

# Energetic fitness: Field metabolic rates assessed via 3D accelerometry complement conventional fitness metrics

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## Funding information

NSF, Grant/Award Number: 9526865, 9814882, 0125608, 0440643 and 0944411; CNRS; French Polar Institute; ADACLIM, Grant/Award Number: 388; New Zealand Ministry of Science and Innovation, Grant/Award Number: C01X1001

Handling Editor: Shaun Killen

## Abstract

1. Evaluating the fitness of organisms is an essential step towards understanding their responses to environmental change. Connections between energy expenditure and fitness have been postulated for nearly a century. However, testing this premise among wild animals is constrained by difficulties in measuring energy expenditure while simultaneously monitoring conventional fitness metrics such as survival and reproductive output.
2. We addressed this issue by exploring the functional links between field metabolic rate (FMR), body condition, sex, age and reproductive performance in a wild population.
3. We deployed 3D accelerometers on 115 Adélie penguins *Pygoscelis adeliae* during four breeding seasons at one of the largest colonies of this species, Cape Crozier, on Ross Island, Antarctica. The demography of this population has been studied for the past 18 years. From accelerometry recordings, collected for birds of known age and breeding history, we determined the vector of the dynamic body acceleration (VeDBA) and used it as a proxy for FMR.
4. This allowed us to demonstrate relationships among FMR, a breeding quality index (BQI) and body condition. Notably, we found a significant quadratic relationship between mean VeDBA during foraging and BQI for experienced breeders, and individuals in better body condition showed lower rates of energy expenditure.
5. We conclude that using FMR as a fitness component complementary to more conventional fitness metrics will yield greater understanding of evolutionary and conservation physiology.

## KEYWORDS

Adélie penguin, animal energetics, animal personalities, daily energy expenditure, pace-of-life syndrome, phenotypic plasticity, Ross Sea

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## 1 | INTRODUCTION

The notion of energetic fitness is implicit across the scientific literature of the 20th century. Notably, Lotka (1922) predicted linkages between energetics and evolution in a seminal paper, and those were further explored by Van Valen (1976), who stated “I define natural selection and fitness wholly in terms of trophic energy.” Later on, Brown, Marquet, and Taper (1993) proposed an energetic definition of fitness based on the reproductive power of animals, as determined by (1) the rate of energy acquisition from the environment and (2) the rate at which these resources are transformed into offspring. They modelled the relationship between reproductive power and body size, and their pioneering work launched a flood of controversy and discussions about allometry and the evolution of body size (e.g. Bokma, 2001; Kozłowski, 1996; Lampert & Tlustý, 2013). The allometry of body size is a fascinating phenomenon, yet research attention to the concept may have distracted the scientific community from actually using animal energetics to quantify fitness in free-ranging animals.

Fitness is set, to a certain extent, by the genotype, yet it is also strongly shaped by phenotypic plasticity, and potentially by epigenetics (Danchin et al., 2011). Phenotypic plasticity is often understood as developmental plasticity affecting the morphology of organisms (Levins, 1968). Such plasticity acting on morphological features has indeed been shown to affect fitness (Le Galliard, Clobert, & Ferrière, 2004), yet there is ample evidence that phenotypic plasticity also affects physiological and behavioural traits (Price, Qvarnström, & Irwin, 2003; Réale, Reader, Sol, McDougall, & Dingemanse, 2007). At the organismal level, it is therefore the complex interplay of morphological, physiological and behavioural plasticity that acts on fitness, with feedbacks onto genotypic microevolution (Piersma & Van Gils, 2011).

In the context of global change, there is a renewed interest for evaluating the capacity of individuals to cope with shifting biotic and abiotic constraints (Visser, 2008). Studying phenotypic plasticity is particularly relevant in long-lived vertebrates whose genotype evolves too slowly to help individuals adjust to rapid environmental change (Charmanier et al., 2008; Gilg et al., 2012). With respect to the behavioural component of phenotypic plasticity, the last decade has seen the rise of intense research activities on animal personalities and on the impact of behavioural traits upon fitness (Stamps & Groothuis, 2010). Animal personalities are identified via consistent individual differences in behaviour across contexts (Réale et al., 2007); personalities are intertwined with individual differences in morphology and physiology to result in individually different lifestyles supporting a “pace-of-life syndrome” hypothesis (Hamel et al., 2010; Le Galliard, Paquet, Cisel, & Montes-Poloni, 2013).

