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Energy metabolism, testosterone and corticosterone in white-crowned sparrows

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Abstract The influence of the steroid hormones testosterone and corticosterone on energy metabolism and activity of birds is largely enigmatic. We measured resting metabolic rate during night and day in 12 long-term castrated and 12 intact male white-crowned sparrows (*Zonotrichia leucophrys gambelii*) under short-day (8:16 SD), long-day (20:4 LD), LD + testosterone implant and LD−testosterone implant conditions. Each male was sequentially measured under all four conditions. Photostimulation increased testosterone, resting metabolic rate, food intake, hopping activity and body mass in castrates and intact males. Surprisingly, testosterone levels and metabolic rates did not differ between intact and castrated males. Testosterone implantation increased activity and food intake, but decreased body mass and resting metabolic rate in both groups. Removing testosterone implants reversed the effects on resting metabolic rate, activity and food intake. Corticosterone levels, measured immediately at the end of metabolism measurements, showed birds were not stressed. Corticosterone had no apparent relationship with resting metabolic rate and there was no interaction between corticosterone and testosterone. Overall, positive changes in testosterone levels resulted in a decrease of resting metabolic rate. We speculate that testosterone increases activity, and birds compensate for increased activity metabolism by reducing resting metabolic rate.

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Abbreviations *BMR* basal metabolic rate · *D* duration of subjective night · *L* duration of subjective day · *RMR* resting metabolic rate · *T* testosterone

Introduction

Hormones regulate developmental and seasonal changes in morphology, behavior and physiology (Hadley 1992). However, hormones may affect physiological systems or organs in contrasting ways, e.g., they may promote the performance of one system but may inhibit the performance of other systems. This is to be expected from the ubiquitous trade-offs between physiological functions, and between various behaviors which have both benefits and costs (Wingfield et al. 1997b).

Such tradeoffs are particularly prominent for testosterone (T) and corticosterone (Wingfield et al. 1994, 1997b). In many male birds, for example, T increases activity and territorial persistence (Wingfield et al. 1990), which in turn increases the likelihood of extra-pair fertilizations (Beletzky et al. 1989; Ketterson et al. 1992). On the other hand, sustained elevated T increases predation and injuries, appears to decrease immune function and may cause cancer (Hillgarth et al. 1997). Costs of hormones like T may also be reflected in the energy balance of organisms (Marler et al. 1995). Feuerbacher and Prinzinger (1981) showed that T caused a decrease of body temperature in quail, possibly related to metabolic changes (Hänssler and Prinzinger 1979). On the other hand, Deviche (1992) did not find an effect of T on standard metabolic rates in dark-eyed juncos (*Junco hyemalis*). Prolonged elevated corticosterone may also affect energy balance. Buttemer et al. (1991) suggested that corticosterone decreases nightly metabolic arousals in birds, which could decrease the daily energy budget of a white-crowned sparrow by as much as 22%. One should keep in mind, however, that there are two

metabolic components of overall metabolim that can be affected by hormones: (1) the basic body energy expenditure, whose output is generally described as the resting metabolic rate (RMR); and (2) activity metabolism, which represents energy expended for active behaviors, particularly locomotion, which are added on top of RMR. These components may be somewhat independent of each other, at least in birds (Ricklefs et al. 1996). Often only one of these components is investigated, but understanding is enhanced when more than one is assessed (Deerenberg et al. 1998).

So far, the relationship between T, corticosterone and RMR, as well as activity and other components of total daily energy expenditure (DEE) in birds remains poorly understood (Ricklefs et al. 1996). Castrated quail had lower energy metabolism, but their RMR was not influenced by T substitution (Feuerbacher and Prinzinger 1981). The most important effect of corticosterone on RMR is its reduction of nocturnal metabolism as shown for domestic fowl (Mitchell et al. 1986).

