

RESEARCH ARTICLE

Sex-specific energy management strategies in response to training for increased foraging effort prior to reproduction in captive zebra finches

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ABSTRACT

Free-living animals often engage in behaviour that involves high rates of workload and results in high daily energy expenditure (DEE), such as reproduction. However, the evidence for elevated DEE accompanying reproduction remains equivocal. In fact, many studies have found no difference in DEE between reproducing and non-reproducing females. One of the hypotheses explaining the lack of difference is the concept of an 'energetic ceiling'. However, it is unclear whether the lack of increase in energy expenditure is due to the existence of an energetic ceiling and/or compensation by males during parental care. To investigate whether an energetic ceiling exists, we experimentally manipulated foraging effort in captive zebra finches, *Taeniopygia guttata*, creating two groups with high and low foraging efforts followed by both groups breeding in the low foraging effort common garden condition. DEE was measured in both sexes throughout the experiment. We show sex-specific energy management strategies in response to training for increased foraging effort prior to reproduction. Specifically, males and females responded differently to the high foraging effort treatment and subsequently to chick rearing in terms of energy expenditure. Our results also suggest that there is an energetic ceiling in females and that energetic costs incurred prior to reproduction can be carried over into subsequent stages of reproduction in a sex-specific manner.

KEY WORDS: Exercise, Workload, Parental care, Energetics, Reproduction, *Taeniopygia guttata*

INTRODUCTION

Free-living animals often engage in behaviour that involves intense activity or high rates of workload, for instance, reproduction (Lemon, 1993; Noren, 2008; Williams and Vézina, 2001), foraging (Haupt and Seitz, 1984; Maurer, 1996), thermoregulation (Bicego et al., 2007; Swanson, 2010; Weathers, 1981) and migration (Piersma, 2011; Wikelski et al., 2003; Yap et al., 2017a). These activities are predicted to be energetically expensive, and therefore, animals engaged in these activities would be predicted to have high daily energy expenditure. For the most part, there is considerable

support for this prediction. For example, the sustained metabolic scope of lactating mammals ranges from 3 to 6 times basal metabolic rate (Hammond and Diamond, 1997; Piersma, 2011); migratory birds engaging in transoceanic migrations expand their basal metabolic rate up to 9 times normal levels (Gill et al., 2005, 2009; Piersma, 2011); and peak metabolic rate of birds induced by cold challenge in experimental settings can reach up to 6 times basal metabolic rate (Barceló et al., 2017; McKechnie and Swanson, 2010; Petit and Vézina, 2014; Piersma, 2011).

However, the evidence for elevated daily energy expenditure (DEE) accompanying the aforementioned activities is equivocal. In fact, several studies have found either no or moderate differences in DEE among animals engaged in putatively very different levels of activity, for example, non-breeding versus reproducing birds and bats (Bryant, 1997; Bryant and Tatner, 1991; McLean and Speakman, 1999; Meijer et al., 1989; Weathers and Sullivan, 1993; Weathers et al., 1999; Williams and Vézina, 2001) and non-lactating versus lactating mammals (Krockenberger, 2003). Multiple hypotheses have been proposed to explain the lack of differences in DEE in these animals. One of the most prominent hypotheses proposed is the concept of an 'energetic ceiling', which posits that there is a 'maximal sustained working level', which, if exceeded, would result in loss of body condition and consequently increased mortality risk (Drent and Daan, 1980; Krockenberger, 2003; Piersma, 2011; Piersma and van Gils, 2010; Tinbergen and Verhulst, 2000). In a brood size manipulation experiment, Tinbergen and Verhulst (2000) measured DEE in great tits (*Parus major*) finding that experimental reduction in brood size results in a lower daily energy expenditure in females, while an experimentally enlarged brood size had no effect, indicative of an energetic ceiling in chick-rearing females. However, it is unclear whether the lack of increases in energy expenditure was due to a constant DEE regardless of workload (i.e. foraging and chick-provisioning) or a constraint of workload within a fixed DEE. In other words, does the energetic ceiling exist because of hardwired energetic constraint (i.e. a 'magical daily energy expenditure value' that can never be exceeded)? Or alternatively, could individuals elect not to expend more energy in the short term to avoid incurring immediate costs (e.g. increased mortality), or to better manage energy over longer periods of time?

Furthermore, a lack of difference in DEE in non-breeding versus breeding female birds could also be masked by the fact that most avian species are socially monogamous and both sexes participate in parental care during reproduction (Gilby et al., 2011; Matysioková and Remeš, 2014; Zann, 1994). An absence of energetic adjustment by females during chick-rearing can be compensated by increased provisioning rate and energy expenditure by their male counterparts to ensure reproductive success (Mainwaring and Hartley, 2016; Moreno et al., 1995). Furthermore, males and females could

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respond differently to different activities in terms of their behaviour and physiology (Moreno et al., 1995; Tarnopolsky, 2000; Yap et al., 2017b), potentially resulting in differences in DEE adjustments.