Physiologically, this hypothesis is based upon the observation that, within a population, some individuals may show consistently higher rates of energy expenditure than others (Bech, Langseth, & Gabrielsen, 1999; White, Schimpf, & Cassey, 2013). This characteristic is sometimes, but not always, heritable, which

indicates the existence of phenotypic plasticity acting upon animal energetics (McKechnie, Chetty, & Lovegrove, 2007; McKechnie, Freckleton, & Jetz, 2006). A link between energetics and fitness has long been postulated (McNab, 2002; Pearl, 1928; Peterson, Nagy, & Diamond, 1990; Prinzinger, 2005) and is implicit across recent writings by Piersma and colleagues (Piersma, 2011; Piersma & Van Gils, 2011). Yet, as with the morphological and behavioural determinants of fitness, rating the incidence of energy expenditure on fitness should ideally be performed at the scale of an individual’s whole life, using life-history traits such as longevity or lifetime reproductive success as proxies for fitness (Brown et al., 1993). This is unpractical when studying organisms that live in unstable and rapidly changing environments. Especially in long-lived organisms, it is immensely costly to gather longitudinal data for decades before being able to rate the fitness consequences of a specific energetic strategy or pace-of-life. Investigators have turned to modelling exercises (Dall, Houston, & McNamara, 2004), or to using surrogate, short-lived organisms (Artacho & Nespolo, 2009; Merritt, Matthews, & White, 2013; Sadowska, Baliga-Klimczyk, Labocha, & Koteja, 2009; Schimpf, Matthews, & White, 2012), yet the validity of their findings to large vertebrates, including humans, is questionable. In response to these issues, energetic fitness is an attractive concept, when defined as the short-term fitness of an individual organism evaluated via its field metabolic rate. This “operational” definition of energetic fitness is distinct from the approach by Brown et al. (1993), and is linked to a series of methodological challenges.

Energy expenditure is classically measured in relation to the activity level of an animal, with distinctions being made between basal metabolic rate (BMR: post-absorptive animal at rest within its thermoneutral zone), resting metabolic rate (RMR: animal at rest) and field metabolic rate (FMR: animal living in its natural environment). Average FMR per 24 hr-period is also routinely used to calculate daily energy expenditure (DEE). A majority of measurements and meta-analyses have focused on both BMR and RMR, their allometry and potential link with life-history traits (White & Kearney, 2013). This approach is nonetheless suspected to be reductive, and Speakman (2005) suggests that the more integrative FMR or DEE should be considered instead, arguing that the latter better reflect the energetic challenges faced by a free-living organism in its natural environment.

In this context, we propose to evaluate energetic fitness using FMR. This approach is ideal for field research, yet still marginal compared to laboratory and theoretical work when it comes to assessing energetic fitness, and hence the short-term capacity of organisms to deal with shifting environmental constraints, for example climate change, or an unstable habitat. To this end, we studied individual Adélie penguins *Pygoscelis adeliae* within a population subjected to long-term monitoring in the Ross Sea, Antarctica. Specifically, we assessed foraging effort and FMR in Adélie penguins of known age, body condition and reproductive performance at Cape Crozier, Ross Island, one of the largest colonies of this species (Lynch & LaRue, 2014; Schwaller, Southwell, & Emmerson, 2013). Previously, it had been determined

that energy expenditure during the breeding season was increasing in this population, compared to neighbouring colonies in its metapopulation, owing to its large size and consequent interference competition for food resources (Ballance, Ainley, Ballard, & Barton, 2009). In this context, we tested the hypothesis that FMR correlates with conventional fitness metrics, especially reproductive performance. On the basis of previous research (Drent & Daan, 1980; Lescroël et al., 2010; Piersma & Van Gils, 2011), we made the prediction of a quadratic relationship between FMR and reproductive performance. Such a functional link can be represented as a dome-shaped curve, with fitness initially increasing along with FMR, reaching a maximum and subsequently decreasing. Importantly, in our study, reproductive performance of individuals was assessed over multiple years.

## 2 | MATERIALS AND METHODS

The study was conducted at the Cape Crozier Adélie penguin colony (77°27'S, 169°12'E; c. 275,000 pairs; Lyver et al., 2014), Ross Sea, Antarctica. All penguin survey, capture and handling methods performed during data collection for this study were approved under Antarctic Conservation Act permits (# 1997-010, 2000-007, 2003-002, 2006-010, 2011-002) issued by the US National Science Foundation and the U.S. Antarctic Program, and administered by H.T. Harvey & Associates; as well as Institutional Animal Care and Use Permits (IACUC # 4130, 4462) through Oregon State University. Studies did not involve endangered species.

### 2.1 | Assessing long-term breeding performance

All measurements were performed under the auspices of the long-term research programme in place since the 1996–1997 (hereafter, seasons are referred to by the initial year, e.g. 1996), which gathered information on penguins each year throughout the breeding season, from early November to late January (Dugger, Ainley, Lyver, Barton, & Ballard, 2010). A sample (500–1,000) of near-fledglings were individually marked with numbered stainless-steel flipper bands (see Appendix S1) at Cape Crozier beginning in 1996 (banding at the nearest colonies at Beaufort Island, Cape Royds, and Cape Bird occurred as well; Dugger et al., 2010), and their breeding success was recorded from egg laying in November through crèching (i.e. when chicks are big enough to be left alone by their parents and gather in groups called “crèches;” Ainley, 2002) in early to mid-January. Chicks gather in crèches near their nests, awaiting parents to return with food. Breeding birds were considered “successful” when they raised at least one chick to the crèching stage. Adult banded birds seen during a given season but never with an egg or a chick were classified as “non-breeders.” Birds seen with at least one egg or chick but which failed before crèching were classified as “unsuccessful.”

