The energetic and survival costs of growth in free-ranging chipmunks

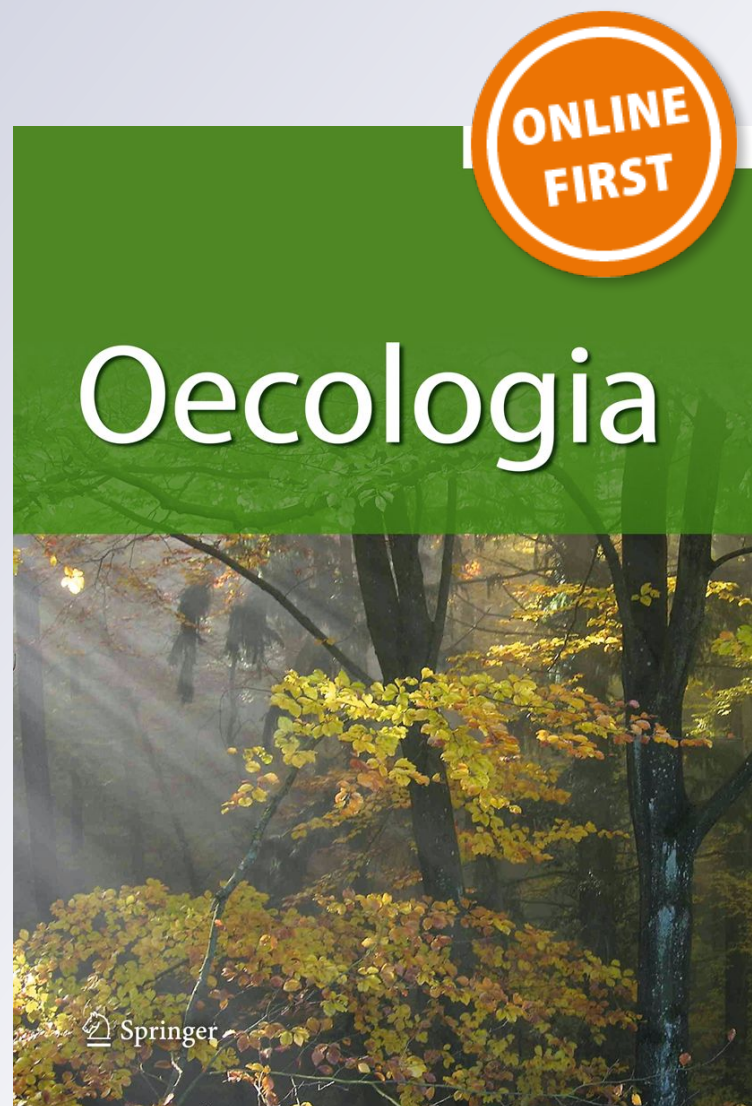Vincent Careau, Patrick Bergeron, Dany Garant, Denis Réale, John R. Speakman & Murray M. Humphries

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The energetic and survival costs of growth in free-ranging chipmunks

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Abstract The growth/survival trade-off is a fundamental aspect of life-history evolution that is often explained by the direct energetic requirement for growth that cannot be allocated into maintenance. However, there is currently no empirical consensus on whether fast-growing individuals have higher resting metabolic rates at thermoneutrality (RMRt) than slow growers. Moreover, the link between growth rate and daily energy expenditure (DEE) has never been tested in a wild endotherm. We assessed the energetic and survival costs of growth in juvenile eastern chipmunks (*Tamias striatus*) during a year of low food abundance by quantifying post-emergent growth rate ($n = 88$), RMRt ($n = 66$), DEE ($n = 20$), and overwinter survival. Both RMRt and DEE were significantly and positively related to growth rate. The effect size was stronger for DEE than RMRt, suggesting that the energy cost of growth in wild animals is more likely to be related to the maintenance of a higher foraging rate (included in DEE) than to tissue accretion (included in RMRt). Fast growers were significantly less likely to survive the following winter compared to slow growers. Juveniles with high or low RMRt were less likely to survive winter than juveniles with intermediate RMRt. In contrast, DEE was unrelated to survival. In addition, botfly parasitism simultaneously decreased growth rate and survival, suggesting that the energetic budget of juveniles was restricted by the simultaneous costs of growth and parasitism. Although the biology of the species (seed-storing hibernator) and the context of our study (constraining environmental conditions) were ideally combined to reveal a direct relationship between current use of energy and future availability, it remains unclear whether the energetic cost of growth was directly responsible for reduced survival.

Keywords Allocation · Botfly · BMR · FMR · Hoarding

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Introduction

Young animals often face considerable challenges in acquiring resources, especially when born during periods of low food abundance (Lindström 1999). Given that limited food intake could negatively impact fitness-related traits (e.g., delayed age at maturity, reduced survival), selection might be expected to favor individuals that are able to grow fast even under poor conditions (Roff 1992). However, rapid growth must be sustained by increased

foraging rates, which can lead to an increased risk of predation in the short term (McPeek 2004). In addition, life-history theory generally assumes that the energy required to fuel fast growth cannot be allocated to traits associated with maintenance, such as immunocompetence (Mangel and Stamps 2001). Both potential costs (predation risk and diverted energy) may reduce survival, which is thought to shape the evolution of the optimal growth curve along a growth/mortality trade-off (Stearns 1992). The simple observation that some individuals grow at lower rates than others, even with unlimited access to food, implies that a high growth rate may be costly (Dmitriew 2011). Although great emphasis has been placed on understanding the potential survival costs of growth rate in wild animals, especially in terms of increased predation risk (Lima and Dill 1990; Lima 1998; Dmitriew 2011), physiological costs have been largely ignored (Stoks et al. 2006).

It is theoretically expected that growing individuals have higher resting metabolic rates at thermoneutrality (RMRt) or maintenance metabolism (in ectotherms) than nongrowing ones, because these measures include the additional energy costs of (1) synthesizing new tissues and (2) maintaining the larger digestive organs (e.g., the liver) required to assimilate energy. In fact, the additional cost of growth, just like reproduction, is the main reason why measurements made on growing endotherms cannot be referred to as "basal metabolic rate" (BMR, McNab 1997). Accordingly, a number of studies have found that growing animals have a higher RMRt or maintenance metabolism than nongrowing ones (Jorgensen 1988; Chappell and Bachman 1995; Vézina et al. 2009). Growth can also have long-lasting effects on metabolism; Criscuolo et al. (2008) showed for example that juveniles experiencing compensatory growth have a higher BMR at adulthood in captive zebra finches (*Taeniopygia guttata*).

