



Effect of photoperiod on body weight gain, and daily energy intake and energy expenditure in Japanese quail (*Coturnix c. Japonica*)

Polly Boon^{a,*}, G. Henk Visser^{a,b}, Serge Daan^a

^aZoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren (Gr), The Netherlands

^bCenter for Isotope Research (CIO), University of Groningen, Nijenborg 4, 9747 AG Groningen, The Netherlands

Received 28 October 1998; received in revised form 1 December 1999; accepted 9 March 2000

Abstract

Effect of photoperiod and food duration on body weight gain, energy intake, energy expenditure, and sexual development were investigated in two strains of Japanese quail (*Coturnix c. japonica*), bred for meat (broilers) or egg production (layers), from 7 to 71 days of age. In a first experiment chicks were subjected to 18L:6D, 15L:9D, 12L:12D, 9L:15D, or 6L:18D, with ad lib food during the light period. In a second experiment birds were exposed to a long photoperiod (18L:6D or 15L:9D) with ad lib food during part of the light period (first 6 or 9 h, respectively). Longer photoperiods were associated with larger weight gains. In 18L:6D broilers total body weight gain was 262 g compared to 213 g in 6L:18D broilers. In layers, corresponding values were 182 and 131 g. This effect of photoperiod on weight gain was primarily due to the effect of photoperiod on food availability. The photoperiod below which detrimental effects on weight gain occurred was 9L:15D for both strains. Chicks subjected to 9L:15D or 6L:18D exploited crop filling to enhance energy intake. They also decreased nocturnal metabolic rates to a greater extent compared to levels during the light phase than chicks subjected to light periods of 12 h or more. Sexual maturation was stimulated by photoperiod. At the age of 71 days, eight out of nine females subjected to 18L:6D were producing eggs, but none of the 6L:18D females. It is concluded that changes in feeding behavior and energy expenditure shown under short photoperiods are part of a strategy that allow chicks to gain weight continuously. © 2000 Elsevier Science Inc. All rights reserved.

Keywords: Photoperiods; Body weight gain; Energy intake; Japanese quail

1. Introduction

Rates of body weight gain in altricial birds in the tropics are, on average, 23% lower than rates in similar sized birds inhabiting temperate areas [33]. This difference in weight gain rate could be explained by a difference in photoperiod between the two latitudes, which determines the period in which parents can gather food for their offspring. Photoperiod is known to affect rates of weight gain in juveniles [3,18,23,24,30,35,38,42]. This effect is primarily produced by the effect of photoperiod on energy intake and energy expenditure [2,3,35]. The interaction between these two parameters as a function of photoperiod determines overall body weight gain. By modulating the duration of the light, and consequently the dark period, opportunities for birds to either increase energy intake or reduce energy expenditure will vary, with consequences in overall body weight gain. Growing chickens and laying hens were able to decrease energy expenditure during a 10-h dark period by 22% compared to only 12% of the light period value when exposed to

a daily 1-h dark period [21]. Adult male pigeons (*Columba livia*) subjected to prolonged (nocturnal) fasting periods decreased both energy expenditure and body temperature during the dark phase to a larger extent compared to pigeons in ad lib conditions [31]. This resulted in an overall lower 24-h energy expenditure. Photoperiod can also influence weight gain via an effect on the balance between food intake and digestion [6]. Throughout the light period food intake occurs, whereas during the dark period, when both food intake and activity are suppressed, digestion can take place. On the other hand, long photoperiods stimulate sexual maturation in both quail and other bird species [7,9,15,20,29,37,39,43], which may also affect weight gain positively.

