; Kitaysky *et al*. 2000; Tinbergen & Verhulst 2000; Green *et al*. 2009). Indeed, it is remarkable how precisely murres regulated energy expenditure to a given level; handicapped birds decreased time spent flying on average by 40%, which was the amount needed to maintain no net change in estimated energy expenditure. Had flight time been reduced by 30% or 50%, at the same activity-specific costs, we would have been able to detect a statistically significant difference. In contrast, chick growth rates, incubation daily energy expenditure, ambient temperature and adult mass all varied substantially among years, implying that conditions were quite variable. Similarly, in years when adult mass was low at our study site, chick growth rates were also low – again suggesting an energy ceiling that prevented adults from expending more energy to maintain chick growth rates (Gaston & Hipfner 2006). Our results are typical (Table 2), and many animals may use similar behavioural mechanisms – alteration of activity budgets – to remain within their energy ceiling (cf. Ropert-Coudert *et al*. 2007).

Animals are unable to maintain high levels of energy expenditure during poor-food years (Fig. 3). When food is abundant relative to need (some incubating birds, supplementally fed animals, animals with experimentally reduced broods), animals can down-regulate energy expenditure (Fig. 3). However, it appears that, for many breeding animals working near their energy limit, energy expenditure cannot be up-regulated (Fig. 3, Table 1). This was the case for chick-rearing murres at our study site (Figs 1c and 3). Similarly, energy availability can be variable at levels below an intrinsic ceiling where resources are highly variable, leading to the potential for a mismatch between need (brood size) and energy availability (Tinbergen & Dietz 1994; Kitaysky *et al*. 2000; Thomas *et al*. 2001; Jodice *et al*. 2002); Pacific kittiwakes (*Rissa tridactyla*) have a small brood size, presumably optimized for low energy availability, and when energy availability increases, because brood size is established a month previous (via clutch size), they have no need to up-regulate energy expenditure as demand is still low (Kitaysky *et al*. 2000).

Energy availability may in some conditions provide a boundary for energy expenditure, but animals normally operate at a lower level defined by intrinsic factors linked to their physiology (Fig. 3). Nonetheless, energy ceilings

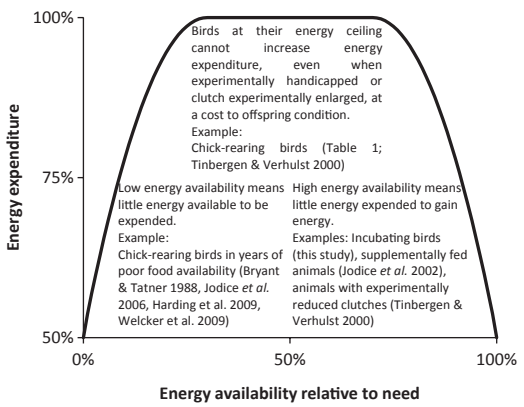

Fig. 3. A theoretical model describing how daily energy expenditure may change depending on energy availability relative to need, illustrating why animals with both low and high energy availability may have low daily energy expenditure.

vary among individuals (Fig. 1b,c) and over evolutionary time-scales (among species or between colonies); energy expenditure often differs among colonies with differing food availability because animals can predict such differences and are adapted to their local level of energy availability (Kitaysky *et al*. 2000; Jodice *et al*. 2002; Ballance *et al*. 2009). For instance, individuals can adjust basal metabolism to reduce energy expenditure during periods of high energy demand (Bech *et al*. 2002), yet individuals are unable to make adjustments over shorter time-scales (Table 2). We suggest that physiological limitations best explain these observations: while animals can likely adapt individually variable physiological, morphological or thermal characteristics to correspond with energy availability over evolutionary time-scales, they are unable to do so over short time-scales.

MECHANISMS UNDERLYING AN ENERGY CEILING

Many animals appear to be at an energy ceiling, unable to increase energy expenditure even at a cost to their own or their offspring's condition. That ceiling appears to be associated with a physiological constraint rather than energy availability or fitness trade-offs. One potential physiological constraint is time required to digest food (Kleiber 1975; Kenward & Sibly 1977; Hammond & Diamond 1997). Like many diving birds, murres interrupt foraging (diving) bouts to spend hours resting on the surface between diving bouts. In seabirds feeding on difficult to digest prey, much of that surface time is spent digesting prey, and digestion rates determine time allocated to dive bouts relative to resting (Guillemette 1998; Heath, Gilchrist & Ydenberg 2010). Digestive constraints also appear to play a role in murres as (i) older individuals used their own reserves to expend more energy even when handicapped, suggesting the constraint occurs at the level of energy intake rather than expenditure, and (ii) 118% of surface resting time in murres is required to digest food (some of which is digested at the colony, see Detailed Methods) leaving no time available to digest any additional food obtained (Hansen 2003). Digestive constraints, however, do not account for all physiological constraints on energy expenditure. As murres spent less time foraging for their offspring, handicapped birds spent more time resting on the surface than non-handicapped birds despite expending the same amount of energy. If energy expenditure in handicapped birds was limited by time available for digestion, then presumably they could use some of the excess time obtaining and digesting more energy instead of simply resting. We believe that various metabolic constraints evolve in tandem to the same level of energy expenditure. The removal of one constraint does not alter energy expenditure as expenditure is still limited by other constraints, such as thermal constraints, muscle properties and oxidative stress (e.g. Krol, Murphy & Speakman 2007; Speakman & Król 2010; Beaulieu *et al*. 2011; Selman *et al*. 2012).