Taking into account these breeding success data for all banded birds (12,609 subsequently resighted between 1998 and 2015) from the first to the most recent resighting year, we calculated a Breeding Quality Index (BQI) for each of the 3,707 individual birds in

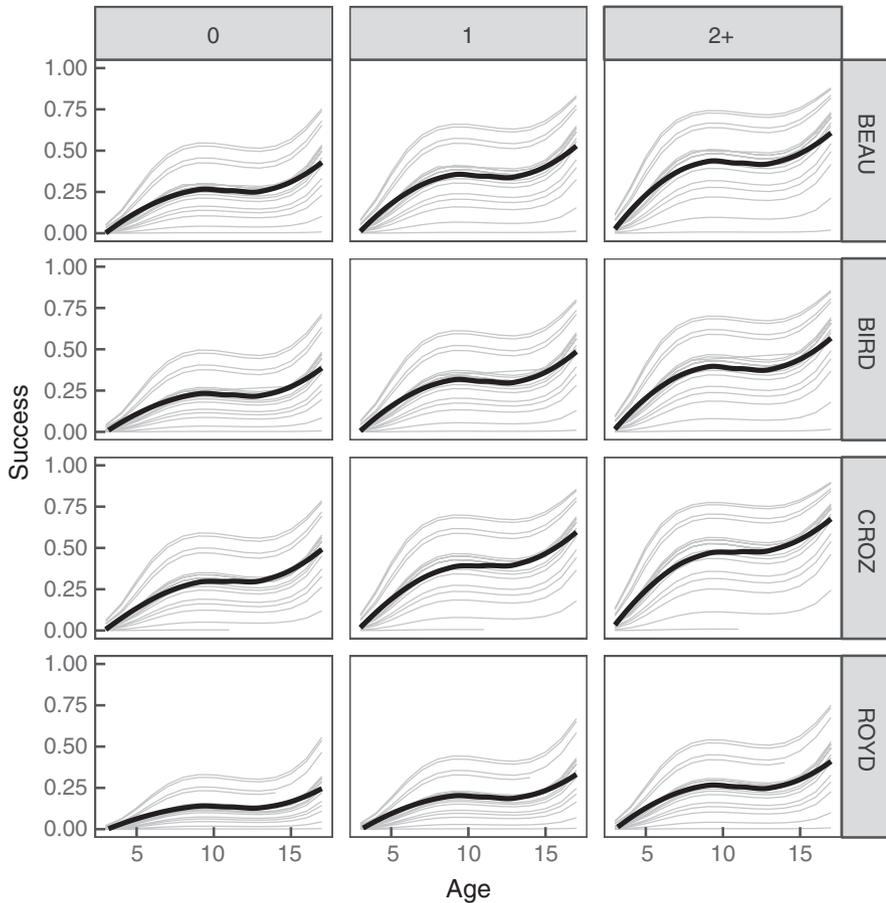
our database, based on the methods developed by Lescroël, Dugger, Ballard, and Ainley (2009), Lescroël et al., (2010) for birds of known breeding history but unknown age. A BQI was calculated as the mean per individual of the difference between the actual breeding success (0 for unsuccessful or deferred breeders, 1 for successful breeders) and the predicted breeding success (a numeric value between 0 and 1) for every year. This led to a unique value per individual per year. The predicted breeding success was modelled from actual breeding success (0 or 1), using four independent variables (age, previous breeding experience, colony of origin and breeding year). We verified that the independent variables were not cross-correlated and that the most general model fit the data. Age varied from 3 (minimum age of sexual maturity; Ainley, 2002) to 18 years old. Breeding experience was included as a categorical variable with three levels: 0, 1 or 2 or more years of previous breeding experience. Colony of origin was one of the four colonies of the Ross Island metapopulation where Adélie penguins were banded: Cape Crozier, Cape Bird, Cape Royds or Beaufort Island (Dugger et al., 2010). Breeding year was treated as an 18-level factor encompassing all study years from 1998 to 2015. These independent variables were then incorporated into a GLM with a logit link function. The model was fitted using a lasso-penalized maximum likelihood (Rockova, Lesaffre, Luime, & Löwenberg, 2012) followed by cross-validation (using the misclassification error between successful and unsuccessful breeders) to determine the coefficients of predictors corresponding to the best model (i.e. the model that minimized the mean cross-validated error), and to derive a probability of success for each year and individual (Figure 1).

The resulting BQI has several interesting characteristics: (1) it corresponds to the long-term relative breeding performance of an individual compared to others of similar characteristics, (2) it is a relative concept (as individual fitness) and does not average environmental variability (contrary to indices such as lifetime reproductive success), and (3) it is a very useful measure of performance for individuals that are still alive and allows an investigation of the variation of individual breeding performance over time.

