

Short photoperiod increases energy intake, metabolic thermogenesis and organ mass in silky starlings *Sturnus sericeus*

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ABSTRACT

Environmental cues play important roles in the regulation of an animal's physiology and behavior. One such cue, photoperiod, plays an important role in the seasonal acclimatization of birds. It has been demonstrated that an animal's body mass, basal metabolic rate (BMR), and energy intake, are all affected by photoperiod. The present study was designed to examine photoperiod induced changes in the body mass, metabolism and metabolic organs of the silky starling, *Sturnus sericeus*. Captive silky starlings increased their body mass and BMR during four weeks of acclimation to a short photoperiod. Birds acclimated to a short photoperiod also increased the mass of certain organs (liver, gizzard and small intestine), and both gross energy intake (GEI) and digestible energy intake (DEI), relative to those acclimated to a long photoperiod. Furthermore, BMR was positively correlated with body mass, liver mass, GEI and DEI. These results suggest that silky starlings increase metabolic thermogenesis when exposed to a short photoperiod by increasing their body and metabolic organ mass, and their GEI and DEI. These findings support the hypothesis that bird species from temperate climates typically display high phenotypic flexibility in thermogenic capacity.

Keywords: Basal metabolic rate (BMR); Body mass; Energy budget; Organ mass; Photoperiod; Silky starling; *Sturnus sericeus*.

INTRODUCTION

Many organisms experience considerable seasonal changes in environmental conditions, such as fluctuations in temperature, food availability and photoperiod (Swanson, 2010). Physiological demands may also change because of increased energetic

requirements during reproduction or seasonal acclimatization (Starck & Rahmaan, 2003; Williams & Tieleman, 2000; Zheng et al., 2008a; 2014a). Reversible phenotypic flexibility allows individual organisms to adjust their phenotypes to meet different environmental, or ecological, demands (McKechnie, 2008; Piersma & Drent, 2003; Piersma & Gils, 2011). Many resident, small, birds in warm and temperate zones use phenotypic flexibility to cope with seasonal changes in temperature and photoperiod, and to develop morphological, physiological, and behavioural adaptations that assist in coping with various energy demands and enhance reproductive success (Swanson et al., 2014; Zheng et al., 2014a).

Photoperiod acts as an environmental cue for the seasonal acclimatization of thermoregulation in birds (Eyster, 1954; Heldmaier et al., 1989; Swanson et al., 2014). It has been demonstrated that an animal's body mass (Swanson et al., 2014; Wolfson et al., 1952), energy balance (Farner et al., 1961; Johnston, 1962; Ni et al., 2011), and basal metabolic rate (BMR) (Saarela & Heldmaier, 1987) all are affected by photoperiod. BMR is the minimum rate of energy expenditure of a non-growing, non-reproductive homeotherm measured under post-absorptive and thermoneutral conditions during the inactive phase of the circadian cycle (AL-Mansour, 2004; McKechnie & Wolf, 2004). The use of BMR as an index of energy expenditure has been the focus of considerable interest from environmental physiologists and comparative physiologists (McKechnie, 2008; Smit & McKechnie, 2010). The shorter day lengths that precede the onset of winter can induce an increase in the energy expenditure of animals (Heldmaier et al., 1989; Ni et al., 2011; Wolfson et al., 1952). Many birds have a variety of strategies to

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cope with this condition, such as increasing their body mass (Saarela & Heldmaier, 1987) and BMR (Swanson et al., 2014). For example, Chinese bulbuls *Pycnonotus sinensis* acclimatized to a short photoperiod developed significantly higher body mass and BMR than those acclimatized to a long photoperiod (Ni et al., 2011). Similar results have been found in other birds, like the dark-eyed junco *Junco hyemalis* (Swanson et al., 2014) and Japanese quail *Coturnix japonica* (Saarela & Heldmaier, 1987). Furthermore, increased energy intake can compensate for the increased energy expenditure associated with thermogenesis in harsh conditions (Hammond & Diamond, 1997; Williams & Tieleman, 2000). Finally, increasing the mass of metabolically active organs, such as the liver, kidney, heart and gastrointestinal tract, can increase BMR (Liu & Li, 2006; Williams & Tieleman, 2000; Zhang et al., 2006; Zheng et al., 2008b; 2014b).