It is evident that daily patterns of food availability and activity have consequences for the daily amount of food that can be consumed, the total 24-h metabolic rate, and the net balance of energy intake and energy expenditure. In growing animals this balance affects the weight gain animals will be able to accomplish. In this study, we measured in Japanese quail (*Coturnix c. japonica*) the 24-h energy intake and expenditure in a range of photoperiods, with food intake restricted to the light period to evaluate how photoperiod and food availability contribute to energy balance. For this pur-

* Corresponding author. Tel.: 31-317-47-54-43; Fax: 31-317-41-77-17
E-mail address: P.E.BOON@RIKILT.WAG-UR.NL

pose, two experiments were conducted. In the first experiment (“photoperiod”), chicks were subjected to five different photoperiods ranging from 6L:18D to 18L:6D with ad lib food during the light period. In a second experiment (“food duration”), chicks were subjected to a long photoperiod (equal to the longest two photoperiods of Experiment 1) with only ad lib food during part of the light period (equal to the shortest two photoperiods of Experiment 1). In this way the effect of photoperiod was separated from the effect of food duration. Japanese quail were used, a species with the fastest growth rate in the family Phasianidae [32], and likely to be responsive to variations in photoperiod and food availability. Two strains were investigated to compare breeds with different growth strategies resulting from selective breeding. The effects of the experimental conditions were studied on body weight gain, energy intake and expenditure, respiratory quotient, and sexual development. The study was extended until adult age to examine the effect of photoperiod on adult body weight. As far as we are aware, this is the first study in which a wide range of natural occurring photoperiods has been studied in an avian species from 1 week of age until adulthood.

2. Materials and methods

2.1. Animals, experimental setup, and housing

Japanese quail neonates, of a fast growing strain bred for meat production (broilers) and a normal growing strain bred for commercial egg production (layers), were obtained from a commercial quail farm (N.V. Nouwen, Lommel, Belgium). Until the age of 6 days, birds were kept in wooden cages (1 × b × h: 67 × 39 × 44 cm³) with sawdust bedding

in continuous light and ad lib access to quail starter food and water, to ensure maximum possible body weight gain. A 40-W heating lamp was placed in each cage to provide a temperature gradient sufficient for selection of the preferred temperature by the chicks. At 6 days of age the chicks were assigned to the experimental conditions in such a way that the average body weight did not differ between the groups. In Experiment 1, the following photoperiods were studied: 18L:6D (18LF), 15L:9D (15LF), 12L:12D (12LF), 9L:15D (9LF), and 6L:18D (6LF), with ad lib food during the light period (Table 1). In Experiment 2 chicks were subjected to a long photoperiod (either 18L:6D or 15L:9D), with only ad lib food during part of the light period (first 6 or 9 h, respectively): 18L-6F and 15L-9F, respectively. In all conditions food became available at lights on. At 6 days of age, the animals were permitted to habituate to the experimental conditions and allowed to eat ad lib during the whole 24-h period. The experiment started at 7 days of age. Throughout the experimental period a pellet diet (Institute for Animal Science and Health, ID-DLO, The Netherlands) containing 27.7% (w/w) crude protein and 17 kJ-wet g⁻¹ (gross energy content) was fed. Water was freely available.

During the experiment the animals were housed in pairs in wooden cages (l × b × h: 67 × 39 × 44 cm³) with a wire bottom and a 40-W heating lamp. The heating lamp was gradually raised and finally removed to allow the ambient temperature to decrease to room temperature (~21°C) within 3 weeks of age. One feeder and one water container were mounted on the left and right side of the cages, respectively, and separated from the inside of the cage by a partition containing two openings, one for each bird. Feeders were automatically removed and returned using a clock-controlled compressed air system. In groups with an uneven

Table 1
Characteristics (mean ± SD) of broilers and layers of Japanese quail subjected to different photoperiods and food duration