### 2.2 | Assessing FMR with triaxial accelerometry

We attached accelerometers to a subsample of breeders each season that demonstrated a range of BQI values (see below). To evaluate FMR, we used dynamic body acceleration (Wilson et al., 2006) as determined using recordings of three-dimensional whole-body acceleration in free-ranging penguins. This technique follows the rationale that the more animals move, the higher their FMR. It has been used previously in a wide range of wild animals, and subjected to a series of validations that support this relationship (Elliott, Le Vaillant, Kato, Speakman, & Ropert-Coudert, 2013; Halsey et al., 2009; Shepard et al., 2008).

During four consecutive breeding seasons, we deployed 3-axis accelerometers (G6A, CEFAS Technology Limited, Lowestoft, UK; 40 × 28 × 15 mm, mass 18 g, sampling frequency 20 Hz), which also recorded temperature and hydrostatic pressure once per second



**FIGURE 1** Probability for an Adélie penguin breeding at Cape Crozier of raising at least one chick to the crèching stage depending on age, previous breeding experience (on top: 0, 1 or 2+ years), year (one curve per year 1998–2015, in grey, with a smooth line in black for all years) and colony of origin (BEAU, Beaufort island; BIRD, Cape Bird; CROZ, Cape Crozier; ROYD, Cape Royds;  $n = 3,707$  birds)

as an index of dive depth, on a total of 125 breeding Adélie penguins ( $n = 10$  in 2010,  $n = 45$  in 2011,  $n = 24$  in 2012,  $n = 46$  in 2013) aged 3–15 years and BQI  $-0.36$  to  $0.98$ . All deployments took place during the guard stage of chick-rearing, from 19 December to 5 January. The devices were attached to the lower back using black Tesa® tape (Hamburg, Germany; Wilson & Wilson, 1989), following techniques previously shown to have no detectable impacts on foraging trip duration and reproductive success (Ballard, Ainley, Ribic, & Barton, 2001). Handling lasted  $<10$  min and devices were recovered after one foraging trip at sea, lasting between 0.47 and 5.83 day. Body mass (kg), torso circumference (m) and flipper length (m) were measured upon recovery. Based on body mass and flipper length, we subsequently calculated a Scaled Mass Index (SMI, in grams) for each bird following Peig and Green (2009). This index of body condition controls for size, it is therefore size-independent. SMI and torso circumference were used as body condition indexes while flipper length was used as a body size index. We were able to recover 116 non-corrupted data files ( $n = 5$  in 2010,  $n = 45$  in 2011,  $n = 20$  in 2012,  $n = 46$  in 2013). Sex of the equipped birds was determined in 2010 by a commercial laboratory (DNA Solutions, Wantirna, Victoria, Australia) from blood or feather samples collected upon detachment of the devices, and in 2011–2013 at the University of Canterbury (New Zealand).

Data from the accelerometers were analysed with the software Igor Pro version 6.31 (Wavemetrics, Portland, Oregon, USA). As a

metric for bird activity levels, we calculated the vector of dynamic body acceleration (VeDBA, g; Qasem et al., 2012):

$$\text{VeDBA} = \sqrt{(A_x - S_x)^2 + (A_y - S_y)^2 + (A_z - S_z)^2}$$

Acceleration ( $A$ ) is the sum of static acceleration ( $S$ ) resulting from body angle with respect to gravity and dynamic acceleration ( $D$ ) resulting from body movements along all three spatial axis ( $x$ : antero-posterior,  $y$ : lateral,  $z$ : vertical), that is  $A = S + D$ . For each axis, we calculated static acceleration ( $S$ ), which is a running mean of 2-s time intervals, using the box smooth function with 39 points in Igor Pro. The time-interval of 2 s was determined by a calibration made during 1-min periods, following Shepard et al. (2008). VeDBA, our proxy for the rate of energy expenditure, was expressed as mean VeDBA per foraging trip and was calculated as the mean of all VeDBA values between the onset of the first dive and the end of the last dive.

### 2.3 | Measuring diving activity

Diving effort of penguins at sea strongly conditions FMR (Ballance et al., 2009; Chappell, Shoemaker, Janes, Maloney, & Bucher, 1993), so we used mean maximum dive depth (i.e. the average of the maximum depth reached for every dive during a foraging trip) as an index of diving effort in our analyses. Diving data collected by the electronic devices in parallel to 3D accelerometry were processed using the

**TABLE 1** Output of the linear model explaining variations of breeding performance (breeding quality index: BQI) as a quadratic function of mean energy expenditure (expressed as vector of dynamic body acceleration (VeDBA), in  $g = 9.81 \text{ m/s}^2$ ) during foraging

Response variable	Explanatory variable	Estimate	SE	t-Value	p-Value	95% confidence intervals (2.5%, 97.5%)
BQI	Intercept	-1.4173	0.5887	-2.408	.0187	(-2.5911, -0.2435)
	Mean VeDBA	12.8274	5.1360	2.498	.0148	(2.5864, 23.0683)
	Mean VeDBA <sup>2</sup>	-28.0307	10.9143	-2.568	.0123	(-49.7931, -6.2682)

We used data from birds equipped with accelerometers and with at least 2 years of previous breeding experience ( $n = 74$  birds;  $R^2 = .09$ ).

program `divesum` (Grant Ballard, unpublished software; see Lesco el et al., 2010 for more details). This program corrected for baseline drift in pressure data. Only dives  $\geq 1$  m deep and  $\geq 3$  s were considered.