To investigate whether an energetic ceiling exists either because of constant DEE regardless of workload, or because of a constraint on workload within a fixed DEE, we first experimentally manipulated foraging effort in captive zebra finches, *Taeniopygia guttata*, using a previously described technique (Koetsier and Verhulst, 2011; Yap et al., 2017b), then allowed individuals to breed in low foraging effort common garden condition. Additionally, to allow us to detect potential compensation by males during reproduction, we looked at DEE in both males and females throughout the experiment. Our findings suggest the presence of an energetic ceiling in females. We also show that males in high foraging effort conditions increased energy expenditure during chick-rearing, likely to compensate for a lack of energetic adjustments in their female counterpart.

MATERIALS AND METHODS

Animal husbandry

Zebra finches [*Taeniopygia guttata* (Vieillot 1817)] were maintained in controlled environmental conditions (temperature 19–23°C; humidity 35–55%; constant light schedule, 14 h:10 h light:dark, lights on at 07:00 h). All birds were provided with a mixed seed diet (Panicum and white millet, 1:3, 11.7% protein, 0.6% lipid and 84.3% carbohydrate by dry mass), water, grit (coral sand) and cuttlefish bone (calcium) *ad libitum*, and received a multi-vitamin supplement in the drinking water once per week. Experiments and animal husbandry were carried out under a Simon Fraser University Animal Care Committee permit (No. 1231B-94), in accordance with guidelines from the Canadian Committee on Animal Care (CCAC).

Experimental timeline and protocol

At the beginning of the study, 36 males and 36 females were randomly assigned to either a high foraging effort group (HF) or control group. Foraging effort was experimentally manipulated using a previously established training protocol (Koetsier and Verhulst, 2011; Yap et al., 2017b; Zhang et al., 2018). Briefly, mixed seed was provided in transparent Plexiglas containers (L×W×H: 40×10×13 cm) suspended from the roof of the cage (122×46×41 cm), with feeding holes low on the front panel to allow access to seeds. Perches made of wooden pencils (diameter 0.8 cm) were fitted adjacent to feeding holes to allow birds to perch while foraging for 21 days prior to the start of the experiment (similar to the standard feeders in control cages). Over a 14 day period, perches were gradually shortened (0.5 cm every 2 days) and eventually removed completely to train birds to modify their foraging behaviour and obtain seeds in the high foraging cost condition. Birds in control foraging condition were given standard feeders (seed fountains) with perches adjacent to them throughout the experiment (Yap et al., 2017b). Upon complete removal of perches in the HF group, all birds were kept in their respective foraging condition for a further 21 days until the end of the HF treatment period. All birds assigned to the HF treatment acclimated to the training condition, and therefore, no individuals were removed from

the study during the training and HF treatment periods. Previous studies using this technique have found that HF birds adjusted their foraging behaviour and made significantly more trips to the feeder (Koetsier and Verhulst, 2011; Yap et al., 2017b).

At the end of the HF treatment, HF birds were switched to control conditions and paired for breeding (HF males with HF females, control males with control females) in common garden, low foraging effort breeding condition (i.e. all HF and control birds were given regular feeders). The breeding protocol followed previously described methods (Tissier et al., 2014; Yu et al., 2016), with slight modification. Briefly, birds were paired randomly and housed in individual breeding cages (51×39×43 cm), each with an external nest box (14×14.5×20 cm). Nest boxes were monitored daily between 08:00 h and 14:00 h for eggs laid, and new eggs were weighed (to the nearest 0.01 g) and numbered in consecutive order. Nest boxes were monitored after clutch completion until all the eggs had hatched. Chicks were reared by parents until they reached 30 days of age, at which time they were separated and maintained in non-breeding juvenile groups. Once birds could be sexed by the appearance of bill colour and sexually dimorphic plumage, they were separated into sex-specific groups. Overall, 94% of HF birds (17 of 18 pairs) and 78% of control birds (14 of 18 pairs) laid eggs. Hatching success was 52% and 54% in HF and control pairs, respectively. These numbers are comparable to breeding success of other captive zebra finch colonies around the world (Griffith et al., 2017).

We measured daily energy expenditure (DEE) using the doubly labelled water method (see detailed methods below) at four time points throughout the experiment: (1) prior to the start of the 14 day perch shortening period (pre-treatment), (2) 14 days after complete removal of perches (post-treatment), (3) when the chicks were 6 days of age during (chick-rearing). A summary of the experimental timeline is provided in Fig. 1.