A relevant question to ask in light of the evolution of the growth/survival trade-off is whether fast growers have higher metabolic rates than slow growers. This question has been investigated in many taxa (mammals, birds, reptiles, fishes, insects, and invertebrates) and using several different approaches (interindividual and interspecific variation, quantitative genetics, and artificial selection). The results for the relationship between growth rate and maintenance costs are strikingly inconclusive, as many studies have reported a relationship that was either positive (McNab 1980; Derting 1989; Yamamoto et al. 1998; McCarthy 2000; Stoks et al. 2006; Sadowska et al. 2009), nonsignificant (Derting and McClure 1989; Álvarez and Nicieza 2005; Nespolo et al. 2005), or even negative (Koehn 1991; Konarzewski 1995; Bayne 1999, 2000; Konarzewski et al. 2000; Steyermark 2002; Álvarez and Nicieza 2005). This diversity of results is perhaps due to

the fact that both positive and negative correlations between RMRt and life-history traits might be expected under different circumstances (Speakman 1997; Nilsson 2002; Blackmer et al. 2005; Boratyński and Koteja 2010). The "increased intake hypothesis" predicts a positive relationship between growth rate and RMRt, because fast growers need more "metabolic machinery" to enable greater assimilation of energy for growth (Biro and Stamps 2010). This increase in "machinery" has a maintenance cost (detected in the RMRt) that could underlie the growth/survival trade-off. On the other hand, the "compensation hypothesis" predicts a negative relationship between growth rate and RMRt, because a trade-off may also arise due to energy allocation constraints between growth and maintenance (Olson 1992; Wieser 1994; Speakman 1997; Bayne 2000; Konarzewski et al. 2000; Nilsson 2002; Steyermark 2002; Blackmer et al. 2005). In this case, fast growers have a lower RMRt than slow growers, because the animal has access to a relatively fixed amount of resources and so the energy used for RMRt is not available for growth. Given these opposing predictions, the relationship between growth rate and RMRt, taken alone, cannot be used to critically assess whether energy can be used as a "currency" in life-history models, as (1) both positive and negative correlations can be obtained and interpreted in light of a more general growth/survival trade-off, and (2) there is the possibility that both processes occur simultaneously, canceling each other out.

An additional complexity is that results derived from constant-conditions laboratory experiments may not be directly applicable to variable natural conditions (Álvarez and Nicieza 2005; Burton et al. 2011). More studies are therefore needed to assess the relationship between growth and RMRt or maintenance metabolism in wild animals. Perhaps even more informative would be attempts to measure the daily energy expenditure (DEE), or the "cost of living," in wild animals (Speakman 2000). On the one hand, the energy cost of synthesizing new tissues and maintaining larger organs should be more apparent in the RMRt than the DEE (akin to a dilution effect). On the other hand, it is possible that the energy costs of increased tissue accretion are exacerbated by the energy costs of increased activity and higher foraging rates, leading a stronger effect of growth rate on DEE than on RMRt (akin to a snowball effect). In the only study that has simultaneously quantified growth rate, DEE, and maintenance metabolism, Peterson et al. (1998) found that growth was positively correlated with DEE but not with maintenance metabolism in garter snakes (*Thamnophis sirtalis*). In endotherms, surprisingly, the impact of growth rate on DEE remains virtually unexplored in the wild, despite its ecological relevance. Although the study of energetic costs of growth in wild animals is mostly restricted to a correlative approach, the

relationships observed can be placed in a natural context, and the potential energetic costs can be related to survival.

We examined the relationships between growth rate, RMRt, DEE, and overwinter survival during a year of low food abundance in a free-ranging eastern chipmunk (*Tamias striatus*) population. We estimated body growth from emergence from the natal burrow until immergence for winter hibernation, and then sampled our population the following year to assess overwinter survival. After leaving their natal burrows, juvenile chipmunks start foraging and hoarding seeds to meet their immediate energy requirements and to accumulate sufficient energy to survive winter. Eastern and yellow-pine chipmunks (*T. amoenus*) rely primarily on hoarded or cached food to survive winter (Humphries et al. 2002; Kuhn and Vander Wall 2008), but can also be characterized by autumn increases and winter declines in body mass (Levesque and Tattersall 2010). Given that food items eaten to sustain growth cannot be hoarded for winter use, and the main masting tree (*Fagus grandifolia*) on our site did not produce seeds during the year of our study, we expected to detect the classic growth/mortality trade-off in our population. We also measured RMRt and DEE in a subset of juveniles to test whether these traits and the nonresting energy expenditure (DEE − RMRt) were correlated with growth rate. We also estimated juvenile overwinter survival: if the energetic costs of growth underlie the growth/mortality trade-off, then we expect high RMRt and high DEE to be associated with reduced survival. Finally, juveniles of the cohort studied here experienced various levels of botfly parasitism (Careau et al. 2010). We therefore evaluated the effects of botfly parasitism on growth rate and survival.

Materials and methods

Study area and population monitoring

We monitored an individually marked population of free-ranging eastern chipmunks in the Sutton Mountains (Québec, Canada, 45°05′N, 72°26′W). Our study site contained 228 Longworth traps distributed in a circular grid pattern over 25 ha of mature American beech (*Fagus grandifolia*) forest (Landry-Cuerrier et al. 2008). Although we have studied chipmunks in this region for multiple years, we report here the results of a single intensive field season when we monitored a large cohort of juveniles by systematically trapping the entire grid continuously from natal emergence (late May) to hibernal immergence (early October) in 2007. Similar intensive methods were not pursued in subsequent years, rendering this a single-year study with an additional trapping session in the following spring to assess overwinter survival. We systematically trapped the entire grid every week from early May through early October 2007. Traps were baited with peanut butter around 8:00 and visited at intervals of 2 h until sunset. At first capture, individuals were permanently marked with numbered ear tags (National Band and Tag Company 1005-1) and a Trovan® PIT tag inserted in the interscapular region. For all captures, we noted trap location, body mass (M_b, measured with a 300 g Pesola scale, accuracy ±1 g), sex, reproductive status (males scrotal or abdominal; females lactating, nonlactating, or pregnant) and the number of botfly larvae. We also recorded the number of warble pores (scars), which indicate that botfly larvae recently emerged from the chipmunk. The sum of botfly larvae and warble pores on any given capture was taken to be the maximum parasite load experienced by this chipmunk over the summer (hereafter referred to as the "maximum number of botfly larvae"). Animals were captured and handled in compliance with the directives of the Canadian Council on Animal Care (#2007-DT01-Université-de-Sherbrooke) and the Ministère des Ressources Naturelles et de la Faune du Québec (#2008-04-15-101-05-S-F). Closely monitoring the population allowed us to differentiate juveniles from adults (see Careau et al. 2010 and Fig. S1 of the Electronic supplementary material, ESM). We also trapped throughout the active period of 2008 (from May to October) to estimate juvenile overwinter survival.