## 2.4 | Statistical analyses

All statistical analyses were performed within R 3.3.1 (R Development Core Team 2016).

We calculated a probability of breeding success for each year and individual by fitting a GLM with a logit link via penalized maximum likelihood using the library `{glmnet}` (Friedman, Hastie, & Tibshirani, 2010). The BQI of each individual was calculated as the mean per individual of the difference between the actual breeding success and the predicted breeding success for every year during which a given individual had been resighted when at least 3 years old, up to the year when we equipped it with an accelerometer.

To test for a quadratic relationship between FMR, as assessed by accelerometry, and BQI, we tested for the linear and quadratic effects of mean VeDBA on BQI in a linear model, using data for birds equipped with accelerometers and with at least 2 years of previous breeding experience (74 birds) as we wanted BQI to be representative of an individual's long-term breeding performance, hypothesized as being a relatively stable value for a given individual. In order to check if inter-individual differences in breeding quality were indeed maintained over time past the first two reproduction attempts, we fitted a GLMM with BQI as the dependant variable, bird age as the independent variable and bird ID as a random effect, using only data for birds with at least 2 years of previous breeding experience (627 birds, 1987 observations). The GLMM was fitted using the library `{lme4}` (Bates, M achler, Bolker, & Walker, 2014) and we calculated the intraclass correlation coefficient (ICC), an index of repeatability, as the ratio of the between-individual variance to the total variance, as given by the model.

To understand better what factors influence the mean level of energy expenditure during a foraging trip, we tested relationships between mean VeDBA over each foraging trip, and year, Julian day, bird age, sex, body condition (torso circumference and SMI), body size (flipper length) and diving effort (mean maximum dive depth), using data collected with accelerometers (115 birds). To this end, we used a GLM containing all above-listed variables, then generated a set of models with all additive combinations (subsets) of terms in the full model and ranking them using the small-sample-size corrected version of Akaike Information Criterion (AICc) as implemented by

the `dredge()` function from library `{MuMIn}`. Means are given  $\pm$  SE unless otherwise stated.

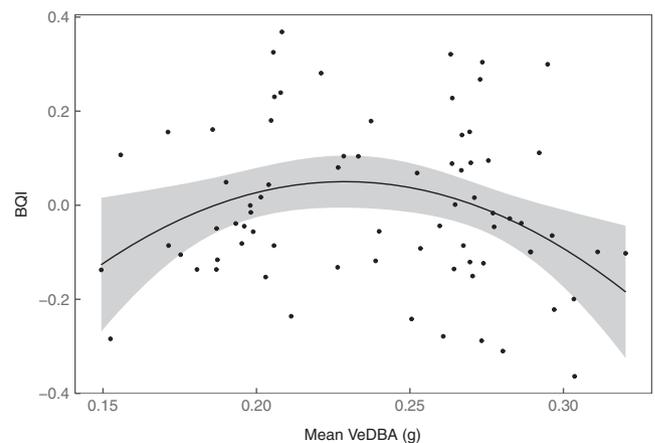
## 3 | RESULTS

### 3.1 | Relationship between FMR and BQI

In experienced birds (bred at least twice), we found evidence of a significant quadratic relationship between mean VeDBA during foraging and BQI (Table 1, Figure 2), with birds showing intermediate rates of energy expenditure having the highest long-term breeding performance. Conversely, an alternative linear relationship was found to be non-significant ( $p = .488$ ). A large amount of the inter-individual variation in BQI remains unexplained by mean VeDBA calculated over a single foraging trip ( $R^2 = .09$ ).

### 3.2 | Repeatability of BQI in experienced individuals

We found a very high repeatability of BQI in experienced breeders. Indeed, the between-individual variance for BQI in individuals with at least 2 years of breeding experience was  $0.0316 \pm 0.1778$  and the residual variance was  $0.0070 \pm 0.0834$ , giving an ICC of 0.82 (Table 2).



**FIGURE 2** Quadratic relationship (regression line in black, 95% confidence interval in grey) between the mean vector of dynamic body acceleration (VeDBA in  $g = 9.81 \text{ m/s}^2$ ) during foraging and the breeding quality index in experienced breeders (at least 2 years of previous breeding experience,  $n = 74$  birds) at the Cape Crozier colony

**TABLE 2** Variance partitioning of the fixed effects of age, and the random effect of individual bird (ID) on breeding quality index (BQI) using a linear mixed model with REML estimation

Response variable: BQI				
	Intercept	Variance	SD	
Random effects	ID	0.0316	0.1778	
	Residual	0.0070	0.0834	
		Estimate	SE	t-Value
Fixed effects	Intercept	0.1721	0.0117	14.69
	Age	-0.0113	0.0010	-10.92

ID is the individual bird identification number (i.e. its band number). We used data collected since 1998, as part of our long-term monitoring study ( $n = 627$  birds with at least 2 years of previous breeding experience).