Here we aim to clarify whether T or corticosterone have an influence on nocturnal or diurnal RMR. To test this, we measured RMR both in intact and long-term castrated male white-crowned sparrows (*Zonotrichia leucophrys gambelii*) and at the same time measured T, corticosterone, activity and food intake under short-day and long-day (simulated 'spring') conditions. We also manipulated T levels by implanting males with silastic tubes filled with crystalline T. The combination of these measurements allows us to assess how the total energy budget of our birds was likely affected by changes in hormone levels. White-crowned sparrows are an ideal study system to address these questions because we have detailed knowledge about their ecology, annual rhythms, seasonal hormonal and body mass changes (Wingfield and Farner 1993; Wingfield et al. 1996, 1997a).

Materials and methods

Birds and experimental time-course

A total of 24 male white-crowned sparrows were caught at Sunnyside Game Refuge, Yakima Country, Washington (47°N). One group (12 birds) consisted of adults that were caught in autumn 1995 and subsequently castrated in spring 1996. They were housed in outdoor aviaries in Seattle, Washington, under natural light and temperature conditions for almost 4 years. One castrated bird died on 3/2/98 (4 weeks after photostimulation, see below), reducing the sample size in this group to 11. The other group of 12 birds were yearling males that had been caught in October and November 1997. This group was also held in outdoor aviaries until the beginning of the experiment. On 1/19/98 and 1/20/98, all birds were laparotomized (see Wingfield and Farner 1976; Hau et al. 1998). We regard laparotomy as a 'sham' treatment for intact males because surgery procedures are almost identical to castration. All intact males had entirely regressed gonads, while no remains of gonads were detected in the long-term castrated birds. The castrated bird that died on 3/2/98 was entirely dissected and no remains of gonadal tissue were found. Furthermore, there had been no gonadal re-growth in the castrated males under the natural spring photoperiod of the preceding year, as determined by unilateral laparotomy (N. Hillgarth, personal communication). We therefore concluded that castration in the remaining castrates was also complete. Immediately after surgery, birds were transferred into individual cages (50 cm × 25 cm × 25 cm) in a 4 m × 5 m indoor experimental chamber. The ambient temperature was set to 20 °C for the entire experiment. All birds had seeds, Mazuri small bird chow (PMI Feeds, St. Louis, Mo.) and water ad libitum. Cages were cleaned every 3rd day. Birds were initially kept under a short-day photoperiod of 8:16 h LD (SD condition). Oxygen consumption, food intake and hopping activity were measured between 1/24/98 and 1/28/98. The photoperiod was then changed to long days (20:4 h LD) on 2/3/98 for the remainder of the experiment (LD condition). Oxygen consumption, food intake and hopping activity were measured again between 3/2/98 and 3/5/98. Birds were implanted with silastic tubes filled with crystalline T on 3/15/98. Intact males received a 10-mm implant, while castrated birds received a 20-mm implant (for details on implantation methods see Buttemer et al. 1991). With this differential treatment, we intended to increase plasma T to similar levels in intact and castrated males. For T-implanted birds, oxygen consumption and hopping activity were measured twice, once 3–6 days after implantation (3/18/98 and 3/21/98, T_{ini} condition) and again 29–32 days after implantation (4/13/98 and 4/16/98, T_{fin} condition). The measurements conducted on birds during T_{fin} condition aimed to clarify whether there is any adaptation to, or compensation for, high T levels through time. Food intake was only measured once for T-implanted birds during the T_{ini} condition. The silastic tubes were explanted immediately after the last round of measurements. Subsequent oxygen measurements were conducted 3 days after explantation (between 4/16/98 and 4/18/98; post-implantation = PI condition). We used a short interval between explantation and subsequent measurements because we wanted to measure metabolic rates in relation to hormonal, but not body mass changes. Birds were released into aviaries after termination of the measurements.

Food intake and activity measurements

The hopping activity of individual birds was monitored via an infrared light beam (Radio Shack) that was interrupted when birds hopped between perches. The number of interruptions was recorded for 24 h for eight birds at a time using a Macintosh activity recording system (LabView, National Instruments) (Breuner et al. 1998, 1999).