The annual mast seed production of beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*) trees within the study site from spring to autumn was sampled as in Landry-Cuerrier et al. (2008) and Bergeron et al. (2011b). We placed a total of 60 seed-collecting buckets (0.06 m^2) under the canopies of trees with diameters at breast height of at least 10 cm, at 30 sampling points evenly distributed across the study site. In 2007, the seed production was nil (Bergeron et al. 2011b). Because chipmunks typically empty their cheek pouches into the trap when they are captured, we observed that during nonmast years they forage on fruits (black cherries, strawberries), bulbs (spring beauty, trout lily), invertebrates (snails, slugs, caterpillar), and mushrooms (VC, personal observation). Food items found in the traps, however, offer only a qualitative description of the resources available, and we do not have quantitative estimates of the productivity and abundance of these alternative food sources.

Resting metabolic rate

Chipmunks were captured on the grid in late afternoon and transported to a nearby laboratory facility where their RMRts were measured overnight. The chipmunks were then released at their original trap location the following morning. Aside from when they were in the metabolic chambers, the animals were provided with apple and

peanut butter at all times. We measured RMRt using a computerized open-circuit respirometry system that allowed us to measure two chambers sequentially for each of two oxygen analyzers, as described in Careau et al. (2010). All respirometry runs were conducted by one of us (VC) with the aid of a single assistant to minimize the observer effect. For a given metabolic run, four individuals were weighed on a digital balance (± 0.1 g) and then placed individually in a 650 or 850 ml plexiglass cylindrical metabolic chamber. Chambers were placed in a constant-temperature cabinet regulated at 30 °C, which lies within the thermoneutral zone for chipmunks (Wang and Hudson 1971). A manifold and four mass-flowmeters provided a constant flow of 450 mL min^{-1} of dry, CO_2-free air to each chamber, as well as to two baseline airflows. The outflows of each chamber and the two baselines were directed to a computer-controlled multiplexor, which allowed us to sequentially sample baselines and the chambers using two oxygen analyzers. A 100 mL min^{-1} subsample of baseline air or chamber outflow was dried and pulled through the oxygen analyzer, alternating between baseline (5 min) and the two chambers (25 min each) over a 3.5 h period (each animal was monitored about 45 % of the time). By running two cycles between 2000 and 0500 hours, we were able to measure RMRt during the resting phase for up to eight animals each night. RMRt was not influenced by the timing relative to the start of the respirometry trial, the size of the chamber, or whether the run was conducted early or late at night (results not shown). We calculated individual O_2 consumption according to Eq. 4a of Withers (1977). We did not scrub the chamber outflows of CO_2, and we assumed an RQ of 0.8 to calculate O_2 consumption and convert data from mL O_2 min^{-1} to mW (Koteja 1996b; Speakman 2000). The RMRt was calculated from the lowest baseline level of O_2 consumption recorded for 5 min during a 3.5 h run (see Careau et al. 2010 for details on respirometry). We excluded three measurements because the individuals did not rest in the metabolic chambers (i.e., they were active throughout the run, as indicated by visual inspection of the metabolic trace and the animal itself at the end of the run).

Daily energy expenditure

We measured DEE using the doubly labeled water (DLW) method (Speakman 1997; Butler et al. 2004). This technique estimates the CO_2 produced by a free-ranging animal based on the differential washout of injected hydrogen (^{2}H) and oxygen (^{18}O) isotopes. The DLW method provides an accurate measure of DEE over periods of several days (Speakman et al. 1994), and has previously been used successfully on eastern chipmunks (Humphries et al. 2002). The dataset used in this study is a subset (i.e., juveniles

only) of the dataset used by Bergeron et al. (2011a). All manipulations in the field were performed by one of us (VC) to minimize variation. Briefly, we injected chipmunks intraperitoneally with 240 μl of DLW (37.78 and 4.57 % enriched ^{18}O and ^{2}H, respectively), after which subjects were held in the trap for a 1 h equilibration period (Speakman and Król 2005). Then, an initial blood sample was collected via a clipped toenail for isotope analysis (see Careau et al. 2012b for details). Chipmunks were then released at the site of capture and recaptured, weighed, and bled 1–3 days later, at multiples of 24 h (or as close as feasible to such multiples), and a final blood sample was taken to estimate isotope elimination rates. Taking samples over multiples of 24 h periods minimizes the influence of circadian variation in DEE (Speakman et al. 1994; Berteaux and Thomas 1999). The range of absolute deviation from 24 h was 5–71 min (25th percentile, 9 min; median, 36 min; 75th percentile, 59 min). A total of two juveniles were blood sampled without prior injection to estimate background isotope enrichments of ^{2}H and ^{18}O (method C in Speakman and Racey 1987).

Limitations

The methods we used to quantify RMRt (respirometry overnight) and DEE (DLW) are relatively invasive and could have induced negative effects on the behavior, survival, and/or growth of juveniles, especially for those who recently emerged from the maternal burrow. As a result, we did not measure RMRt and DEE in the peak phase of juvenile growth, which probably occurred around the time they emerged from the maternal burrow. Instead, we let juveniles grow naturally and sampled RMRt and DEE in the plateau phase of their growth (see Figs. S1 and S2 of the ESM). Such a protocol is similar to those previously used in studies of the energetic cost of growth (e.g., Steyermark 2002). Time elapsed between first day of capture and metabolic measurement averaged ($\pm$SD) 30 ± 21 days for RMRt (range 3–91) and 47 ± 20 days for DEE (range 22–93). The main limitation of this protocol is that we tested correlations between a growth rate measure that includes the period of maximum growth rate (from emergence of the burrow to metabolic measurement) and RMRt and DEE measures taken after the period of maximum growth, coinciding instead with the plateau phase of growth. Because some individuals may have been characterized by little or no growth in the week prior to metabolic measurements, the direct energetic costs of synthesizing new tissues might have been negligible. Therefore, it remains unclear whether a positive correlation between growth and RMRt or DEE is a direct reflection of previous costs of growth. One interesting possibility is that, due to limited plasticity, the metabolic machinery required

during the peak phase of the growth is carried over to the plateau phase. If this is the case, any correlations we detect may be influenced by a combination of direct effects of ongoing growth and carryover effects from previous growth.