The silky starling, *Sturnus sericeus*, is resident in most of south and southeast China but also disperses to northern Vietnam and the Philippines in winter (MacKinnon & Philipps, 2000). This species feeds on fruits and seeds (Zheng & Zhang, 2002), prefers broadleaf and coniferous-broadleaf mixed forest, but is also found in orchards and tillable fields. It has a lower than predicted BMR for its body size (McKechnie & Wolf, 2004; McKechnie & Swanson, 2010), a high body temperature (T_b), a high upper critical temperature (T_{uc}), high thermal conductance, high evaporative water loss (EWL), and a relatively wide thermal neutral zone (TNZ) (Bao et al., 2014; Zhang et al., 2006). These characteristics suggest that it is adapted to warm climates, where selection for metabolic thermogenesis and water conservation is not strong. However, it is not known if the silky starling can change its body mass and BMR in response to different photoperiods.

In this study, we acclimated wild-caught silky starlings to different two different photoperiods (short vs long day-lengths) and examined the effects of these treatments on body mass, energy budget, metabolic rate and the mass of metabolically active organs. We hypothesized that short photoperiods are a key factor driving metabolic flexibility in silky starlings and consequently predicted that body mass, energy budget, metabolic rate, and organ mass would be higher in starlings acclimated to a short photoperiod than in those acclimated to a long photoperiod.

MATERIALS AND METHODS

Animals

Fifteen adult male silky starlings were used in the experiment. All birds were captured in Wenzhou city (N27°29', E120°51'), Zhejiang Province, China. The climate in Wenzhou is warm-temperate with an average annual rainfall of 1 700 mm across all months and slightly more precipitation during winter and spring. Mean daily maximum temperature ranges from 39 °C in July to 8 °C in January. The mean temperature from March to May is 15 °C (Wu et al., 2015; Zheng et al., 2014a). Body mass to the nearest 0.1 g was determined immediately upon capture with a Sartorius balance (model BT25S). After capture, birds were transported to the laboratory at Wenzhou University and

housed in separate plastic cages (50 cm×30 cm×20 cm) at 25 °C with 12L: 12D photoperiod. Food and water were supplied *ad libitum* and replenished daily. After one week of acclimation, starlings were moved into individual cages and then randomly assigned to one of two experimental groups; a short photoperiod (SD, 8L: 16D with lights on at 1000h, $n=8$) group, and a long photoperiod (LD, 16L: 8D with lights on at 0400h, $n=7$) group. Each group was acclimated to its respective photoperiod for 4 weeks. Each bird's body mass was monitored weekly during the four week acclimation period (Ni et al., 2011). All experimental procedures were approved by the Wenzhou City Animal Care and Use Committee, Zhejiang Province, China (Wu et al., 2015).

Measurement of metabolic rate

Birds' metabolic rates were measured with an open-circuit respirometry system (AEI Technologies S-3A/I, USA). To take these measurements, individual birds were placed in 1.5 L plastic metabolic chambers inside a temperature-controlled cabinet at ± 0.5 °C (Artificial climatic engine BIC-300, China). No ambient light reached birds within the cabinet so they were effectively in the dark, and therefore more likely to be inactive, while confined within the apparatus. Dry CO₂-free air was pumped through the chamber at 300 mL/min using a flow control system (AEI Technologies R-1, USA) (McNab, 2006). The fractional concentration of O₂ in the inlet chamber (dry CO₂-free air) was determined using an oxygen sensor (AEI Technologies N-22M, USA). Oxygen consumption rates were measured at 30 ± 0.5 °C within the thermal neutral zone and recorded at 20 s intervals (Zhang et al., 2006; Zheng et al., 2013). Each measurement period lasted for 1 hour and began after birds had first acclimated inside the metabolic chamber for about 1 hour. BMR was calculated for each individual as the average of the 30 lowest consecutive oxygen consumption recordings made over about 5 min. Food was removed 4h before each measurement period to minimize the heat increment associated with feeding. Metabolic rates were calculated from equation 2 of Hill (1972), and expressed as O₂(mL)/h, corrected to STPD conditions (Schmidt-Nielsen, 1997).