	18LF ¹	15LF	12LF	9LF	6LF	15L-9F	18L-6F
Experiment 1: photoperiod						Experiment 2: food duration	
Broilers							
Sample size (n)	8	9	10	8	8	8	7
Females (n)	5	7	5	6	2	6	1
b.wt. start (g) ²	38.8 ± 5.5 ^{ab}	35.3 ± 3.1 ^a	33.1 ± 1.3 ^a	33.8 ± 4.5 ^a	33.1 ± 4.6 ^a	33.8 ± 3.6	35.3 ± 5.0
b.wt. gain (g)	262 ± 62 ^{ab}	294 ± 45 ^a	261 ± 28 ^{ab}	241 ± 27 ^{ab}	213 ± 25 ^b	275 ± 46	204 ± 21
b.wt. gain rate (g·day ⁻¹)	4.1 ± 1.0	4.6 ± 0.7	4.1 ± 0.4	3.8 ± 0.4	3.3 ± 0.4	4.3 ± 0.7	3.2 ± 0.7
24-h RQ	0.92 ± 0.05	0.92 ± 0.04	0.88 ± 0.04	0.87 ± 0.05	0.86 ± 0.04	0.89 ± 0.06	0.83 ± 0.03
End of the night RQ	0.80 ± 0.06	0.78 ± 0.04	0.73 ± 0.03	0.72 ± 0.03	0.72 ± 0.03	0.76 ± 0.04	0.72 ± 0.03
Layers							
Sample size (n)	13	10	8	7	10	11	15
Females (n)	4	5	3	3	8	8	11
b.wt. start (g)	27.0 ± 4.2 ^a	26.4 ± 2.4 ^a	27.1 ± 3.5 ^a	23.1 ± 4.6 ^a	24.6 ± 1.5 ^a	24.4 ± 3.3	26.4 ± 3.3
b.wt. gain (g)	182 ± 53 ^a	195 ± 46 ^a	187 ± 36 ^{ab}	154 ± 14 ^{ab}	131 ± 12 ^b	174 ± 31	133 ± 17
b.wt. gain rate (g·day ⁻¹)	2.8 ± 0.8	3.1 ± 0.7	2.9 ± 0.6	2.4 ± 0.2	2.0 ± 0.2	2.7 ± 0.5	2.1 ± 0.3
24-h RQ	0.94 ± 0.05	0.92 ± 0.05	0.88 ± 0.09	0.88 ± 0.04	0.84 ± 0.02	0.89 ± 0.05	0.84 ± 0.04
End of the night RQ	0.78 ± 0.05	0.80 ± 0.05	0.76 ± 0.03	0.73 ± 0.03	0.70 ± 0.02	0.75 ± 0.03	0.74 ± 0.05

¹For definitions, see the Materials and methods section.

²b.wt.: body weight; RQ: respiratory quotient.

*Numbers with the same letter (^{ab}) within Experiment 1 are not significantly (Tukey, $p > 0.05$) different from each other.

number of animals, one cage contained three birds. This had no effect on body weight gain. Birds were sexed by plumage color.

2.2. Body weight and food intake

Birds were weighed (to 0.1 g) every 2–4 days at lights on until the age of 8 weeks, and thereafter once every week until the end of the experiment. On these days food became available just after weighing. Total 24-h food intake (g) was measured every 2–4 days until the age of 8 weeks, and thereafter once every 1 or 2 weeks until the end of the experiment. For this, the feeders were weighed at lights on on 2 consecutive days. Food intake was measured for both strains in two cages in the 6LF, 9LF, and 18L-6F group, and in four cages in the 12LF, 15LF, 18LF, and 15L-9F group. Spilled food was carefully collected from all parts of the cage and at the side of the cage where the feeder was located. The 24-h gross energy intake (GEI; $\text{kJ}\cdot\text{day}^{-1}$) per cage was calculated by transforming 24-h food intake per cage (g) to its energetic equivalent ($17 \text{ kJ}\cdot\text{g}^{-1}$). This value was expressed as GEI per bird.