Air temperature

To assess the effect of air temperature (T_a) on RMRt, we used the two-week average of the daily averages obtained from a weather station located ca. 20 km from the study site (Environment Canada, Sutton station, http://climate. weatheroffice.gc.ca; 45°04′N, 72°41′W). To test the effect of T_a on DEE, we could not use the data from Sutton station (as for RMRt), because it did not report hourly estimates (which we needed to calculate an average T_a from the initial to final capture). Therefore, we used the hourly average of two weather stations near our site: Lac Memphremagog 45°16′00″N, 72°10′00″W, 32 km north; Frelighsburg 45°03′01″N, 72°51′41″W, 37 km west). Both stations gave T_a estimates that were highly correlated with each other and to a weather station located in the middle of our grid that was operational only in 2006 (Lac Memphremagog vs. Frelighsburg stations: $r = 0.96$, $n = 3719$; onsite station vs. Lac Memphremagog: $r = 0.97$, $n = 3719$; onsite station vs. Frelighsburg: $r = 0.98$, $n = 4366$; correlations estimated for each hourly estimate available for each station from 1 May 2006 to 1 October 2006).

Statistical analysis

We restricted the analysis to growth rates of individuals for which we had at least three M_b measurements. We used a random regression approach to assess the extent of individual variation in growth rate (i.e., the slope at which M_b increases through time). In a model including individual identity (ID) as a random effect, we included several fixed effects (Julian day, Julian day^2, sex, and date of first capture), and sequentially removed the least significant term from the model based on its p value until only marginally nonsignificant effects (i.e., $p \leq 0.1$) remained in the model. After the structure of the fixed effects had been determined, we included ID in the interaction with Julian day ("ID × Julian") as an additional random term to test for the presence of individual differences in growth rate (Pinheiro and Bates 2000). We also included an interaction between ID and Julian day^2 to test if individuals differed in their nonlinear growth pattern. The significance of adding each random term was tested using a likelihood ratio test (LRT). Upon finding significant individual differences in growth rate, we calculated the growth rate for all juveniles ($n = 88$) as their gain in M_b during summer divided by number of days (in g day^{-1}), and used a linear model to test whether growth was related to the number of captures, the maximum number of botfly larvae, and sex.

We used linear models to test for the relationships between RMRt or DEE and growth prior to the metabolic measurement, calculated as the gain in M_b from first capture up to metabolic measurement divided by the number of days (i.e., in g day^{-1}). To control for potential confounding effects, we included the following covariates: M_b at metabolic measurement, sex, date of first capture, M_b on first capture, time elapsed between first capture and metabolic measurement, maximum number of botfly larvae, number of botfly larvae at the time of measurement, date of measurement, and air temperature (T_a; daily average of the previous two weeks for RMRt, and hourly average for DEE). Backward model selection was performed as described above. Residuals of models were normally distributed (Shapiro–Wilks normality test: $W \geq 0.98$, $p \geq 0.73$). Recognizing that some individuals may have been characterized by little or no growth in the period immediately prior to metabolic measurements, we fitted a quadratic relationship between M_b and Julian day prior to RMRt or DEE measurement, and recalculated growth by considering only the portion before the inflection point (determined by visual inspection of the curves), and retested its effect on RMRt and DEE. We also tested the effect of growth on the level of nonresting energy expenditure (DEE − RMRt) using the same model selection approach as for RMRt and DEE. To explore the possibility that the effect of growth rate on RMR, DEE, and nonresting energy expenditure was different in males and females, we added an interaction between growth rate and sex in our final model.

Individuals that were never captured in the following active season were considered not to have survived the winter. To limit the potential bias resulting from dispersal, we also tested the effect of growth and RMRt on the survival of the subset of individuals that were still present on the grid by 1 August 2007 (after which dispersal is very low: the numbers of new individuals captured on the grid before and after this date were 188 and 11, respectively). We used a generalized linear model with a binomial error structure (logit link function) to test the effect of sex, maximum number of botfly larvae, date of first capture, mass at first capture, and either growth, RMRt, or DEE on survival. We tested for the significance of linear selection acting on a given variable by comparing a model that included covariates and the variable of interest to a model that excluded the variable of interest. Because our measure of survival followed a binomial distribution, significance was established using the change in deviance between the reduced and complete models, and tested against a χ^2 distribution with one degree of freedom. We also tested whether the effects of growth, RMR, DEE, and nonresting

energy expenditure on survival were different in males and females (Boratyński et al. 2010) by including an interaction between sex and the factor of interest in our model. Selection gradients were calculated using a linear model on standardized growth rate or RMRt (mean, 0; SD, 1) and relative survival (Lande and Arnold 1983).

We used the program R 2.13.1 (http://www.r-project.org) to perform all analyses. Means and estimates are presented ±SE if not otherwise stated. We used the package pwr to evaluate the power to detect a significant effect of DEE on survival. We calculated effect sizes (r) via formula 11 in Nakagawa and Cuthill (2007), which takes covariates into account and is often referred to as a partial correlation coefficient. Accordingly, we graphed the partial residual correlations to show the effect of growth on metabolic variables. Partial residual correlations were plotted as residuals from the regression of a metabolic variable on covariates against the residuals from the regression of growth rate on covariates. This procedure yielded correlation estimates that were numerically equivalent to the effect size (r) calculated in the multiple regression models that included covariates.

Results

Seasonal pattern

From 24 May 2007 to 10 October 2007, we recorded 1,295 measures of M_b on a total of 88 juveniles (mean number of measurements per individual 14.7, range 3–43; see Table S1 of the ESM for descriptive statistics for each sex separately). At the population level, a clear period of rapid growth occurred from late May to early July, after which M_b remained stable until October (Fig. S1 of the ESM). Although M_b was not significantly influenced by the day of first capture ($F_{1,86} = 0.16$; $p = 0.69$) or sex ($F_{1,86} = 0.09$, $p = 0.77$), it was significantly affected by Julian day ($F_{1,1205} = 887.89$, $p < 0.001$), and Julian day^2 ($F_{1,1205} = 688.66$, $p < 0.001$).