Energy budget

We regarded digestible energy intake as an index of total daily energy expenditure. A set quantity of food was provided during the 28 day experimental period but water was provided *ad libitum*. Food residues and feces were collected during the 2-days before temperature acclimation began (week 0) and weekly (every seventh day) thereafter throughout the 4-week experimental period. These residues were separated manually, then oven-dried at 60 °C until a constant mass was obtained. The caloric content of residual food and feces were determined using a C200 oxygen bomb calorimeter (IKA Instrument, Germany). Gross energy intake (GEI), feces energy (FE), digestible energy intake (DEI), and digestibility of energy were calculated according to Grodzinski & Wunder (1975) and Wu et al. (2014):

GEI (kJ/day)=dry food intake(g/day)×caloric value of dry food (kJ/g) (1)

FE (kJ/day)=dry mass of feces(g/day)×caloric value of dry feces (kJ/g) (2)

DEI (kJ/day)=GEI (kJ/day)–FE(kJ/day) (3)

Digestibility(%)=DEI(kJ/day)/GEI(kJ /day)×100% (4)

Measurements of organ mass

All birds were euthanized by cervical dislocation at the end of the 4 week experimental period, and their heart, liver, spleen, lungs, brain, kidneys, stomach, small intestine and rectum removed and weighed to the nearest 0.1 mg. The gizzard, small intestine and rectum were then rinsed with saline to remove all gut contents before being dried and reweighed. These organs were then dried to a constant mass over 2 d at 75 °C and reweighed to the nearest 0.1 mg (Liu & Li, 2006; Williams & Tieleman, 2000).

Statistics

Data were analyzed using SPSS (version 12.0 for Windows). Distributions of all variables were tested for normality using the Kolmogorov-Smirnov test. Non-normally distributed data were normalized by being transformed into their natural logarithm prior to analysis. A repeated-measures analysis of variance (RM-ANOVA) was used to determine the significance of changes in body mass, GEI, FE, DEI and digestibility over time. Direct comparisons of the body mass of starlings acclimatized to LD or SD group were made using independent sample *t*-tests. With the exception of body mass, differences in the above variables between the LD and SD groups were evaluated using ANOVA or ANCOVA, with body mass as a covariate, where appropriate. Least-squares linear regression was used to test for correlations between log dry organ mass, log BMR and log body mass. For organ mass, body mass minus wet organ mass was used for the organ in question to avoid the statistical problem of part-whole correlations (Christians, 1999). Residuals were calculated from correlations and the residuals of log dry organ mass were regressed against those of log BMR to determine if organ mass was significantly correlated with BMR. Least-squares linear regression was used to evaluate the relationships between log body mass, log GEI and log DEI, and between log BMR, log body mass, log GEI and log DEI. All results are expressed as mean±SE; *P*<0.05 were considered statistically significant.

RESULTS

Body mass and metabolic rate

Overall, birds acclimated to the short photoperiod (SD) underwent a significant increase in body mass ($t_{13}=2.850$, *P*<0.05; Figure 1) and weighed on average 15% more than those acclimated to the long photoperiod (LD) by day 28 of the experiment. Significant group by time interactions were also evident for body mass ($F_{4,28}=20.174$, *P*<0.01). No group differences in body mass were apparent prior to photoperiod acclimation ($t_{13}=0.040$, *P*>0.05). However, a significant increase in body mass was apparent in the SD group by day 21 of

acclimation, and this increase was sustained for the 4 week duration of the experiment (Figure 1). An ANCOVA (with body mass as the covariate) indicated that the SD group had undergone a mass-specific (O_2 (mL)/g/h) 32% increase in BMR relative to the LD group ($F_{1,12}=7.814$, *P*<0.05, Figure 2). Individual birds in the SD group had undergone an average 36% increase in BMR (O_2 (mL)/h) by day 28, causing their BMR to be significantly higher than that of LD birds (Figure 2). There was a significant positive correlation between log body mass and log total BMR ($R^2=0.486$, *P*<0.01; Figure 3).

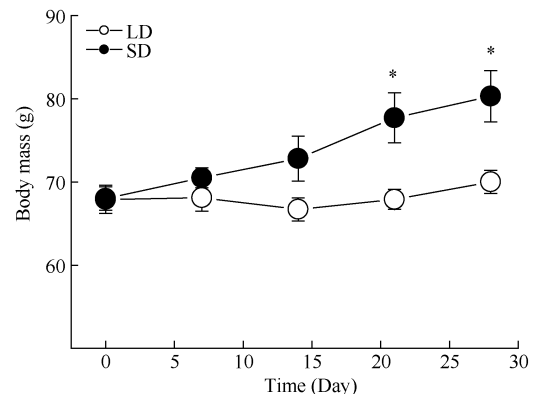


Figure 1 Trends in the body mass of silky starlings *Sturnus sericeus* acclimated to either a short, or a long, photoperiod for four weeks

Data are shown as mean±SE, *: *P*<0.05; SD: short photoperiod; LD: long photoperiod.