The food consumption of individual birds was determined by measuring (to the nearest 0.01 g) the decrease in seeds and chow in the food tray over the course of 1 day. To achieve this, the cages were cleaned from all remains of seeds, food trays were filled with new chow and weighed. Additionally, to minimize food being thrown from cages, we fitted the outside of each cage with a 7-cm-tall paper box. After 24 h, food trays were weighed again (after removing feces, if necessary) and food items found on the cage floor and in the paper box were carefully added to the weight of the food tray. The difference in these two measurements was taken as an estimate of apparent food consumption. Seeds that were thrown out of the cage could not be accounted for.

Metabolic and hormone measurements

Measurements were always made in the dark, during both the birds' nocturnal and diurnal phase (Aschoff and Pohl 1970). Resting oxygen consumption of each bird was measured in an open-flow respirometry system with a 2-l respirometer volume. A two-channel Applied Electrochemistry S-3A oxygen analyzer was used to record oxygen concentrations at 10-s intervals over a period of 90 min (nocturnal measurements 60 min) at 28 °C, i.e., in thermoneutral conditions. As a measure of RMR, we used the average oxygen concentration over the 5-min period of lowest stable oxygen concentration during each run. Two individual birds (one castrate, one intact male) were measured at the same time. For the diurnal measurements two birds each were captured starting at 3 h after lights on. Birds were put into cloth bags, transported to

the respirometry system (ca. 2 min duration), weighed to the nearest 0.1 g, scored for subcutaneous fat stores (Wingfield et al. 1996), and put into the respiration chamber. We expected that this treatment would stress the birds, i.e., increase their corticosterone levels, and that corticosterone levels would stay elevated for the duration of the metabolic measurements (Breuner et al. 1998, 1999; Romero et al. 1997). To evaluate the birds' plasma corticosterone levels during the metabolic measurements, we took 50-µl blood samples from both birds within 2 min after opening the chamber. It is important to take a sample for corticosterone within 2–4 min because 'stress' like handling will increase corticosterone levels after that time. To the contrary, T levels are not immediately affected by handling stress and thus blood samples for T analysis were taken subsequently, i.e., immediately after the blood samples for corticosterone analysis. All T samples (200 µl) were taken within less than 10 min after opening the chambers. We only report T levels for diurnal metabolic measurements because diurnal and nocturnal T levels did not differ significantly (Wilcoxon-test, $P = 0.64$). Similarly, corticosterone levels during the diurnal and the early nocturnal phase did not differ significantly (Wilcoxon-test, $P = 0.53$) as expected from the circadian pattern of corticosterone release in white-crowned sparrows (Breuner et al. 1999). Therefore, we only report daytime corticosterone levels here. Individuals were brought back to their cages immediately after termination of the measurements.

For the nocturnal measurements, all six birds measured during one night were taken from their cage less than 10 min before lights-off, transferred into cloth bags which were hung inside a dark room adjacent to the respirometry system. All nocturnal measurements including blood sampling were done using a dimmed head lamp. Light levels were just enough to perform the blood sampling. As during diurnal measurements, blood samples were taken after metabolic measurements. Metabolic rate was measured for 60 min. After nocturnal measurements, all six birds together were returned to their cages within 15 min after lights-on the next morning.

We tried to determine the lean mass-specific oxygen consumption of individual birds by estimating the lean mass of the birds. For this, we subtracted the amount of externally visible fat from the bird's body mass. The fat score was converted into fat mass according to previously determined relationships for white-crowned sparrows (Wingfield and Farner 1993; Wingfield et al. 1996).

Hormone assays

Plasma levels of T and corticosterone were measured with a direct RIA as described by Wingfield et al. (1992) and Hau et al. (1998). Non-radioactive T and corticosterone standards, as well as water blanks, were taken through the whole assay procedure to estimate non-specific interference, assay accuracy and intra-assay variation. Blanks were usually below detection limit. The accuracy of the T (corticosterone) standards was 5.3 ± 2.1% (11.3 ± 4.5%), and intra-assay variation was 10% (6%), respectively. Assay sensitivity (two standard deviations from lowest dilution) was at 0.13 ng ml^{-1} for T and 5 ng ml^{-1} for corticosterone. Whenever samples were below detection limit (e.g., 11 T samples during SD conditions, 6 corticosterone samples during LD conditions), they were set to detection limit levels as the highest possible value. This represents a conservative estimate for statistical comparisons.