2.3. Energy expenditure

The 24-h energy expenditure (EE) was measured at regular time intervals with indirect calorimetry. Oxygen consumption and carbon dioxide production were measured in an open air flow system. The birds were removed from their home cages and placed in airtight metabolic boxes of 10 to 20 liters with absorptive paper for bedding. The boxes were placed in light- and temperature-regulated metabolic chambers. The light and feeding schedule, and temperature were identical to conditions in the home cages. The animals were placed in and removed from the metabolic boxes during the light period. Metabolism was measured over a period of at least 25 h to obtain a full 24-h record after possible handling and gas equilibration effects had subsided. Metabolism was determined of two animals per box until the age of 4 weeks to minimize the stressful effect of solitary confinement in young birds. Thereafter, the measurements were conducted on isolated animals until the end of the experiment. During the measurement water was freely available. Body weight was recorded at the start and end of the measurement. Measurements were performed every week during the experimental period until the age of 5 weeks. Thereafter, at least one measurement was taken at adult weight. We attempted usually to obtain at least two energy measurements per week and strain for each experimental condition.

Dry air was pumped through the boxes at rates varying with age (from ca. $25 \text{ liters}\cdot\text{h}^{-1}$ at 1 week to ca. $120 \text{ liters}\cdot\text{h}^{-1}$ at 10 weeks of age) to obtain a difference in the in- and outflowing air of about 0.5% oxygen. The flow rate was measured on the inlet air with a mass-flow controller (Type 5850E Brooks) to an accuracy of 1%. The excurrent air was dried over molecular sieves (3 \AA , Merck). The oxygen concentration in the in- and outflowing air was measured by a

zirconium oxide sensor (S-3A/II Oxygen Analyzer, Applied Electrochemistry), and the carbon dioxide concentration by an infrared gas analyzer (BINOS-IR), both to an accuracy of 0.01%. At regular time intervals we calibrated the oxygen and carbon dioxide analyzers with certified gas standards. Six channels were employed simultaneously, using valves to switch between the channels once per minute (washout time 45 s), so that for each channel the values were recorded automatically at 6-min intervals. The system recorded the oxygen and carbon dioxide differentials between dried reference air and dried air from the metabolic box.

Oxygen consumption and carbon dioxide production ($\text{liters}\cdot\text{h}^{-1}$) were computed using equation 6 of [13], in which the gas data are corrected for changes in gas volume resulting from the carbon dioxide production with the use of the respiratory quotient (RQ). The obtained values were converted to energy expenditure ($\text{kJ}\cdot\text{h}^{-1}$) by applying an energy equivalent of $20.1 \text{ kJ}\cdot\text{liters}^{-1} \text{ O}_2$ [12]. We calculated the average energy expenditure and RQ over the last 24 h of the measurement. The mean RQ was also computed over the last half hour of the dark period for an impression of the metabolic status of the birds at the end of the dark phase. Resting metabolic rate (RMR) was calculated as the lowest value of a 30-min running mean over the last 24 h of the measurement.

2.4. Sexual maturity

To assess the effect of photoperiod on sexual maturity, the age and body weight at which females laid their first egg was measured. Because of the experimental setup (two birds per cage), it was not always possible to identify which bird had laid which egg. In the case of two females per cage, we assumed that the first egg found was laid by the heaviest animal. Because of the characteristic color pattern of the shells, we could for most eggs establish retrospectively which bird had laid which egg. Eggs were weighed every morning during weekdays just after lights on.

2.5. Data analysis

Data are expressed as means and interindividual standard deviations. Differences between group means were analyzed posthoc by Tukey's honestly significant difference test, after an effect of treatment on the variable of interest was ascertained by one-way analysis (SPSS Inc., 1988). Student's *t*-test was used when comparing two groups. Because of variations in body weight for the different experimental conditions at the same age, gross energy intake and energy expenditure were compared based on log-log regressions on body weight. To this end, analysis of covariance (ANCOVA) was used with experimental condition and strain as main effects and body weight as covariate. The same procedure was used, but without logarithmic transformation, to test for main effects on other variables with or without body weight as covariate. In all ANCOVA analyses two- and three-way interaction terms were taken into ac-

count. The main effects and interaction terms were entered in the model. Subsequently, the nonsignificant terms were removed in a stepwise backward procedure. This ANCOVA procedure is an a posteriori test without preplanned comparisons, and the statistics should be evaluated conservatively [25]. Therefore, interaction terms were removed when $p \geq 0.02$ and main effects when $p > 0.05$. A two-tailed significance level of $p < 0.05$ was used in all other tests. More details of the analyses are presented in the Results section.