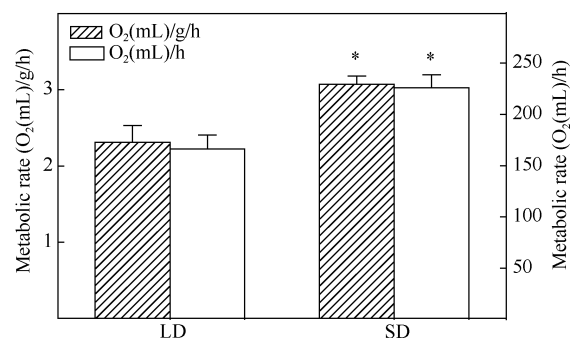


Figure 2 Basal metabolic rates of silky starlings *Sturnus sericeus* acclimated to either a short, or a long, photoperiod for four weeks

Data are shown as mean±SE, *: *P*<0.05; SD: short photoperiod; LD: long photoperiod.

Energy budget

By the end of the 4-week acclimation period the SD group had significantly higher gross energy intake (GEI) ($F_{1,13}=8.600$, *P*<0.05; Figure 4A), feces energy (FE) ($F_{1,13}=5.692$, *P*<0.05; Figure 4B), and digestible energy intake (DEI) ($F_{1,13}=4.026$, *P*<0.05, Figure 4C), relative to the LD group. There was, however, no significant difference in digestive efficiency

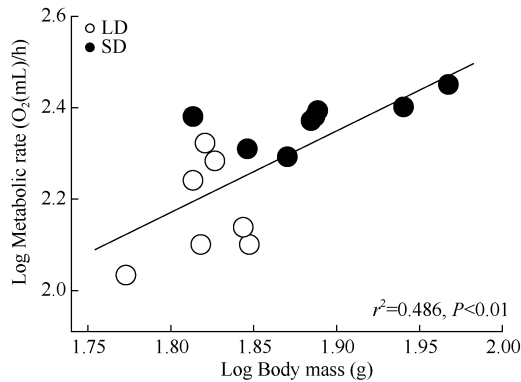


Figure 3 Correlation between the body mass and basal metabolic rate (BMR) of silky starlings *Sturnus sericeus* acclimated to either a short, or a long, photoperiod for 4 weeks
SD: short photoperiod; LD: long photoperiod.