Individual pattern in growth rate

There were significant interindividual differences in M_b throughout the summer, as indicated by a significant ID (intercept, at day 0) random effect (LRT: $\chi^2 = 853.59$, $p < 0.001$), that explained 64.5 % of the variance. There were also interindividual differences in growth rate, as the addition of the ID × Julian day interaction as a random effect significantly improved the fit of the model (LRT: $\chi^2 = 132.72$, $p < 0.001$). However, the addition of the ID × Julian day^2 interaction did not further improve the fit of the model (LRT: $\chi^2 = 1.04$, $p = 0.79$).

On average, juveniles gained 0.31 ± 0.04 g day^{-1} from the first to last capture. Growth rate was not different between sexes (Table S1 of ESM; $t_{84} = 0.117$, $p = 0.91$), and was not influenced by the number of captures throughout summer ($t_{84} = -1.53$, $p = 0.13$). Growth rate was negatively correlated with the maximum number of botfly larvae ($t_{84} = -2.51$, $p = 0.01$). Individuals that were never observed with a larva had a 3.5-fold higher growth rate (uninfected individuals; $n = 44$, 0.49 ± 0.07 g day^{-1}) than those observed with at least one botfly larva (infected individuals; $n = 44$, 0.14 ± 0.02 g day^{-1}; Fig. 1).

Resting metabolic rate

We measured RMRt for 66 juveniles from 12 June 2007 to 6 September 2007. The average RMRt (±SD) was 619 ± 56 mW (Table S1 in the ESM; mean M_b was 80.1 g in this sample). These 66 individuals were captured on average 10.4 times prior to RMRt measurement (range 2–32, total: 688; Fig. S2a in the ESM). In this sample, the average growth rate was 0.31 ± 0.05 g day^{-1}. After accounting for the significant effect of M_b (Fig. S3a in the ESM) and the marginally nonsignificant effect of T_a on RMRt (Table 1a), the residual variation was positively correlated to growth rate (Table 1a; Fig. 2a). An increase in growth rate from 0.10 g day^{-1} (25th percentile) to 0.46 g day^{-1} (75th percentile) represented a 3 % (18 mW) increase in RMRt. The interaction between growth rate and sex was not significant ($t_{60} = 0.18$, $p = 0.86$). All other potential fixed effects (see "Materials and methods") were not significant (all $p > 0.44$), including time elapsed between the first capture and RMRt measurement ($t_{61} = 1.09$, $p = 0.28$), indicating that the correlation with
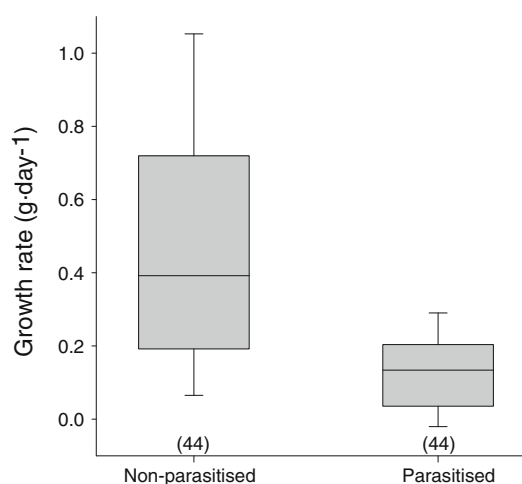
Fig. 1 Growth rate (in g day^{-1}) in wild juvenile eastern chipmunks (*Tamias striatus*) that were either never observed as being infected with a botfly larva (unparasitized) or observed once with at least one botfly larva (parasitized) throughout summer 2007

Table 1 Multiple regression models of (a) the resting metabolic rate at thermoneutrality (RMRt, in mW), (b) the daily energy expenditure (DEE, in mW), and (c) the nonresting energy expenditure (i.e., DEE minus RMRt) as a function of growth rate (in g day^{-1}) in free-ranging eastern chipmunks in the plateau phase of their growth during a nonmast year

	Estimate $\pm$ SE	t	df	P	Effect size
(a) RMRt $\sim$					
M_b	4.55 ± 1.18	3.86	62	<0.001	0.440
T_a	14.44 ± 7.77	1.86	62	0.068	0.230
Growth rate	49.47 ± 18.74	2.64	62	0.010	0.318
(b) DEE $\sim$					
M_b	46.47 ± 10.17	4.57	16	<0.001	0.752
Sex	361.84 ± 122.22	2.96	16	0.009	0.595
Growth rate	1211.05 ± 376.65	3.22	16	0.005	0.626
(c) Nonresting energy expenditure $\sim$					
M_b	34.99 ± 13.10	2.67	13	0.019	0.595
Sex	338.25 ± 178.83	1.89	13	0.081	0.465
First capture	8.97 ± 4.98	1.80	13	0.095	0.447
Growth rate	1343.95 ± 568.69	2.36	13	0.034	0.548

Final models included covariates such as body mass (M_b), air temperature (T_a), sex, and date of first capture (see text for covariates excluded)

growth rate is not an artefact related to sampling dates (see also Fig. S2a in the ESM for the growth rate pattern during days prior to RMRt measurement). The effect of growth rate on RMRt remained significant (multiple regression estimate 40.09 ± 17.88, $t_{62} = 2.24$, $p = 0.029$) when considering only the growth calculated before the inflection point of the relationship between M_b and Julian day.

Daily energy expenditure

We measured DEE for 21 juveniles from 21 July 2007 to 31 August 2007. The average DEE ($\pm$SD) was $1{,}528 \pm 312$ mW (range 730–2,057 mW, $2.5 \times$ RMRt; mean M_b was 81.1 g in this sample). These 21 individuals were captured on average 14.0 times prior to DEE measurement (range 6–26, total 293; see Fig. S2b in the ESM). In this sample, all individuals had positive growth rates (average 0.26 ± 0.08 g day^{-1}), except for one that was captured only six times before DEE measurement, which had a growth rate of -0.6 g day^{-1} (see Fig. S4 in the ESM). After excluding this outlier, DEE was significantly affected by M_b (Fig. S3b in the ESM), sex, and growth rate (Table 1b; Fig. 2b). An increase in growth rate from the 25th to 75th percentile (i.e., from 0.10 to 0.46 g day^{-1}) corresponded to a 29 % (436 mW) increase in DEE. Although males and females had similar DEEs on a whole-animal basis (Table S1 in the ESM), males in this sample were smaller (79.8 ± 1.3 g) than females (84.7 ± 1.5 g), which resulted in a 3.3 % higher mass-specific DEE in males (18.6 ± 0.96 mW g^{-1}) than in females (18.0 ± 0.98 mW g^{-1}). The interaction between growth rate and sex was not significant ($t_{15} = 0.38$, $p = 0.71$). All other fixed effects (see "Materials and methods") were not

significant ($p > 0.22$), including time elapsed between first capture and DEE measurement ($t_{15} = 0.07$, $p = 0.94$), indicating that the correlation with growth rate is not an artefact related to sampling dates (see Fig. S2b in the ESM). The effect of growth rate on DEE remained significant when we considered the growth before the inflection point (estimate 754.77 ± 235.67, $t_{15} = 3.20$, $p = 0.006$).