Daily energy expenditure measurement

To measure DEE, we used the two-sample doubly labelled water (DLW) protocol (Speakman, 1997). To isotopically enrich the birds, we injected 2 $\mu\text{l g}^{-1}$ DLW ($^2\text{HH}^{18}\text{O}$) into the pectoralis muscle. After injection, birds were held for 1 h to allow the injected isotopes to equilibrate with the body water pool. Following equilibration, we collected an initial blood sample using heparinized microhematocrit tubes from the brachial vein for measurement of initial isotope enrichment. Birds were then returned to the control conditions. After 24 h a second (final) blood sample was collected from each bird using the same protocol described above. Blood samples were also collected from 20 uninjected birds for measurement of background isotope enrichment. After collection all blood samples were flame sealed and stored at 4°C for future analysis. For analysis blood samples were shipped to George Fox University, Newberg, OR where they were microdistilled to obtain pure water (Nagy, 1983), and the ^{18}O and ^2H enrichment of the resulting water samples measured using a Los Gatos Research Liquid Water Isotope Analyzer (LWIA-24-EP). Isotopic enrichment values for the initial and final samples were used to estimate CO_2 production using the equations for the 2-sample method in Speakman (1997, p. 315).

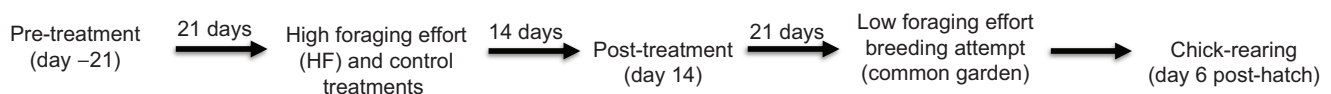


Fig. 1. Summary of the experimental timeline.

Statistical analyses

Analyses were carried out using R version 0.99.467 (<https://www.r-project.org/>). Data were first examined for normality using the Shapiro-Wilk test. Mass-specific DEE was calculated by dividing DEE by body mass. First, we analysed how body mass varies with HF treatment and chick-rearing by using repeated measure with sex, treatment, and time as main effects, pre-treatment body mass as covariate and individual bird ID as a random factor. Similarly, to investigate how mass-specific DEE varied with HF treatment and chick-rearing, mass-specific DEE was analysed using repeated measure with sex, time and treatment as main effects, and pre-treatment mass-specific DEE as covariate, and individual bird ID as a random factor. Additionally, linear regression was employed to look at whether mass-specific DEE during chick-rearing is related to brood size. *F*- and *t*-statistics and *P*-values were generated using the lmerTest package (<https://cran.r-project.org/web/packages/lmerTest/>). If there was a significant main effect of sex and/or interaction of sex and treatment, separate models were run for males and females, respectively. Following a significant mixed model, Tukey's HSD (package multcomp; <https://cran.r-project.org/web/packages/multcomp/>; Hothorn et al., 2008) was used to evaluate pairwise comparisons between treatments and timepoints. In addition, we estimated repeatability of body mass and mass-specific DEE from generalized linear mixed-effects models fitted by restricted maximum likelihood using the rptR package (<https://cran.r-project.org/web/packages/rptR/vignettes/rptR.html>; Stoffel et al., 2017). Repeatability was estimated over the three timepoints and without correcting for any fixed effects (Table S2). Detailed statistical output showing all variables and statistical models are presented in Tables S1 and S2.

RESULTS

Effects of increased foraging effort (HF treatment) and chick-rearing on body mass

Body mass was independent of sex×time×treatment interaction ($F_{1,29}=0.418$, $P=0.523$), sex×treatment interaction ($F_{1,51}=0.254$, $P=0.616$), sex×time interaction ($F_{1,29}=2.259$, $P=0.144$) and time×treatment interaction ($F_{1,29}=0.877$, $P=0.357$). However, there was a main effect of time on body mass ($F_{1,29}=41.283$, $P<0.001$; Fig. 2), where body masses of birds were significantly lower during chick-rearing compared with post-treatment ($t_{27}=8.97$, $P<0.01$).

Repeatability of mass-specific daily energy expenditure

Moderate but significant repeatability was found for body mass of both HF ($R=0.328$, $P=0.005$, 95% CI=0.051–0.543) and control birds ($R=0.569$, $P<0.001$, 95% CI=0.309–0.749). When birds from both treatment groups were pooled and considered, repeatability of body mass was also moderate but significant ($R=0.457$, $P<0.001$, 95% CI=0.288–0.609; Fig. 3C,D).