3. Results

3.1. Experiment 1: Photoperiod

3.1.1. Body weight gain

At 6 days of age absolute body weight (g) did not differ between the experimental groups for both broilers and layers (Table 1, Fig. 1A). At 7 days of age, when food restriction was introduced, groups subjected to a daily light period of 9 h or less did not grow during the first 2 days of the experiment (Fig. 1A). This effect was clearest in the 6LF group (Fig. 1A). From the age of 9 days onwards weight increased again. Total body weight gain over the whole experimental period in relation to photoperiod is plotted in Fig. 2A. ANCOVA revealed that the total body weight gain varied significantly with photoperiod, $F(4, 71) = 16, p < 0.001$, strain, $F(1, 71) = 138, p < 0.001$, and sex, $F(1, 71) = 44, p < 0.001$: body weight gain was higher with longer photoperiods, in broilers, and in females. Only photoperiod \times sex interaction, $F(4, 71) = 8.5, p < 0.001$, signifi-

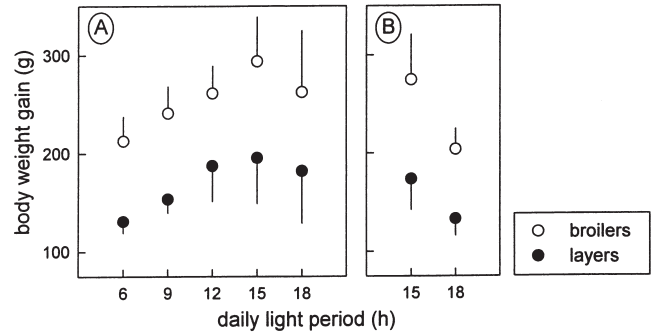


Fig. 2. Mean (\pm SD) total body weight gain (g) in relation to daily light period (h) in Japanese quail subjected to different photoperiods and food duration. For more details, see Fig. 1.

cantly contributed to the explained variance, indicating that the effect of photoperiod on body weight gain differed per sex: females showed a stronger retardation in body weight gain with decreasing photoperiod than males. Because of the unbalanced distribution of the sexes over the different groups with few females in the 6LF group of the broilers (Table 1), sex differences were only analyzed in total body weight gain. Because sexual dimorphism has been shown to disappear under severe food restriction [11], we do not expect that the small number of females in this group influenced the results.

Chicks subjected to a daily light period of 9 h or less started off at lower rates of body weight gain ($\text{g} \cdot \text{day}^{-1}$) than birds subjected to longer light periods (Fig. 3A). The 6LF group even lost body weight initially. In the 12LF, 15LF, and 18LF groups weight gain rate attained its highest value