Statistical analysis and data presentation

Data were processed with SPSS (Chicago) for Windows. Two-tailed test statistics were used. Data are given as means ± 95% confidence interval if not indicated otherwise. We used repeated measures ANOVAs (rANOVA) and least-significant post-hoc tests to determine differences between T_{ini}, T_{fin} and PI treatments for the two groups. Missing data for the bird that died were substituted by the group mean. Significance for all tests was accepted at the $\alpha = 0.05\%$ level.

Results

Hormones

Contrary to expectation, there was no significant difference in T levels between castrated and intact males throughout the experiment. However, T levels between treatments differed significantly (rANOVA $F_{4,24} = 8.5$, $P < 0.001$; for group: $P = 0.15$; for group × treatment: $P = 0.72$). Significant differences between groups and treatments, as determined by post-hoc tests, are indicated by stars in Fig. 1. At the beginning of the experiment, T was minimal in both groups, as expected from wintering birds (Fig. 1). After photostimulation both groups increased significantly but only slightly, up to 0.53 in intact males and 0.92 ng ml^{-1} in castrates, and there was no difference between the two groups. After T implantation, plasma T_{ini} levels significantly rose in both groups about five- to tenfold to levels found in free-living birds in spring (5–10 ng ml^{-1}). T_{fin} levels (4 weeks after implantation) did not differ from T_{ini} levels. T levels decreased significantly after removal in intact males, but not in castrates (Fig. 1). It is possible that the 3-day interval following removal was too short for T levels to be reduced to the baseline levels of photostimulated birds. The plasma levels of corticosterone were always low or at baseline levels (ca. 10 ng ml^{-1}) and did not differ between groups or treatments (Fig. 1b;

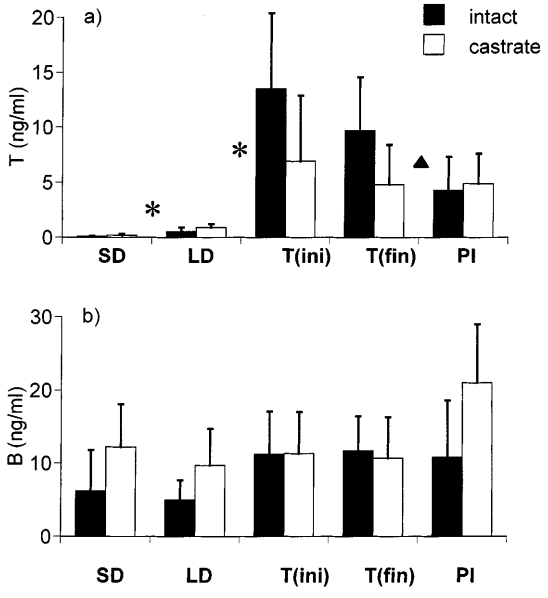

Fig. 1 Plasma concentrations of the hormones testosterone (T; in **a**) and corticosterone (B; in **b**) of white-crowned sparrows during the course of the experiment. *Bars* indicate means ± 95% confidence interval. Intact males are shown in *black bars*, castrated males in *open bars*. *SD* short-day condition, *LD* long-day condition, T_{ini} 3–6 days after T implantation, T_{fin} 29–32 days after T implantation, *PI* after removal of T. Significant differences between subsequent treatments are indicated by *stars* (for both groups) and *triangles* (for intact males only)

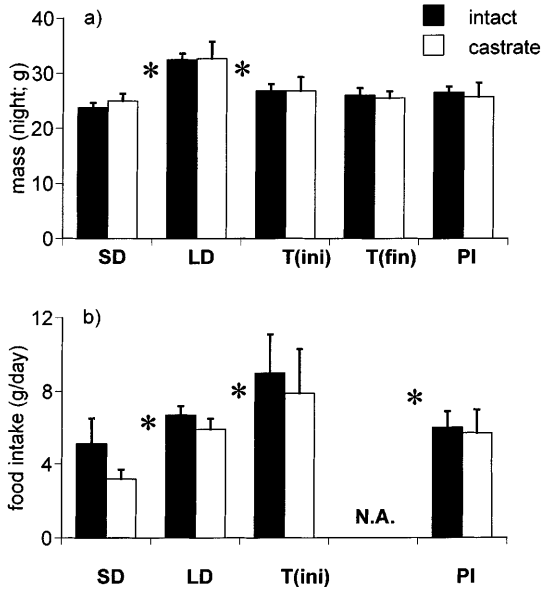

Fig. 2 Body mass (**a**) and food intake (**b**) during the experiment. Symbols as in Fig. 1. *N.A.* indicates that measurements are not available