Likewise, when birds from both treatment groups were considered, repeatability of mass-specific DEE was moderate but significant ($R=0.302$, $P=0.006$, 95% CI=0.069–0.503; Fig. 3A,B). We expected the mass-specific DEE of HF birds to be low because of individual variation in energetic adjustments to HF treatment. Indeed, when only HF birds were considered, mass-specific DEE was not repeatable ($R=0.15$, $P=0.179$, 95% CI=0–0.451) but when only control birds were considered, mass-specific DEE was moderately repeatable ($R=0.421$, $P=0.013$, 95% CI=0.072–0.669). The moderate repeatability could be attributed to differences in brood size during chick-rearing, as shown by the positive correlation between mass-specific DEE during chick-rearing and brood size ($R=0.420$, $P<0.0001$; Fig. 3E). Strong repeatability was

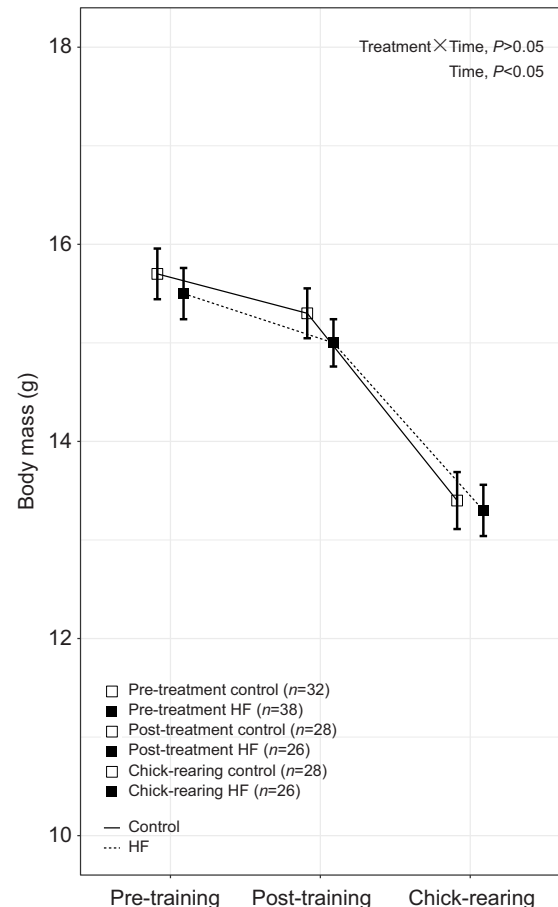


Fig. 2. Effects of increased foraging effort and chick-rearing on body mass in zebra finches (*Taeniopygia guttata*). Data shown are least-squared means±s.e.m. Solid squares and solid line represent control group; open squares and dashed line represent HF group.

found when we tested for repeatability of mass-specific DEE for control birds during pre- and post-treatment time points ($R=0.60$, $P=0.003$, 95% CI=0.248–0.808; Fig. 3A).

Effects of increased foraging effort (HF treatment) and chick-rearing on mass-specific daily energy expenditure

There was a significant sex×time×treatment interaction of mass-specific DEE ($F_{1,11}=11.163$, $P=0.007$). Therefore, males and females were analysed independently. For females, there was a significant time×treatment interaction of mass-specific DEE ($F_{1,8}=9.20$, $P=0.016$; Fig. 4B). HF females had significantly higher mass-specific DEE during post-treatment than control females ($t_{27}=2.114$, $P=0.044$), but marginally lower mass-specific DEE during chick-rearing when compared with control females ($t_{27}=1.955$, $P=0.061$). There was a significant increase in mass-specific DEE of control females from post-treatment to chick-rearing ($t_{20}=2.45$, $P=0.023$) but there was a marginal decrease in mass-specific DEE of HF females from post-treatment to chick-rearing ($t_{17}=1.89$, $P=0.075$). For males, there was a marginal time×treatment interaction of mass-specific DEE ($F_{1,3}=9.194$, $P=0.056$; Fig. 4A). However, unlike results in females, mass-specific DEE was not different between control and HF males post-treatment ($t_9=0.484$, $P=0.639$). Control males maintained mass-specific DEE from post-treatment to chick-rearing ($t_6=0.006$, $P=0.995$) whereas HF males increased mass-specific DEE significantly from post-treatment to chick-rearing ($t_4=4.509$, $P=0.011$).