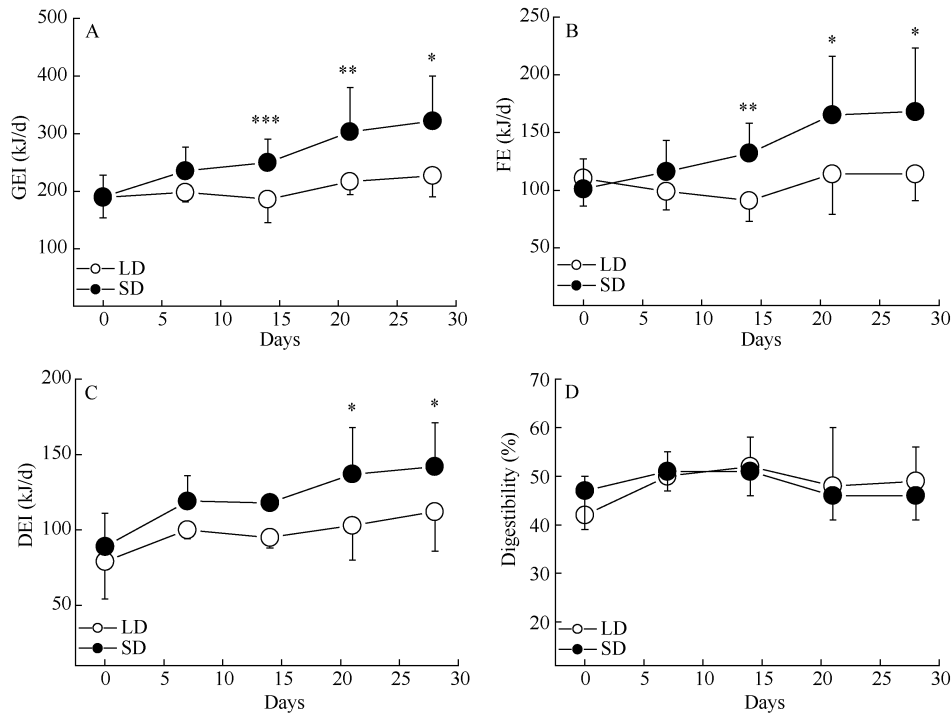


Figure 4 Trends in GEI (A), FE (B), DEI (C), and digestibility (D) of silky starlings *Sturnus sericeus* acclimated to either a short, or a long, photoperiod for four weeks
Data are shown as mean±SE, *: $P<0.05$, **: $P<0.01$, ***: $P<0.001$; SD: short photoperiod; LD: long photoperiod; GEI: gross energy intake; FE: feces energy; DEI: digestible energy intake.

Organ mass

ANCOVA (with body mass as the covariate) detected significant differences in the mass of several internal organs between the two treatment groups. These included differences in the wet and dry mass of the liver, gizzard, small intestine and digestive tract (Table 1). The average wet mass of the liver, gizzard, small intestine and digestive tract of the SD group was 24%, 26%, 22%, and 25%, respectively, higher than those of the LD group. The dry mass of the liver, gizzard, small intestine and digestive tract of

between the two groups ($F_{1,13}=1.594$, $P>0.05$; Figure 4D). Significant group by time interactions were apparent for GEI ($F_{4,28}=9.862$, $P<0.01$), FE ($F_{4,28}=7.372$, $P<0.01$), and DEI ($F_{4,28}=6.211$, $P<0.01$). No pre-acclimation (i.e., on day 0) differences were found between the two groups in any of the above indices. After 14 days of acclimation the SD group had significantly higher GEI ($P<0.001$) relative to the LD group, a difference that was sustained for the remaining 4 weeks of the experiment (Figure 4A). The SD group also had significantly higher FE than the LD group in week 2 ($P<0.01$), and week 3 ($P<0.05$) (Figure 4B), and significantly higher DEI in week 3 ($P<0.05$) (Figure 4C). No group by time interaction was found for digestibility ($F_{4,28}=1.713$, $P>0.05$; Figure 4D). There was a significant, positive relationship between log GEI and log body mass ($R^2=0.498$, $p<0.01$; Figure 5A), log GEI and log total BMR ($R^2=0.536$, $P<0.001$; Figure 5C), and log DEI and log total BMR ($R^2=0.394$, $P<0.05$; Figure 5D), but not between log DEI and log body mass ($R^2=0.171$, $P>0.05$; Figure 5B).

the SD group was 37%, 38%, 28%, and 32%, respectively, higher than those of the LD group. Other organs listed in Table 1 did not differ significantly in either wet or dry mass between groups. The partial relationships between log dry organ mass and log body mass (minus organ wet mass) were positive for all organs, however, only the dry mass of the heart, liver, kidney, gizzard, small intestine, and digestive tract were significantly correlated with body mass (Table 2). Residuals of liver dry mass were positively correlated with BMR residuals (Table 2).