### 3.3 | Intrinsic and extrinsic determinants of energy expenditure rates during foraging

From our model set, seven models had delta AICc below 2 in comparison to the best model (Table 3) and explained a large amount of the variation of mean VeDBA ( $R^2 \geq .76$ ). The most parsimonious model included the effects of year, sex and body condition (SMI) on mean VeDBA (Table 4). Mean VeDBA was significantly higher in years 2011 and 2012 than in years 2010 and 2013 (Figure 3). Males exhibited higher rates of energy expenditure than females (Figure 4), and individuals in better body condition showed lower rates of energy expenditure (Figure 5). Interestingly, the effect of age was included in the top two models and in four of the seven best models. Older birds tended to have slightly lower rates of energy expenditure than younger birds (from the best model:  $-0.0012 \pm 0.0006$  SE,  $p = .050$ ).

## 4 | DISCUSSION

Using long-term monitoring data and recent technological developments allowing 3D accelerometry in Adélie penguins, we validated our hypothesis of significant relationships between conventional fitness proxies (reproductive performance, body condition), and FMR as assessed with dynamic body acceleration (VeDBA; Figure 2). Our study is particularly novel in demonstrating a quadratic relationship

between the reproductive performance of experienced birds and FMR (Figure 2), and by showing that birds in good body condition have lower FMR (Figure 5). Our results complement the “working less to gain more” paradigm proposed by Lescroël et al. (2010). Indeed, their framework corresponded to the right-hand (descending) part of the quadratic relationship shown on Figure 2, to which a left-hand (ascending) part can now be added, demonstrating that for very low levels of estimated FMR, breeding performance tends to decrease again.

There is considerable variability in our dataset, strongly suggesting that other factors influence mean VeDBA. This might be the case for varying levels of preening and cleaning activity of birds during foraging trips. Given the observational nature of this study, the low variation in BQI explained by VeDBA is nonetheless consistent with the concept of an adaptive peak (Fisher, 1999; Kingsolver et al., 2001). Yet, the methods that we used could be further improved. Notably, we only estimated mean VeDBA over single foraging trips very early in the chick period before chicks began to demand the most effort from their parents. Independent studies of Adélie penguins show that inter-individual differences in time spent diving are consistent over time, at least within the same breeding season (Takahashi et al., 2003), yet future studies should rather perform this measurement over several foraging trips, potentially across the entire chick-rearing phase. Despite these limitations, our work is an important step towards an operational definition of energetic fitness as it indicates, within this wild population, the existence of an optimum intermediate FMR linked to sustained levels of reproductive performance across years (Figure 2).

The dome-shaped (quadratic) energy/fitness relationship is implicit in a series of previous publications, notably those following the “prudent parent hypothesis” (PPH) by Drent and Daan (1980) and the “life-history/physiology nexus” (Ricklefs & Wikelski, 2002), such as summarized in Piersma (2011). A correlate of the PPH is that increasing FMR is beneficial to fitness levels because it increases individual probabilities to survive and reproduce, for instance via higher reactivity and speed promoting, e.g., escape from predators and/or foraging efficiency. On the other hand, previous work also supports the idea that morphological and physiological factors strongly affect or even limit an individual's energy expenditure, particularly important in diving air-breathing vertebrates as indicated, for example, in studies of guillemots *Uria*

Response variable	Explanatory variables	AICc	$\Delta$ AICc	$R^2$
Mean VeDBA	Year + Day + Age + Sex + SMI	-547.4	0	.77
	Year + Age + Sex + SMI	-547.3	0.1	.76
	<b>Year + Sex + SMI</b>	<b>-546.3</b>	<b>1.1</b>	<b>.76</b>
	Year + Day + Age + Sex + SMI + Torso	-545.9	1.5	.77
	Year + Day + Sex + SMI	-545.6	1.8	.76
	Year + Age + Sex + SMI + Torso	-545.6	1.8	.76
	Year + Day + Age + Sex + SMI + Flipper	-545.5	1.9	.77

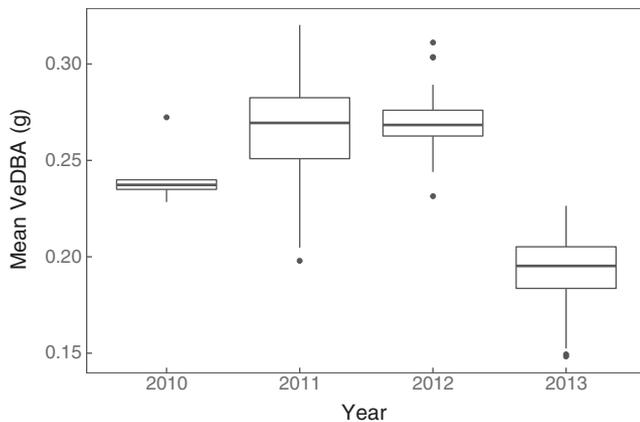
**TABLE 3** Best models (within  $2 \Delta$ AICc of top model) as selected with AICc for explaining the variations of the mean vector of dynamic body acceleration (VeDBA in g) during foraging. The most parsimonious model within  $2\Delta$ AICc of the top model is highlighted in bold

We used data from birds equipped with accelerometers (2010–2013,  $n = 115$  birds).