Nonresting energy expenditure

We obtained RMRt and DEE estimates for the same individuals on 18 occasions. The average ($\pm$SD) level of nonresting energy expenditure was 877 ± 313 mW (range 73–1,422 mW). The average ($\pm$SD) metabolic scope (ratio of DEE on RMRt) was 2.40 ± 0.53 (range 1.11–3.39). There was no relationship between mass-adjusted DEE and RMRt (estimate 0.45 ± 1.29, $t_{16} = 0.35$, $p = 0.73$), perhaps due to the long interval between measurements (range 1–47 days, mean $\pm$ SD 15.4 ± 15.0 days). After accounting for the significant effect of M_b (Fig. S3c in the ESM) and the marginally nonsignificant effects of sex and date of first capture on the level of nonresting energy expenditure, residual variation was positively correlated to growth rate (Table 1c; Fig. 2c). An increase in growth rate from the 25th to 75th percentile (i.e., from 0.10 to 0.46 g day^{-1}) corresponded to a 55 % (484 mW) increase in nonresting energy expenditure.

Survival

Of the 36 females and 52 males for which we had at least three measures of M_b in 2007, only ten of each sex were
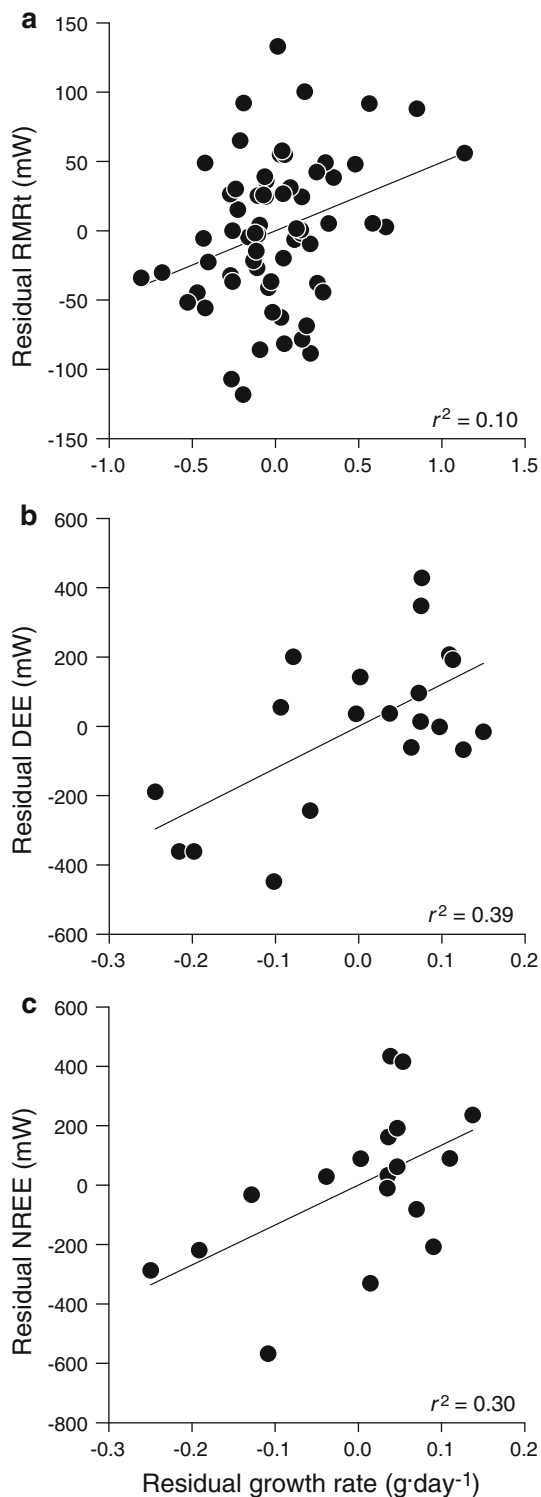
Fig. 2 Relationships between growth rate (in g day^{-1}) and **a** resting metabolic rate at thermoneutrality (RMRt, in mW), **b** daily energy expenditure (DEE, in mW), and **c** nonresting energy expenditure (NREE, in mW) in wild juvenile eastern chipmunks (*Tamias striatus*). For illustrative purposes, the data points and regression lines plotted represent partial residuals from the multiple regression models (see Table 1 for statistical significance)

recaptured in 2008. The difference between the sexes in terms of survival rate (28 % in females and 19 % in males) was not significant ($\chi^2 = 0.58$, $p = 0.45$). Body mass at first capture did not influence the probability of overwinter survival ($\chi^2 = 0.22$, $p = 0.64$). Winter survival was significantly and negatively related to growth rate ($\chi^2 = 10.67$, $p = 0.001$; Fig. 3a). This translated into a negative selection gradient on growth rate ($\beta = -0.53 \pm 0.20$). The nonlinear effect on growth rate was not significant ($\chi^2 = 0.21$, $p = 0.65$). The linear effect of growth rate on survival remained significant when considering only juveniles that were still present on the grid after 1 Aug 2007 ($n = 55$, $\beta = -0.50 \pm 0.29$, $\chi^2 = 4.37$, $p = 0.04$). After accounting for the date of first capture ($\beta = -0.63 \pm 0.20$, $\chi^2 = 4.90$, $p = 0.03$), winter survival significantly reduced as the maximum number of botfly larvae increased ($\beta = -0.45 \pm 0.20$, $\chi^2 = 12.52$, $p < 0.001$; Fig. 3b).