rANOVA $F_{4,24} = 1.3$, $P < 0.27$; for group: $P = 0.07$; for group × treatment: $P = 0.23$).

Mass, food intake and activity

We found no differences between intact and castrated males in the body mass profiles throughout the experiment (Fig. 2a). However, body masses differed significantly between treatments (rANOVA $F_{4,24} = 120.2$, $P < 0.001$; for group: $P = 0.94$; for group × treatment: $P = 0.19$). Body masses increased dramatically after photostimulation and birds became very fat (the median fat score increased from 1 to about 4). After T implantation, body masses dropped again to previous values, and stayed at those values throughout the experiment.

Castrated and intact birds always had similar food intake (Fig. 2b). Food intake in both groups increased after photostimulation, and increased even further after T_{ini} implantation (rANOVA $F_{3,24} = 138.9$, $P < 0.001$; for group: $P = 0.68$; for group × treatment: $P = 0.06$). Food intake was not measured during the T_{fin} period. Food intake dropped again after explantation of T.

The pattern of activity resembled that of T and food intake in that activity showed no difference between intact and castrated males, increased significantly after photostimulation, increased further after T_{ini} implantation, stayed about at the same levels until the end of the implantation experiment (until T_{fin}), and finally decreased sharply after explantation of T (Fig. 3; rANOVA $F_{4,24} = 21.2$, $P < 0.001$; for group: $P = 0.87$; for group × treatment: $P = 0.77$). Significant differences between groups and treatments, as determined by post-hoc tests, are indicated by stars in Figs. 2 and 3.

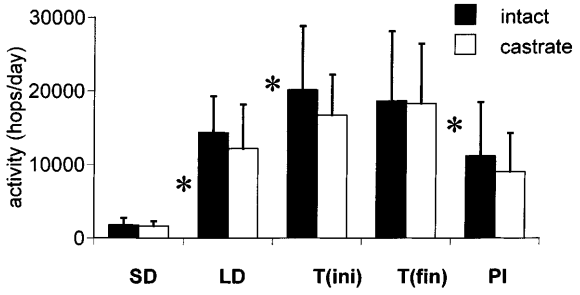

Fig. 3 Hopping activity of white-crowned sparrows during 1 day, as determined by the number of times individuals crossed infrared light beams. Symbols as in Fig. 1

Metabolism

Nocturnal oxygen consumption (RMR) did not differ between castrates and intact males, but changed significantly throughout the experiment (Fig. 4a; rANOVA $F_{4,24} = 32.4$, $P < 0.001$; for group: $P = 0.37$; for group × treatment: $P = 0.48$). It approximately doubled after photostimulation. T implantation strongly decreased RMR. RMR remained at similarly low levels until the end of the T implantation, but increased significantly after removal in intact males. Castrated males showed a slight increase in RMR at the end of the T experiment. When we corrected the nocturnal RMR data for the metabolically active body mass (i.e., estimated lean body mass), a very similar pattern emerged (Fig. 4b; rANOVA $F_{4,24} = 12.1$, $P < 0.001$; for group: $P = 0.32$; for group × treatment: $P = 0.34$).

Daytime RMR basically showed the same temporal pattern as nocturnal RMR except that absolute RMR levels were generally higher. Furthermore, there was a significant group × treatment interaction for both absolute and mass-specific oxygen consumptions, indicating that the reaction of castrated males to T implantation was different from that of intact males (Fig. 4c and 4d; for absolute levels: rANOVA $F_{4,24} = 9.9$, $P < 0.001$; for group: $P = 0.22$; for group × treatment: $P < 0.001$; for mass-specific levels: rANOVA $F_{4,24} = 5.3$, $P = 0.02$; for group: $P = 0.25$; for group × treatment: $P = 0.001$). Significant differences between groups and treatments, as determined by post-hoc tests, are indicated by stars in Fig. 4.