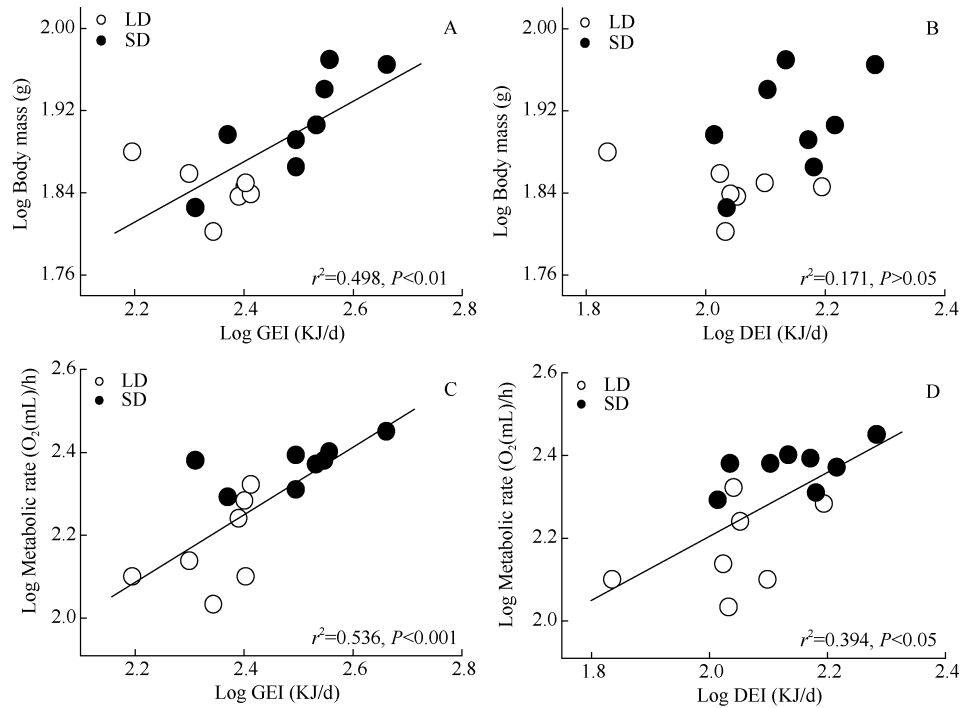


Figure 5 Correlations between body mass and GEI (A), body mass and DEI (B), basal metabolic rate and GEI (C), and between basal metabolic rate and DEI (D), in silky starlings *Sturnus sericeus* acclimated to either a short, or a long, photoperiod for four weeks SD: short photoperiod, LD: long photoperiod, GEI: gross energy intake, FE: feces energy, DEI: digestible energy intake.

Table 1 Mass (mean±SE) of various internal organs of silky starlings *Sturnus sericeus* after four weeks acclimation to either a short (SD), or a long (LD), photoperiod

	SD	LD	Significance
Sample size (n)	7	8	
Wet mass			
Brain (mg)	1 689.1±42.6	1 638.7±46.0	$F_{(1,12)}=0.558, P>0.05$
Heart (mg)	849.3±29.0	750.2±31.3	$F_{(1,12)}=4.658, P>0.05$
Liver (mg)	2 082.3±62.0	1 684.8±67.0	$F_{(1,12)}=16.354, P<0.01$
Spleen (mg)	116.3±21.2	62.4±19.6	$F_{(1,12)}=2.998, P>0.05$
Lung (mg)	625.7±27.5	615.8±30.0	$F_{(1,12)}=0.052, P>0.05$
Kidney (mg)	689.3±31.9	648.6±43.4	$F_{(1,12)}=0.647, P>0.05$
Gizzard (mg)	1 229.5±25.2	907.7±27.3	$F_{(1,12)}=64.566, P<0.001$
Small intestine (mg)	2 120.1±84.6	1 739.5±91.4	$F_{(1,12)}=8.059, P<0.05$
Rectum (mg)	235.8±28.0	218.8±30.2	$F_{(1,12)}=0.148, P>0.05$
Digestive tract (mg)	3 585.5±111.5	2 865.9±120.5	$F_{(1,12)}=16.567, P<0.01$
Dry mass			
Brain (mg)	389.4±9.6	362.4±10.3	$F_{(1,12)}=3.179, P>0.05$
Heart (mg)	246.5±29.3	223.4±31.7	$F_{(1,12)}=0.247, P>0.05$
Liver (mg)	725.1±19.4	545.9±20.9	$F_{(1,12)}=34.011, P<0.001$
Spleen (mg)	16.2±4.7	28.4±5.0	$F_{(1,12)}=2.711, P>0.05$
Lung (mg)	127.6±6.2	118.0±6.7	$F_{(1,12)}=0.967, P>0.05$
Kidney (mg)	191.9±8.3	170.7±8.9	$F_{(1,12)}=2.614, P>0.05$
Gizzard (mg)	389.8±12.7	282.6±13.8	$F_{(1,12)}=28.157, P<0.001$
Small intestine (mg)	548.4±29.8	428.3±32.2	$F_{(1,12)}=6.480, P<0.05$
Rectum (mg)	84.7±11.8	63.6±2.8	$F_{(1,12)}=1.264, P>0.05$
Digestive tract (mg)	1 022.9±44.9	774.5±48.5	$F_{(1,12)}=12.205, P<0.01$

Values in bold type are statistically significant.