The linear term for RMRt did not influence survival ($n = 66$, $\chi^2 < 0.01$, $p = 0.99$), and the interaction with sex was not significant ($\chi^2 = 0.24$, $p = 0.62$). However, we found a significant negative nonlinear effect of RMRt on survival ($\gamma = -0.35 \pm 0.20$, $\chi^2 = 5.33$, $p = 0.02$). Individuals with either low or high RMRt were thus less likely to survive winter (Fig. 3c). The interaction between sex and the quadratic term was not significant ($\chi^2 = 0.16$, $p = 0.69$). The nonlinear effect of RMRt on survival became marginally nonsignificant ($\chi^2 = 3.22$, $p = 0.07$) when considering juveniles that were still present on the grid after 1 Aug 2007, but this reduction in significance also reflects a reduction in sample size ($n = 44$, $\gamma = -0.30 \pm 0.25$).

We found no relationship between survival and DEE ($n = 20$, linear term: $p = 0.79$; nonlinear term: $p = 0.75$) or nonresting energy expenditure ($n = 18$, linear term: $p = 0.88$; nonlinear term: $p = 0.86$). However, the power to detect an effect of DEE and nonresting energy expenditure on survival was much lower than for growth and RMRt. The power to obtain a significant χ^2 value with one *df* given a large effect size (i.e., 0.5) and a sample size of 20 was only 0.61, as compared to 0.99 and 0.98 for sample sizes of 88 (growth rate) and 66 (RMRt).

Discussion

Fast growers had significantly higher RMRt than slow growers. In European starlings (*Sturnus vulgaris*), energy invested in tissue development represents 38.4 and 10.9 % of RMRt during the peak and plateau phases of their growth, respectively (Vézina et al. 2009). Because we measured RMRt in chipmunks that were in the plateau phase of their growth, it is likely that RMRt was increased
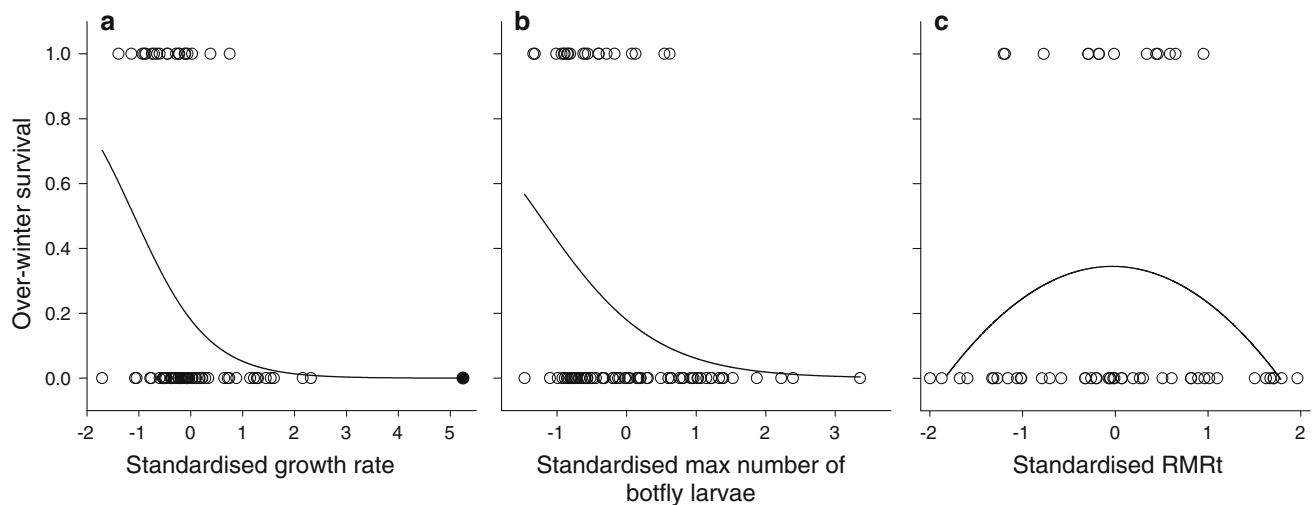
Fig. 3 Probability of overwinter survival of juvenile eastern chipmunks (*Tamias striatus*) as function of **a** growth rate from the immergence of the maternal burrow until immergence in late fall, **b** the maximum number of botfly larvae observed throughout summer, and **c** the resting metabolic rate at thermoneutrality (RMRt). For illustrative purposes, *x* variables were standardized (mean, 0; SD, 1) and adjusted for significant covariates. In **a**, the statistical test remains unchanged when the potential outlier (*filled black dot*) is removed from the analyses

by the costs of tissue accretion and by the maintenance of the body constituents required to sustain previous growth (Vézina et al. 2009). Although larger digestive organs for increased assimilation were associated with an elevated RMRt (Nespolo et al. 2002; Bacigalupe et al. 2004), several comprehensive studies show hardly any consensus on the effects of organ size on RMRt or BMR in mammals (Konarzewski and Diamond 1995; Koteja 1996a; Selman et al. 2001; Król et al. 2003; Speakman et al. 2004; Chappell et al. 2007; Russell and Chappell 2007). A weak or nonsignificant effect of organ size on RMRt combined with possible compensatory allocation mechanisms (Olson 1992; Konarzewski et al. 2000; Steyermark 2002) may have reduced the effect of growth rate on RMRt.

Fast growers had significantly higher DEE than slow growers. The overall stronger effect of growth rate on DEE than RMRt is apparent in the subset of 18 individuals for which we measured both variables: a 25th to 75th quartile increase in growth rate (i.e., from 0.10 to 0.46 g day^{-1}) represented only 1.6 % of RMRt but 26 % of DEE. This difference may occur because DEE also includes the costs of maintaining a higher foraging rate in addition to the cost in RMRt. This possibility is further supported by the fact that nonresting energy expenditure (DEE − RMRt) was also positively correlated with growth rate. It is possible that foraging costs are exacerbated because the exploratory activities that are needed to acquire scarce resources lead to increased thermoregulatory costs (when T_a is low) and other energetically costly behaviours such as agonistic encounters (Briffa and Sneddon 2007) and predator escape. Our results suggest that from an ecological perspective, the energetic costs of maintaining fast growth in wild animals are more likely to be associated with higher DEE and non-resting energy expenditure than the direct cost of tissue accretion (RMRt).