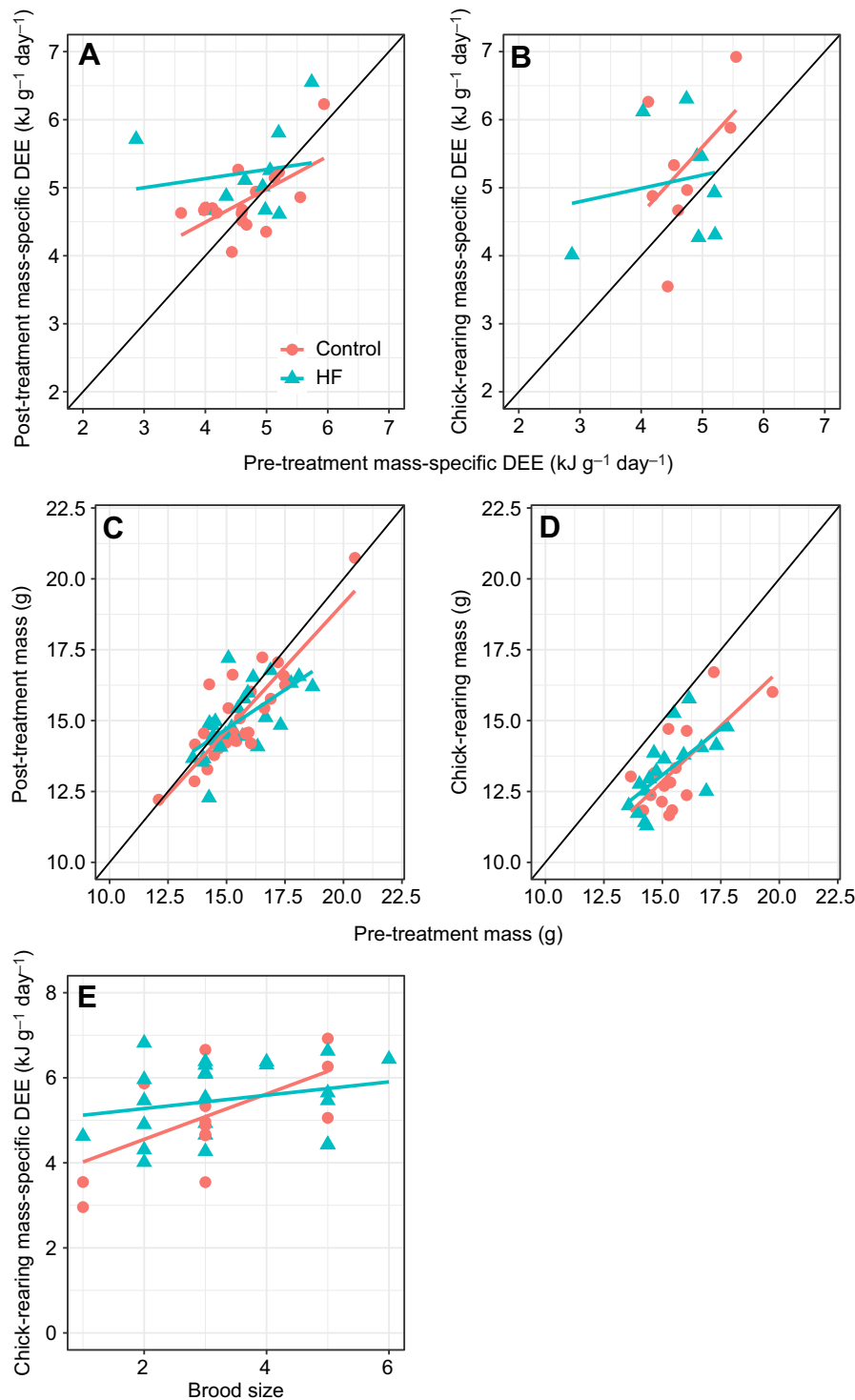


Fig. 3. Repeatability of mass-specific daily energy expenditure (DEE) and body mass measurements in zebra finches at different experimental stages. Repeatability of mass-specific DEE between (A) pre-training and post-training ($n=7M$; $n=20F$) and (B) pre-training and chick-rearing ($n=5M$; $n=11F$). Repeatability of body mass measurements between (C) pre-training and post-training ($n=28M$; $n=27F$) and (D) pre-training and chick-rearing ($n=16M$; $n=18F$). (E) Relationship between brood size and mass-specific DEE. Red circles and lines represent control group; cyan triangles and lines represent HF group. Diagonal black line in A–D is the line of no change. Note that repeatability was estimated over the course of the experiment (3 timepoints), but only 2 timepoints are plotted on each figure for simplicity.

In the HF group, both males and females had similar mass-specific DEE during HF treatment ($t_{32}=0.66$, $P=0.55$) but males had higher mass-specific DEE than females during chick-rearing ($t_{34}=-3.02$, $P=0.004$). In the control group, however, males and females had similar mass-specific DEE both during HF treatment ($t_{33}=-1.58$, $P=0.12$) and chick-rearing ($t_{33}=0.61$, $P=0.54$).

DISCUSSION

This study investigated how behavioural adjustments to ‘exercise’ (*sensu* Halsey, 2016) affected daily energy expenditure of captive

zebra finches during reproduction by experimentally manipulating foraging behaviour and workload in zebra finches using a previously described technique (Koetsier and Verhulst, 2011; Yap et al., 2017b). We first experimentally manipulated foraging effort in captive zebra finches, creating two groups with high and low foraging effort followed by both groups breeding in a low foraging effort common garden condition.