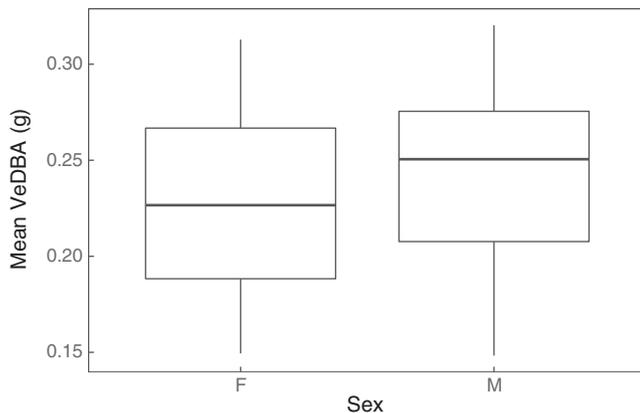
**TABLE 4** Output of the most parsimonious model as selected with AICc for explaining the variations of the mean vector of dynamic body acceleration (VeDBA g) during foraging

Response variable	Explanatory variable	Estimate	SE	t-Value	p-Value
Mean VeDBA	Intercept	0.2894	0.0227	12.764	<.001
	Year (2011)	0.0236	0.0105	2.247	.0267
	Year (2012)	0.0268	0.0111	2.407	.0178
	Year (2013)	-0.0529	0.0109	-4.880	<0.001
	Sex (Male)	0.0084	0.0042	2.008	.0471
	SMI	-0.00001	0.000004	-2.714	.0077

We used data from birds equipped with accelerometers (2010–2013,  $n = 115$  birds).

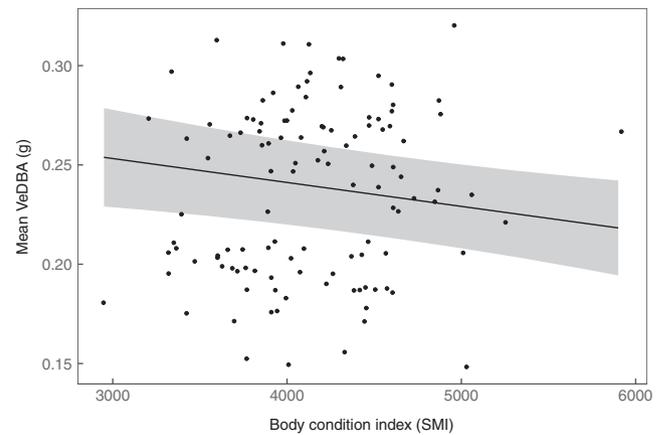


**FIGURE 3** Mean vector of dynamic body acceleration (VeDBA in  $g = 9.81 \text{ m/s}^2$ ) of Adélie penguins at the Cape Crozier colony during foraging was significantly higher in years 2011 and 2012 than in years 2010 and 2013 ( $n = 115$  birds)



**FIGURE 4** Male Adélie penguins exhibit higher mean vector of dynamic body acceleration (VeDBA in  $g = 9.81 \text{ m/s}^2$ ) than females ( $n = 115$  birds)

spp. (Elliott, Davoren, & Gaston, 2007; Elliott et al., 2013, 2014) or penguins (Sato et al., 2009). These limits are predicted by allometric meta-analyses that suggested that one unit (g) of living tissue metabolises a set amount of energy before death (reviewed in Prinzinger, 2005; Speakman, 2005); a body of work that led to formulating the “live-fast-die-young” hypothesis. Further molecular work showed indeed that cell metabolism generates free



**FIGURE 5** Adélie penguins ( $n = 115$ ) in good body condition (scaled mass index) show lower mean vector of dynamic body acceleration (VeDBA in  $g = 9.81 \text{ m/s}^2$ ) than penguins in poor body condition (in grams)

radicals (reactive oxygen species – ROS) as a by-product of mitochondrial activity (reviewed in Krause, 2007), with an impact on survival probabilities and reproductive output (Stier, Reichert, Massemin, Bize, & Criscuolo, 2012). Upper limits to rates of energy expenditure in animals, particularly diving ones, might also be set by structural constraints in the fractal architecture of circulatory networks (Brown, Gillooly, Allen, Savage, & West, 2004), heat dissipation limits to sustained rates of energy expenditure (Speakman & Król, 2010) and other factors. A growing literature indicates the relationship between allometry, energy expenditure and diving efficiency in birds (Sato et al., 2007, 2009), and our findings are consistent with recent studies establishing functional links between levels of energy expenditure and fitness traits (Elliott et al., 2013; Le Vaillant et al., 2012).