NO FITNESS TRADE-OFF BETWEEN ENERGY EXPENDITURE AND SURVIVAL, BUT INCREASED INVESTMENT BY INDIVIDUALS WITH HIGHER BROOD VALUE (HYPOTHESIS FOUR)

High energy expenditure during peak demand (chick-rearing) did not reduce apparent survival (see also Jackson, Trayhurn & Speakman 2001; Welcker *et al*. 2009, 2010). Rather, birds with high energy expenditure had *higher* apparent survival, which we interpret as meaning that birds that were near death were incapable of high levels of energy expenditure (cf. Manini *et al*. 2006). In contrast, those individuals with experimentally increased energy expenditure often have lower apparent survival (Daan, Deerenberg & Dijkstra 1996; Paredes, Jones & Boness 2005; Jacobs, Elliott & Gaston 2013; our deployment period – 24 h – was apparently too short to create such an effect). While we did not find a fitness cost associated with high daily energy expenditure, we also did not find a fitness benefit, as chick post-fledging survival (as approximated by energy delivery rates to the offspring) was not correlated with daily energy expenditure. Thus, although individual birds at our study site specialize on different foraging strategies (one long flight, many short flights, deep dives, etc.) with different energy costs (Woo *et al*. 2008; Elliott *et al*. 2009; Elliott, Crump and Gaston 2010), no particular strategy provided a better pay-off in terms of higher return to the chick.

Despite the constant average level of energy expenditure, there was considerable individual variation (Welcker *et al*. 2009, 2010; Green *et al*. 2009; Fig. 1b,c). In contrast to the results of the meta-analysis (Fig. 2b), some of the individual variation in our study was related to life-history trade-offs. Older individuals that were less likely to produce many more offspring were more willing to invest in current broods by having higher chick-provisioning rates and expending larger amounts of energy to compensate for being handicapped. Similarly, when murres were handicapped with larger handicaps, three out of nine young birds (<10 years old) abandoned the offspring, whereas none of ten old birds (>9 years old) abandoned (Elliott, Davoren & Gaston 2007; K.H. Elliott, unpublished data). Perhaps old murres maintained the secretion of hormones associated with parental behaviour, such as prolactin, throughout the stress of handicapping (Angelier *et al*. 2007).

For breeding animals, an alteration in activity budgets in response to increased activity-specific metabolic rates entails a cost for either investment in the individual or its offspring, and those adjustments were evident in our meta-analysis. Individuals either reduced their own body mass (at least over the short term) or reduced their offspring body mass (Fig. 2b). Where a particular species lies upon the trade-off between investment in one's offspring and investment in one's self may be dictated by life history, with individuals from long-lived species maximizing their lifetime reproductive success by favouring their own

condition over that of their current offspring (Saether, Andersen & Pedersen 1993; Mauck & Grubb 1995). We found little support for that idea when comparing across 25 studies, including the subset of studies used to justify those claims (Fig. 2b). With a larger selection of both long- and short-lived birds than the two petrels and four passerines reported by Mauck & Grubb (1995), handicapped long-lived birds were not more likely to reduce chick growth rates than handicapped short-lived birds.

IMPLICATIONS FOR MURRE LIFE HISTORY

The existence of an intrinsic limitation on energy expenditure explains the unique 'intermediate' life-history strategy of murres (Ydenberg 1989; Houston, Thompson & Gaston 1996; Hansen 2003). Most auks either remain at the breeding site until fledging at near adult size or leave the breeding site soon after hatching, without ever being fed by the parent. Along with fruit-pigeons, three species of semi-precocial auks are unique among birds in adopting an intermediate strategy of leaving their breeding site at only *c*. 20% of adult body mass and prior to being able to fly (Sealy 1973; Crome 1975). The presence of an energy ceiling in murres explains why parent murres are unable to continue provisioning at the higher rate required by larger offspring regardless of energy availability and why their offspring continue their development at sea, closer to potential food sources. The inefficiency of the murre strategy is apparent in that chick-rearing murres expend 733 kJ day^{-1} more than incubating murres to meet the chick energy requirements of 289 kJ day^{-1} (145 kJ day^{-1} per adult); a female mammal with 75% efficiency at converting food into milk could provide energy for nearly four offspring at that same level (733 kJ day^{-1}) of excess energy expenditure.

IMPLICATIONS FOR STUDIES OF DEVICE EFFECTS

Accelerometers that are regularly attached to birds of similar or smaller size than murres (Watanuki *et al*. 2006; Sato *et al*. 2007) had a measurable impact on behaviour. Likewise, there was a strong indication of reduced investment in either chick or adult condition following attachment of devices designed to mimic typical bio-logging devices (Fig. 2a). Most studies of device effects on daily energy expenditure were unable to measure an effect (Table 1), presumably because individuals adjusted their behaviour to remain within their energy ceiling. Increasing body drag by attaching a device augments locomotory costs to a much greater degree than predicted by simple biomechanical modelling, as flow disruption can be much greater than that imposed by a proportional increase in cross-sectional area for a similarly shaped object (Pennycuick *et al*. 2012). Increasing mass without increasing drag has a smaller effect than predicted by biomechanical modelling (Kvist *et al*. 2001; Nudds & Bryant 2002; Schmidt-Wellenburg, Engel & Visser 2008). We suggest that device effect studies focus on activity budgets or activity-specific costs rather than on daily energy expenditure and that researchers measure both adult and chick effects simultaneously given the potential trade-off between those metrics. Effects are likely particularly pronounced on birds with high wing-loadings and that must move underwater (Elliott *et al*. 2012; Vandenabeele *et al*. 2012).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Studies used for meta-analysis on the effect of handicapping on adults and offspring.