Overall, our findings suggest that an energetic ceiling does exist, at least in females, as females that were in the HF condition did not appear to maintain or increase energy expenditure during chick-

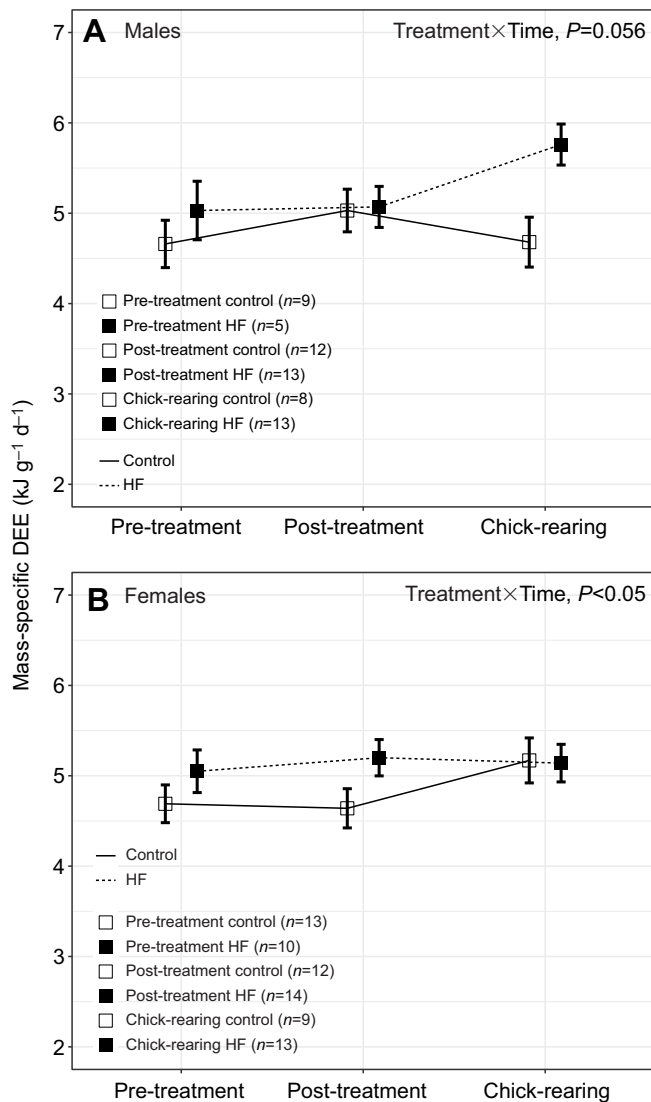


Fig. 4. Effects of increased foraging effort and chick-rearing on mass-specific DEE of male and female zebra finches. Data shown are least-squared means \pm s.e.m. Solid squares and solid line represent control group; open squares and dashed line represent HF group.

rearing. Unlike females, HF males increased mass-specific DEE during chick-rearing. Mass-specific DEE was moderately repeatable across different timepoints. HF treatment had no effect on body mass of birds, but all birds decreased body mass during chick-rearing, regardless of treatment.

Consistent with findings from Yap et al. (2017b), the current study found that body mass was not affected by HF treatment. This finding is also consistent with findings from other studies that employed similar high foraging effort training regimes, where body mass was not affected by increased foraging effort (Briga et al., 2017; Simons et al., 2014). Other studies that manipulated activity levels in birds (Briga and Verhulst, 2017) and mice (Vaanholt et al., 2007), however, found decreased body mass with increased activity. Another study by Koetsier and Verhulst (2011) found that when controlling for body mass, basal metabolic rate decreased in birds trained for high foraging effort. These differences in findings could be due to slight differences in methodology, timing of sampling, experimental duration and/or study species. Body mass decreased during chick-rearing, regardless of treatment. This finding is in line

with findings from field studies in birds (Boyle et al., 2012; Fowler and Williams, 2017; Williams and Fowler, 2015), where birds lose mass adaptively once chicks are hatched to increase flight efficiency during chick provisioning. This finding differs somewhat from findings by Simons et al. (2014), where regardless of treatment, females, but not males, lost mass gradually over the course of the experiment that culminated in breeding. This discrepancy could be due to differences in experimental design, including housing condition, length of the experiment and timing of measurements.