Table 2 Linear regression statistics for partial and residual correlations of log dry organ mass versus log body mass (minus wet mass of the organ), and dry organ mass versus BMR in silky starlings *Sturnus sericeus* after 4 weeks acclimation to either a short (SD), or a long (LD), photoperiod

	Brain	Heart	Liver	Spleen	Lung	Kidney	Gizzard	Intestine	Rectum	Digestive mass
Partial Correlations										
R^2	0.479	0.623	0.608	<0.001	0.009	0.557	0.558	0.586	0.112	0.570
P	0.071	<0.05	<0.05	0.495	0.097	<0.05	<0.05	<0.05	0.664	<0.05
Residual Correlations										
R^2	0.063	0.079	0.321	0.173	<0.001	0.032	0.197	0.009	0.002	0.043
P	0.369	0.779	<0.05	0.123	0.994	0.542	0.098	0.732	0.885	0.458

Values in bold type are statistically significant.

DISCUSSION

Many small birds cope with seasonal stress in winter by adjusting their body mass (Dawson & Carey, 1976; Pohl & West, 1973; Swanson, 1991; Zheng et al., 2008a, 2014a), energy intake (Lou et al., 2013; Wu et al., 2014), metabolic rate (Klaassen et al., 2004; McKechnie, 2008; Zheng et al., 2008, 2014), and internal organ mass (Zheng et al., 2014b). The results of this study show that 4 weeks of acclimation to a short photoperiod is sufficient to cause significant changes in each of these variables in the silky starling; specifically, an increase in body and organ mass, BMR and energy intake associated with bodily metabolic functions. Collectively, these data suggest that the silky starling can change its thermogenic capacity in response to photoperiod, and provide further evidence to support the notion that small birds have high phenotypic plasticity with respect to thermogenic capacity (Liknes & Swanson, 2011; McKechnie et al., 2006; Swanson et al., 2014; Zhang et al., 2015).

Effects of photoperiod on BMR and body mass

Seasonal changes in thermoregulation and body mass are important adaptive strategies for many small birds (Cooper, 2000; Swanson, 1990; Wu et al., 2015; Zheng et al., 2014b). Several environmental factors, such as temperature (Williams & Tieleman, 2000; Zheng et al., 2013), food quantity and quality (Wu et al., 2014), and photoperiod (Ni et al., 2011; Swanson et al., 2014) have been implicated in the regulation of seasonal variation in animals' thermogenic capacity and body mass. Short photoperiod could act independently and/or synergistically with lower temperature to enhance the thermogenic capacity of small birds (Ni et al., 2011; Saarela & Heldmaier, 1987; et al. Swanson et al., 2014). This notion is supported by the results of this study. SD starlings had significantly higher BMR compared to LD starlings after 4 weeks of photoperiod acclimation. Elevated BMR in response to short photoperiods, under either experimental, or natural, conditions, has been reported in other avian species (Ni et al., 2011; Saarela & Heldmaier, 1987; et al. Swanson et al., 2014). As BMR is directly related to the peak winter metabolic rate of thermogenesis in the wild, our data suggest that the effects of photoperiod on thermogenesis were both strong and significant. The same pattern was also found in body mass; SD starlings

underwent a gradual increase in body mass whereas LD starlings did not show any significant change in mass over the course of photoperiod acclimation. The time course data illustrate two interesting findings. First, no significant differences in body mass were found between the SD and LD starlings until day 21 of acclimation, indicating that a period of acclimation is required before short photoperiod exerted a significant effect on the body mass of silky starlings. Second, SD starlings displayed a steady increase in body mass during acclimation whereas LD starlings showed no significant change in mass. This suggests that the significant difference in body mass between the two groups occurred because LD starlings failed to increase their body mass during acclimation. Such increases in body mass will decrease the surface-to-volume ratio, which can reduce heat loss and thereby influence thermogenic demands and RMR (Christians, 1999; Swanson, 2010; Zheng et al., 2008). In addition, increased body mass is often the result of increases in fat deposits and/or metabolically active tissues (Williams & Tieleman, 2000; Wu et al., 2014; Zheng et al., 2014a), and is supported by increases in other parameters, such as GEI, DEI, and internal organ mass (see below).