To address the intraspecific allometry of RMR against body mass, we calculated the regression equations for log RMR against log body mass for each individual bird during the different conditions. The mean mass exponent was 1.21 ± 0.11 (SE; $n = 23$, excluding the bird that had died). To evaluate whether a higher corticosterone level suppressed the variance in RMR, as suggested by Buttemer et al. 1991, we regressed the coefficient of variance in RMR against the individual corticosterone levels, i.e., we used one data point for each individual bird irrespective of whether it was a castrate or a control. There was no relationship [linear regression: CV(RMR) = 20.2 (±4.1) − 0.9 (±0.9) × B,

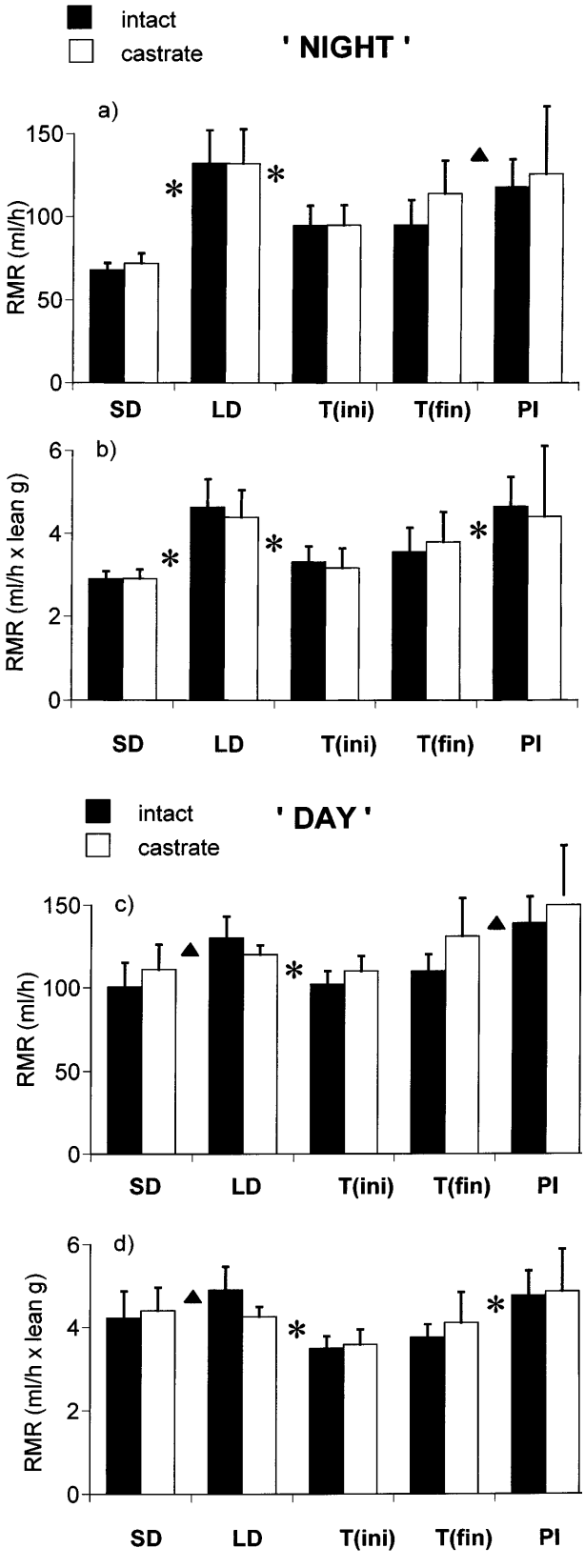

Fig. 4a–d Resting metabolic rate of white-crowned sparrows during the course of the experiment. **a** and **b** show daytime measurements, **c** and **d** nocturnal measurements. **a** and **c** show whole-body values of oxygen consumption (ml h^{-1}), while **b** and **d** show oxygen consumption in relation to the estimated lean mass of birds. Symbols as in Fig. 1

$F_{1,21} = 0.2$, $P = 0.26$, $r^2 = 0.06$]. Furthermore, we did not find evidence that T and corticosterone were interrelated (Spearman Rank correlation for the respective values after photostimulation: $P = 0.65$).