Overall, mass-specific DEE was only moderately repeatable within individuals. DEE measurement using doubly labelled water is sensitive to changes in body composition (Speakman, 1997). Therefore, the low to moderate repeatability could be partially attributed to changes in body composition (decreased fat mass) because of the effects of high foraging effort treatment in HF birds (Yap et al., 2017b; Zhang et al., 2018), as well as changes in body composition (decreased lean mass) owing to reproduction in female birds (Boyle et al., 2012; Vézina and Williams, 2003). Although HF treatment-induced decreased fat mass could be interpreted as either increased fuel consumption or decreased fat storing capacity (Zhang et al., 2018), it should be noted that animals can adjust fuel selection and metabolism readily (e.g. using more fat and less carbohydrate and vice versa) and maintain similar overall energy expenditure. Many studies that manipulated workload in animals have also found decreased basal metabolic rate (a portion of DEE) with increased workload (Briga and Verhulst, 2017; Piersma and van Gils, 2010; Schubert et al., 2009), which would in turn affect repeatability of overall DEE. High repeatability was found for control birds, suggesting that individuals likely have consistent energy management strategies across time. This finding is partially supported by several other studies that found robust repeatability of basal metabolic rate in a number of bird species (Broggi et al., 2009; McKechnie and Swanson, 2010; Nespolo and Franco, 2007; Rønning et al., 2005).

Although we did not detect any significant changes in mass-specific DEE in HF birds in response to HF treatment, mass-specific DEE was not repeatable within individuals, which indicates that when subjected to energetic challenge or environmental perturbation, individuals tend to differ in their energy management strategies. This finding is consistent with other studies that found either no or low repeatability within individuals across multiple years or different life-history and breeding stages (e.g. wintering versus breeding, incubation versus chick-rearing; Auer et al., 2016; Berteaux et al., 1996; Potti et al., 1999; Speakman et al., 1994; White et al., 2013; Williams and Vézina, 2001). Interestingly, HF birds with the lowest pre-treatment mass-specific DEE seemed to have the largest increased in mass-specific DEE post-treatment. It is unclear why such a response is observed but it reinforces the idea that individuals differ greatly in their energy management strategies when subjected to energetic challenge.

HF treatment caused an increase in mass-specific DEE in females but not in males, suggesting that males are perhaps able to adjust their flight behaviour to increase efficiency in response to HF treatment, whereas females are unable to do so and therefore, are forced to work harder in response to HF treatment. This finding is consistent with previous studies from our group that utilized the same technique to manipulate foraging effort in zebra finches (Yap et al., 2017b; Zhang et al., 2018). Both studies found profound physiological adjustments, such as lower myostatin expression, increased flight muscle mass and lung mass in females subjected to HF treatment, whereas no physiological adjustments were detected in males subjected to HF treatment (Yap et al., 2017b; Zhang et al., 2018).

Our data suggested that an energetic ceiling exists for females owing to a constraint on workload, as evidenced by a failure to

maintain high DEE during chick-rearing in HF birds. In other words, there appears to be a constraint on how hard females can work and how much energy they can expend over time without paying a fitness cost in the form of reduced fecundity or survival. It should be noted that an energetic ceiling here does not necessarily imply a ‘hard’ ceiling, but rather females electing not to increase DEE because of constraints imposed either by trade-offs in the form of immediate costs or in relation to how they manage energy expenditure over longer periods of time. Indeed, other studies that manipulated workload in breeding birds have found negative effects of increased workload on survival and/or reproduction (Briga et al., 2017; Deerenberg and Overkamp, 1999; Drent and Daan, 1980; Nilsson, 2002; Simons et al., 2014; but see Schmidt-Wellenburg et al., 2008). Since we did not observe a training-induced increase in mass-specific DEE in males, it is unclear whether an energetic ceiling exists for them based on our findings. However, data from previous studies that manipulated brood size in blue tits suggest that males servicing larger broods showed decreased survivorship (Pettifor, 1993), suggesting that an energetic ceiling likely exists for males in some bird species. It is possible that sex-specific energy management strategies are observed because male birds are selected to invest in current reproductive attempts whereas females are selected to prioritize self-maintenance in favour of future reproduction. Our finding is consistent with a previous study in broad-billed hummingbirds where males appear not to have an energetic ceiling or at least a ceiling that is very high (Shankar et al., 2019).

During the chick-rearing phase, there was an increase in mass-specific DEE for HF males and control females but not for HF females and control males. Presumably, HF males were compensating for low provisioning effort of their female partner. Carry-over of energetics cost and sex-specific energy management strategies during reproduction have been documented in other passerines before. Mainwaring and Hartley (2016) found that reducing nest building costs in blue tits (*Cyanistes caeruleus*) increased provisioning rate during chick-rearing in males but not females. Furthermore, Moreno et al. (1995) found that males increased provisioning rate and energy expenditure in artificially enlarged brood whereas females did not adjust feeding rate nor energy expenditure in response to brood manipulation.