Effects of photoperiod on energy budget

In birds, body mass is an important indicator of their level of energy balance (Doucette & Geiser, 2008). Many birds display phenotypic flexibility in maintaining energy requirements and are capable of regulating their body mass up or down over a period of time in response to thermal acclimation (Vézina et al., 2006; Zheng et al., 2013, season (Petit et al., 2014; Swanson, 1990; Zheng et al., 2008a, 2014b) and photoperiod (Ni et al., 2011; Saarela & Heldmaier, 1987; Saarela & Vakkuri, 1982; Swanson et al., 2014). Adjustments in energy intake and budget can compensate for the increased energy expenditure associated with thermogenesis under short photoperiod conditions (Ni et al., 2011; Saarela & Heldmaier, 1987). The significant increases in GEI and DEI observed in the SD group are consistent with the adaptive changes in energy intake and utilization in response to short photoperiod documented in many other small birds (Farner et al., 1961; Lou et al., 2013). Our repeated measurements of body mass and energy intake over the 4 week course of the experiment show the pattern of temporal change in these variables. The fact that the GEI of the

SD group was 42% higher than that of LD group suggests that the increased body mass of SD starlings was probably due to increased energy intake during the 4 week acclimation period. Increased GEI and DEI also contributed to the observed increase in body mass and BMR, as indicated by the positive correlation between these variables (Figure 5). One interesting finding of this study is the timing of adjustments made by birds in response to short photoperiod. A significant increase in body mass was apparent in the SD group after three weeks of acclimation. Moreover, a significant increase in GEI was apparent in the SD group after just two weeks of acclimation. These data provide further evidence that physiological responses to short photoperiod can occur relatively quickly (Heldmaier et al., 1989; Ni et al., 2011). The ability to make such physiological adjustments in response to changes in ambient photoperiod would clearly be advantageous for small birds (Swanson et al., 2014). The absence of a significant difference in digestive efficiency between the two experimental groups raises the question; “what is the benefit of developing a larger gut in response to short photoperiods?” Starlings consume more food during the short day of winter, which appears to stimulate the enlargement of digestive organs such as the gizzard, small intestines and the overall digestive tract (Table 1). Increasing gut size in response to increasing food quantity can yield several benefits. One is that it allows a constant mean retention time, thereby maintaining digestive efficiency if the ingestion rate increases (Karasov, 2011; Karasov et al., 2011).

Effects of photoperiod on organs

Short photoperiod has also been associated with changes in organ size and mass (Ni et al., 2011; Yang et al., 2009). One idea is that energetically challenged birds may increase their food intake, and at the same time, reorganize their internal organs to improve thermal and digestive efficiency (Liu & Li, 2006; Starck & Rahmaan, 2003; Williams & Tieleman, 2000). Several authors have suggested that much of the energy used in basal metabolism is consumed by visceral organs (Daan et al., 1990; Hansen et al., 2010; Piersma et al., 1996; Rolfe & Brown, 1997). The results of this study indicate that acclimation to a short photoperiod for 4 weeks was followed by significant increases in the mass of the liver, gizzard, small intestine and digestive tract, but not that of the heart and kidney. Increases in liver and small intestine mass are associated with thermogenic capacity. For example, the liver, kidneys, heart, and small intestine contribute to about 60% of total heat production (Clapham, 2012; Rolfe & Brown, 1997). Thus, the observed increase in the mass of the liver, gizzard, small intestine, and digestive tract in SD starlings may reflect adaptive regulation of organ morphology to accommodate increased food intake and digestion, ultimately contributing to an altered metabolic rate. Interestingly, only the dry mass of the liver was significantly correlated with BMR. This finding suggests that liver mass has a greater effect on BMR than that of other digestive organs. The liver is one of the largest and most metabolically active organs in birds. Under basal metabolic conditions, the liver has been shown to contribute 20%-25% of total heat production in

animals (Coutre & Hulbert, 1995). The liver's hepatocyte oxygen consumption is devoted to mitochondrial ATP production, mitochondrial proton leak and non-mitochondrial processes (Brand et al., 2003; Else et al., 2004). The mass of the liver is less often associated with BMR, however, positive correlations between BMR and liver mass have been documented in Eurasian tree sparrows and Chinese bulbuls (Zheng et al., 2013, 2014b). Thus, the positive correlation between liver mass and BMR in this study is not without precedent. The proportionately large nutritional liver mass of birds may facilitate the liver making a significant contribution to BMR (Coutre & Hulbert, 1995; Zheng et al., 2013).

In conclusion, environmental cues play important roles in the mediation of seasonal adaptation of body mass, thermogenesis, and energy intake in small birds. The results of this study indicate that the silky starling displays a general, elevated, whole-body response to short photoperiod, including increased body and organ mass, enhanced BMR and energy intake. The evident morphological and physiological flexibility in photoperiodic acclimation displayed by this species would be advantageous given the wide variation between the winter and summer climate in Wenzhou.

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