Discussion

T profoundly influenced the behavior of birds, as expected from other studies (Wingfield et al. 1990). T increased hopping activity and food intake but at the same time decreased body mass, possibly as a result of very high activity levels. Although we could not measure activity metabolism directly, the greatly increased activity levels suggest that activity metabolism was much higher after T implantation. Interestingly, and contrary to our expectation, high T levels appeared to be also associated with low RMRs. Such a finding of increased activity metabolism and decreased RMR is not without precedence. Deerenberg et al. (1998) showed that zebra finches (*Taeniopygia guttata*) apparently compensated for increased activity metabolism by decreasing nocturnal and even diurnal RMR. Our study suggests a similar result. The major difference between the two studies is that Deerenberg et al. (1998) increased activity metabolism by increasing the work load of captive birds, while we increased T levels, which in turn increased activity levels.

It is important to note that the effect of T on behavior (activity) in our experiment was short lived, at least in control birds. As soon as the silastic tubes containing crystalline T were removed, activity decreased. As a consequence, birds presumably had a lower activity metabolism and consequently did not metabolically compensate any longer. Thus, RMRs increased again after T explantation. The close correspondence of results of Deerenberg et al. (1998) and our study suggests that the most likely effect of T on metabolic rate was secondary, i.e., via the effects of T on behavior. It will be interesting to investigate whether the costs of T as discussed by Wingfield et al. (1997a, b) are at least partly caused by a *decrease* in RMR, which in turn may be linked to a lowered maintenance effort (Daan et al. 1996) or to a decreased vigilance against predators (Bednekoff and Houston 1994). In this context it is important to note that T levels produced by implants were well in the physiological range for free-living white-crowned sparrows, which can have plasma T levels up to 12 ng ml^{-1}.

Our results for the relationship between metabolic rate and T are qualitatively the same if we use absolute oxygen consumption or lean-mass-specific oxygen consumption (Fig. 4). For our calculations of mass-specific metabolic rate we used estimates of lean body masses of white-crowned sparrows based on fat scores, but did not sacrifice the birds. The latter would have been necessary to obtain exact quantitative values. However, we feel confident that our estimates of lean body mass are accurate to approximately $\pm 10\%$ (Wingfield and Farner

1993; Wingfield et al. 1996). Relating metabolic rates to lean body mass is necessary to assess how the basic body machinery changes irrespective of the mass changes caused by fat (Piersma et al. 1995, 1996). The observation that the basic body maintenance (RMR) was enhanced after photostimulation (Fig. 4) is supported by the fact that mass exponents of RMR considerably exceeded proportionality (average 1.21). Thus, metabolic rate increased with body mass beyond what would be expected had the maintenance metabolism remained the same. Similarly high values were reported for knots, *Calidris canutus*, (1.38; Piersma et al. 1995) and kestrels, *Falco tinnunculus* (1.67; Daan et al. 1989) that were either exposed to high maintenance foraging or thermoregulation regimes. These mass exponents are considerably steeper than for interspecific comparisons between bird species (0.73; Kersten and Piersma 1987), for homomorphic change (0.66; Heusner 1984) or for mass proportionality (1.0). At present, however, any direct influence of T on intraspecific scaling of RMR remains speculative and warrants further attention.

Our data suggest an alternative explanation for the results of Feuerbacher and Prinzinger (1981) and Gupta and Thapliyal (1984), who found that mass-specific energy metabolism was lower in castrates than in intact male quail (*Coturnix coturnix japonica*) or spotted munia (*Lonchura punctulata*), respectively. Given the fact that castrated birds are generally heavier, i.e., presumably fatter, it is likely that the mass-specific difference in oxygen consumption found between the two groups simply reflects the presence of fat in castrated males as also argued in Hänssler and Prinzinger (1979). This may also explain why metabolic rate of quail did not change after T implantation in the above-mentioned experiments. However, it is unfortunate that neither body masses nor plasma T levels are reported in Feuerbacher and Prinzinger (1981) and no T levels are reported in Gupta and Thapliyal (1984). Thus, we are presently unable to relate their results directly to those obtained during the present study.