Interestingly, despite finding sex-specific effects of energy management strategies, no sex-specific effects were found in physiological metrics in our companion study (Yap et al., 2021). In that study, we found increases in haematocrit, haemoglobin concentration and oxidative stress in response to HF treatment in both sexes. However, when birds were bred in low foraging effort common garden condition following HF treatment, measures of fecundity and final reproductive output were similar between both groups (Yap et al., 2021). Taken together, findings from both the current study and the companion study suggest that daily energy expenditure and physiological metrics such as haematology and oxidative stress are at least somewhat uncoupled, as evident from the sex-specific effect and lack thereof in DEE and physiology, respectively. Indeed, it has been suggested that the costs of workload and reproduction are not purely energetic and that there are often ‘hidden’ physiological costs associated with increased workload (Veasey et al., 2001). Furthermore, despite showing increased DEE in response to HF treatment in females, fecundity and final reproductive output were similar between HF and control birds. These findings suggest that initial reproductive investment (e.g. egg formation, clutch size) was not impacted by increased energy expenditure prior to reproduction, and/or that compensation by the male partner during chick-rearing mitigated the presumably

low provisioning effort by females during chick-rearing and ensured final reproductive success.

In summary, this study has shown that captive zebra finches showed sex-specific energy management strategies in response to increased foraging effort treatment prior to reproduction. Our results also suggest that energetic costs incurred prior to reproduction can be carried over into subsequent stages of reproduction in a sex-specific manner. Other researchers proposed that energy management strategies of animals can be plastic and vary depending on life-history stages (Careau and Garland, 2015; Mathot and Dingemanse, 2015a,b; Portugal et al., 2016). Future studies should measure basal metabolic rate in addition to DEE in animals during increased foraging effort treatment and breeding to better understand trade-offs between self-maintenance and reproduction within individuals.

Acknowledgements

We thank Sarosha Ali for her invaluable assistance with the experiment. We also thank Julian Christians and Douglas Altshuler for their input on initial experimental design.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: K.N.Y., T.D.W.; Methodology: K.N.Y., T.D.W.; Validation: K.N.Y.; Formal analysis: K.N.Y., M.L.V.; Investigation: K.N.Y., D.R.P., M.L.V., O.H.-I.T.; Resources: K.N.Y., D.R.P., T.D.W.; Data curation: K.N.Y.; Writing - original draft: K.N.Y.; Writing - review & editing: K.N.Y., D.R.P., O.H.-I.T., T.D.W.; Visualization: K.N.Y.; Supervision: T.D.W.; Project administration: K.N.Y., T.D.W.; Funding acquisition: D.R.P., T.D.W.

Funding

This work was funded by a Natural Sciences and Engineering Council of Canada Discovery and Accelerator Grant to T.D.W. (155395-2012- RGPIN and RGPAS/429387-2012) and a National Aeronautics and Space Administration Grant to D.R.P. (NNX11AO28G). The funders did not have any input into the content of the manuscript nor require approval before submission.

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Table S1. Statistical output showing all variables and linear mixed effect models. Response variables are highlighted in bold. Corresponding predictors are underlined.

Model	Random factor	Estimated variance	Residual variance	numDF	denDF	t-value	F-value	P-value
mass ~ sex * <u>time</u> *trt + pre-mass	id	0.400	0.467	1	29	.	0.418	0.523
mass ~ <u>time</u> *trt + pre-mass	id	0.479	0.430	1	29	.	0.877	0.357
mass ~ sex * <u>time</u> + pre-mass	id	0.479	0.430	1	29	.	2.259	0.144
mass ~ sex * trt + pre-mass	id	0.479	0.430	1	51	.	0.254	0.616
mass ~ sex* <u>time</u> *trt + pre-mass	id	0.479	0.430	1	51	.	0.017	0.898
mass ~ sex* <u>time</u> *trt + pre-mass	id	0.479	0.430	1	29	.	41.283	<0.001
mass ~ sex* <u>time</u> *trt + pre-mass	id	0.479	0.430	1	51	.	0.728	0.398
MSDEE ~ sex * <u>time</u> *trt + pre-MSDEE	id	0.072	0.272	1	11	.	11.163	0.007
MSDEE ~ <u>time</u> *trt + pre-MSDEE	Female id			1	8	.	9.20	0.016
MSDEE ~ <u>time</u> *trt + pre-MSDEE	Male id			1	3	.	9.194	0.056

Table S2. Statistical output showing all variables and repeatability fitted by restricted maximum likelihood.

Variable	Treatment group	Random factor	95% Confidence Interval	R	P-value
mass	CTR and HF	id	0.288-0.609	0.457	<0.001
mass	HF	id	0.051-0.543	0.328	0.005
mass	CTR	id	0.309-0.749	0.569	<0.001
mass-specific DEE	CTR and HF	id	0.069-0.503	0.302	0.006
mass-specific DEE	HF	id	0-0.451	0.15	0.179
mass-specific DEE	CTR	id	0.072-0.669	0.421	0.013