#### 4.1 | Caveats to the notion of energetic fitness

Energetic fitness might well be a powerful indicator of fitness, yet there are several well-identified limitations to this approach (Elliott et al., 2013, 2014; Jeanniard-du-Dot, Guinet, Arnould, Speakman, & Trites 2017; see Appendix S1). Energy expenditure also occurs in the absence of movement, and this is not taken into account by the accelerometry method. FMR as calculated using VeDBA therefore does not embrace variability in maintenance metabolism. There are

individually variable levels of RMR and BMR, and energetic costs also occur in certain species via, for example non-shivering heat production (McNab, 2002). Activating and maintaining an immune system has also non-negligible energetic costs, and those tend to increase in individuals facing pathogens and stressful situations (Bonneaud et al., 2003). Furthermore, the dynamics of energy storage through, for example fat deposition, have to be considered. High FMR has a much higher impact upon fitness levels if the energy used is drawn from protein (i.e. from muscle mass), than from fat deposits (Le Maho et al., 1981). Life-history strategies of studied animals therefore have to be taken into account, and specifically those of income/capital breeders (Stearns, 1992). This calls for energetics studies conducted over longer time periods (Green, Boyd, Woakes, Warren, & Butler, 2009), required to match long-term studies of life-history metrics. Finally, there is a massive body of work investigating the “live-fast-die-later” hypothesis (Speakman, Selman, McLaren, & Harper, 2002), which posits that ageing might be uncoupled from rates of energy expenditure.

These different, important points indicate that forthcoming studies should carefully assess the actual impact of such, and other, processes on the adequacy of using energetic fitness as an evolutionary currency. One potential conclusion might be that energetic fitness is one possible metric of fitness, which might be best used in combination with other, more “conventional” fitness proxies (Crossin, Cooke, Goldbogen, & Phillips, 2014).

## 5 | CONCLUSIONS

Following the series of previous work (as referenced across this text) indicating the notion of energetic fitness, we proposed to use FMR as a short-term measurement of fitness. Here, we outlined the conceptual and technological means enabling this approach, which is distinct from the framework set by Brown et al. (1993), as well as its limitations. We also provided an empirical example of how FMR and fitness correlate in a wild population. While we are most aware of the potential weaknesses and agree with the importance of further exploration and validation of the practicability of energetic fitness, we suggest that energetics are a major tool that, so far, has not been used to its full potential in operational evolutionary biology. The integrative power of this approach is due to the fact that energetics uses one single currency, which is eminently suitable for comparative analyses (Brown et al., 2004; McNab, 2002). Energetic fitness will also be most useful as a short-term fitness currency, and for the study of inter-individual variability, since it allows immediate evolutionary rating of the morphological, physiological and behavioural strategies developed by individuals. This is particularly relevant for the study of the fitness consequences of animal personalities and related pace-of-life strategies, as proposed by Careau and Garland (2012). Furthermore, an energetics approach to evolutionary fitness of single organisms seems appropriate in the context of global change and its impacts upon the biosphere. For instance, energetic fitness is an ideal tool within the emerging field

of macrophysiology (Chown & Gaston, 2008; Gaston et al., 2009), which aims at testing “variation in physiological traits over large geographical, temporal and phylogenetic scales.” Indeed, energetic fitness specifically allows testing the consequences of variation in physiological traits upon individuals, populations and communities, across all considered spatio-temporal scales. From an applied point of view, this also leads to using energetic fitness within the framework of conservation physiology (sensu Wikelski & Cooke, 2006), for a better integration of physiological processes and their evolutionary consequences upon the design and the assessment of conservation strategies.

## ACKNOWLEDGEMENTS

Financial support was provided by NSF grants OPP 9526865, 9814882, 0125608, 0440643 and 0944411. D.G. is funded by CNRS and the French Polar Institute (IPEV) within the ADACLIM program (grant 388). M.M. was partly funded through a New Zealand Ministry of Science and Innovation grant (C01X1001). We thank Phil Lyver for providing equipment, and all fieldworkers for their tremendous help in resighting bands since 1997, especially S. Jennings and A. Pollard for her additional help in deploying and recovering accelerometers. We also thank Arvind Varsani for laboratory work linked to bird sexing. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government. This is Point Blue Conservation Science Contribution #2170.

## AUTHORS' CONTRIBUTIONS

D.G., A.L., G.B., K.M.D. and D.G.A. conceived the research. All authors performed the research. D.G. and A.L. wrote the manuscript, with input from all further co-authors.

## DATA ACCESSIBILITY

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.n802d> (Grémillet et al., 2018).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**How to cite this article:** Grémillet D, Lescroël A, Ballard G, et al. Energetic fitness: Field metabolic rates assessed via 3D accelerometry complement conventional fitness metrics. *Funct Ecol*. 2018;00:1–11. <https://doi.org/10.1111/1365-2435.13074>