Our T manipulations revealed two unexpected results. First, T levels did not differ between intact and castrated males after photostimulation. Second, implanting twice the amount of T into castrates barely increased their T levels to that of T-implanted intact males.

Our experiment was initially designed to make use of the differences in plasma T levels of castrated and intact male white-crowned sparrows. We assumed, as many other studies did, that castrates have lower T levels than intact birds. This turned out to be wrong. Although this lack of T differences between castrates and intact males was unexpected, it is not without precedence. Several recent studies show that levels of gonadal hormones may remain high following castration (Tsutsui et al. 1991). These results suggest that elevated T levels as observed in our castrates may occur regularly and are unlikely to be the results of long-term castration. We suggest that T in castrated males may come from the adrenals. This argument relies on the assumption that castration was complete, i.e., that at least visually there were no remaining steroidogenic cells of gonadal origin in castrated birds during laparotomies and one dissection. T levels in photostimulated birds were lower than in wild birds at the same time of year (Wingfield and Farner 1993). This was expected because hormone levels in captivity are usually lower than in the wild, possibly due to a lack of social interactions in cages. However, it is unlikely that the housing protocol was so stressful that adrenal activation could have suppressed plasma T levels (Wingfield 1990). It is of some concern that castrated and intact males were of different ages. However, even intact (yearling) males were in captivity for about half a year and thus similarly accustomed to cages as castrated males. Furthermore, the experimental elevation of T far exceeds any differences between birds of different ages or stages (Wingfield and Farner 1993).

Castrated birds received two T implants (20 mm) while intact males only received one (10 mm). It is unclear why T levels in castrated birds were indistinguishable from those in intact males. This result is particularly puzzling because, as discussed above, both groups of males had similar unmanipulated T levels under the preceding experimental conditions of photostimulation.

T appeared to have no influence on corticosterone levels during our experiment. However, we did not measure a possible influence of T on corticosteroid-binding globulin, which in turn might affect circulating corticosterone levels (Klukowski et al. 1997). During our experiment, circulating corticosterone levels after metabolic measurements were indistinguishable from baseline levels for white-crowned sparrows (ca. 8 ng ml^{-1}, Breuner et al. 1999). This indicates that our physiological measurements did not elicit a strong adrenocortical response in white-crowned sparrows. At least, levels were much lower than reported by Romero et al. (1997) for stressed birds. We did not observe any effect of corticosterone on the variance in metabolic rate, as has been documented by Buttemer et al. (1991) and Astheimer et al. (1992). The difference between these experimental setups was that corticosterone levels were manipulated via implants in the study of Buttemer et al. (1991) and thus more adequately reflected the high corticosterone levels of a 'stressed' sparrow in the wild.

Overall, it appears that T has either no *direct* influence on the RMR of birds, or even *reduces* maintenance metabolism. On the other hand, T profoundly increases the activity of birds and thus presumably their total daily metabolism and the individual component of locomotor or activity metabolism. By doing so, T may also have a strong influence on the body temperature of birds, as found by Feuerbacher and Prinzinger (1981). Birds that are more active are expected to have higher metabolic rates, and thus higher body temperatures, during daytime. Birds that are highly active in the day, either because of their work load (Deerenberg et al. 1998) or because of high T levels (this study), apparently

compensate for their increased energy expenditures at night. This may cause body temperature to decrease and may explain in an overall way why castrated birds have higher nocturnal but lower diurnal body temperatures (Feuerbacher and Prinzinger 1981). Lower RMRs in birds with high T levels may also explain why such individuals suffer an increased risk of predation or disease (Ketterson et al. 1992; Wingfield et al. 1997a, b). T could have a dual action that includes turning off, or sacrificing, basic organismal functions.

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