Juvenile chipmunks that maintained fast growth had significantly lower survivals over their first winter. This may have resulted from an allocation trade-off between food consumption to satisfy immediate demands versus food hoarding to satisfy overwinter requirements, which was made more severe by the low food conditions that prevailed during our study. The decision to consume or hoard a food item of a given type and perishability (Careau et al. 2007) will depend primarily on an individual's hunger level (Vander Wall 1990), which may differ according to the energy needed to sustain fast versus slow growth. The caloric content of a chipmunk's larder is so critical for winter survival that it has been suggested as a quantitative proxy for the likelihood of winter survival (Kuhn and Vander Wall 2008). Indeed, in our study system, juvenile survival is lower in years of mast failure than in years of mast production in our population (Bergeron et al. 2011b). The biology of the species (seed-storing hibernator) and the context of our study (constraining environmental conditions) were ideally combined to reveal a direct relationship between current use of energy and future availability. Accordingly, our observation that juveniles with high RMRts had lower survival could support the idea that the energy cost of growth was directly responsible for reduced survival.

However, there are several caveats to this reasoning. As noted above, the absolute effect of growth on RMRt was relatively small, which greatly reduces the chances that RMRt was the underlying factor in the growth/mortality

trade-off. In addition, individuals with low RMRts also had low survival, a finding that is difficult to reconcile with the reasoning above. A more important caveat is the absence of a relationship between DEE and survival, which may be explained by our reduced power to detect a relationship compared to growth and RMRt (see above). However, if we assume that energy was mediating the growth/survival trade-off, then the power needed to detect a survival cost to DEE may have been higher than that needed for RMRt, given that the effect of growth on DEE was approximately double than it effect on RMRt (Table 1a, b). Assuming effect sizes (r) of 0.626 and 0.319 with sample sizes of 20 (DEE) and 66 (RMRt), respectively, the power to obtain a significant χ^2 value with one df for the effect of DEE and RMRt on survival was 0.80 and 0.73, respectively. Taken together, our results suggest that the causality underlying the correlation between growth and survival is more complex than a direct energy allocation constraint.

Although few studies have assessed the relationship between maintenance metabolism and survival, it seems already clear that high, intermediate, or low metabolism may be favored depending on sexes, seasons, and environmental conditions (Burton et al. 2011). Short-tailed field voles (*Microtus agrestis*) with a higher mass-residual RMRt were more likely to survive the winter (Jackson et al. 2001). In bank voles living on an island, Boratyński and Koteja (2009) found no consistent relationship between RMRt and survival. In bank voles living in outdoor enclosures, RMRt was positively correlated with survival, but in females only (Boratyński et al. 2010). In North American red squirrels (*Tamiasciurus hudsonicus*), juveniles with low RMRt were more likely to survive winter (Larivée et al. 2010; this relationship was not influenced by growth rate). Mixed results were also obtained in fishes (see Álvarez and Nicieza 2005; Bochdansky et al. 2005). In the only study on an invertebrate, Artacho and Nespolo (2009) found a combination of negative directional selection and stabilizing selection on maintenance metabolism in the garden snail (*Helix aspersa*).

In an attempt to reconcile these contrasting results, the "context dependence" hypothesis predicts that high-RMRt individuals will have a higher fitness when environmental conditions are favouable, whereas low-RMR individuals will have a higher fitness when environmental conditions are poor (Burton et al. 2011). However, this hypothesis cannot entirely explain our result of stabilizing selection on RMRt ($\gamma = -0.35$; Fig. 3c), because we conducted our study during a non-mast year (low food resources). Another explanation for these results is that RMRt is an epiphenomenon on which selection acts indirectly (Piersma and van Gils 2011). RMRt reflects the sum of the maintenance costs of all tissues and organs required to keep a homoeothermic animal alive. In

juvenile individuals, RMRt can include the additional costs of maintaining growth and developing components of the acquired immune system. Because selection may act on many different factors that affect RMRt other than growth, it remains unclear why juveniles with either high or low RMRt had lower survival. Boratyński and Koteja (2009) reached a similar conclusion upon finding stabilizing selection on $VO_{2\text{-max}}$ in bank voles (*Myodes glareolus*).

Botfly parasitism had a negative effect on both growth rate (Fig. 1) and survival (Fig. 3b). We have previously shown in our population that each botfly larva is associated with a $\sim 7.6\%$ increase in RMRt in juveniles but not in adults (Careau et al. 2010). Although we did not detect an effect of botfly parasitism on RMRt in our sample, this was probably due to the fact that only 4 of 66 individuals were infected at the time of RMRt measurement. We recently found that botfly parasitism was also associated with a decreased cold-induced $VO_{2\text{-max}}$ and aerobic scope (ratio of $VO_{2\text{-max}}$ on RMRt, Careau et al. 2012a), which may explain the lower survival of infected juveniles. In addition, the metabolic scope (ratio of DEE on RMRt) in our population is slightly lower in juveniles (2.4) than in adults (3.22; Careau et al., unpublished), as has been reported in other rodents (Chappell and Bachman 1995; Larivée et al. 2010). For a given RMRt, an individual with a higher metabolic scope should have a greater ability to compensate for increased energy costs of growth and parasitism. If juveniles are limited in their ability to compensate, as we previously suggested (Careau et al. 2010), then the additional energy demands imposed by botfly parasitism may have reduced the energy available to invest in growth and/or survival.

Conclusion

The concept of trade-offs is central to theories on the evolution of life-history traits, with time and energy being used as "currencies" in determining the optimal pattern of resource allocation to such competing functions as growth, body maintenance, and reproduction. Because growth rate influences the balance between development time and size at maturity, the identification and quantification of the costs limiting fast growth are important for understanding life-history evolution (Dmitriew 2011). In our study, we have focused on interindividual differences in growth rate, RMRt, and DEE within a single cohort of juveniles, and combined these measures with estimates of botfly parasitism and overwinter survival. Our results are consistent with the "increased intake hypothesis," with the additional distinction that the energy component that was most affected by growth rate was not RMRt but nonresting

energy expenditure. However, we measured DEE and RMRt during the plateau phase of growth, after most of the growth had taken place. Therefore, it remains unclear whether we quantified direct energetic costs of growth, which are more likely to occur during periods with the fastest growth, or energetic costs related to the limited plasticity of the metabolic machinery that was required to sustain past growth (carryover effects).

We detected both energetic and survival costs to maintaining a fast growth and being parasitized (Careau et al. 2010), but failed to detect a direct link between DEE and survival. It must be noted that all of our observations are correlational. Ideally, one or more of the variables involved (growth, RMRt, DEE, parasitism) could have been manipulated in order to unravel the mechanisms at play. Such an experimental approach is most easily conducted in the laboratory, where the energy costs of both parasitism and growth rate appear to be different than in the wild (Álvarez and Nicieza 2005; Careau et al. 2010). Our results highlight the importance of combining at least two components of the energy budget with estimates of selection in the wild within the context of life-history trade-offs.

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