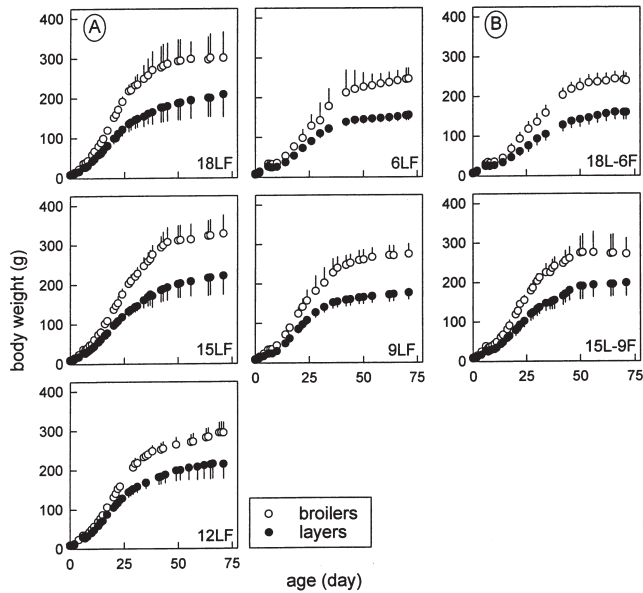


Fig. 1. Mean (\pm SD) body weight (g) as a function of age (day) in Japanese quail subjected to 18L:6D (18LF), 15L:9D (15LF), 12L:12D (12LF), 9L:15D (9LF), and 6L:18D (6LF) with ad lib food during the light period (Experiment 1; A), and long photoperiods (18L:6D or 15L:9D) with ad lib food during part of the light period (first 6 or 9 h, respectively): 18L:6D and 15L-9F, respectively (Experiment 2; B).

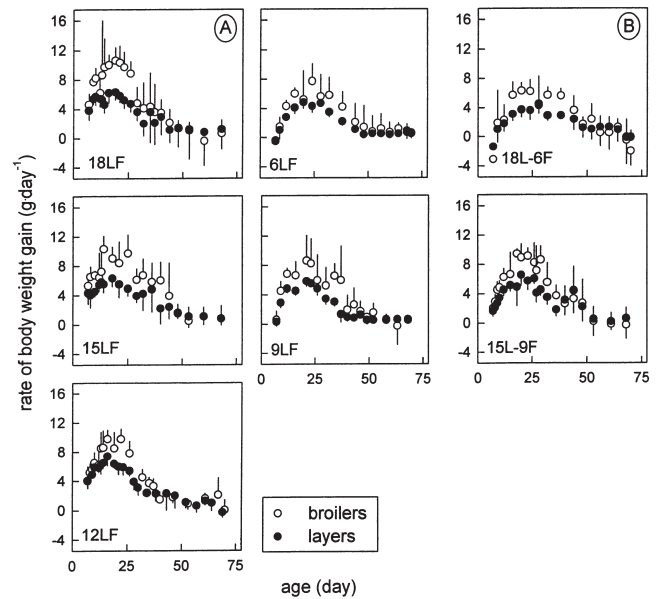


Fig. 3. Mean (\pm SD) rate of body weight gain ($\text{g} \cdot \text{day}^{-1}$) as a function of age (day) in Japanese quail subjected to different photoperiods and food duration. For more details, see Fig. 1.

around 20 days of age, and remained stable from 40 until 71 days of age. In the 6LF and 9LF groups, the peak in weight gain seemed to be shifted to around 25 days of age, while it stabilized around the same age (42 days).

3.1.2. Gross energy intake

The 24-h gross energy intake (GEI; kJ·day⁻¹) for the different photoperiods is plotted as a function of body weight in Fig. 4A. For each photoperiod and strain biphasic regression models were fitted to describe the relationship between GEI and body weight [16,17]. This was done because of a large increase in GEI for body weight in the 6LF and 9LF group at the beginning of the experiment (Fig. 4A). The biphasic model is

$$Y = a + b_1 X - r(b_1 - b_2) \log(1 + e((X - c_1/r)^{-1}))$$

where *Y* is the log of the dependent variable (GEI), *a* is the intercept, *b*₁ and *b*₂ are the slopes of phase 1 and 2, respectively, *X* is the log of the independent variable (body weight), *c*₁ is the estimated break point between phase 1 and 2, and *r* is a smoothness parameter that was set at 0.01, forcing an abrupt transition [16]. All curves were fitted according to the nonlinear regression algorithm procedures of the NONLIN package (shareware program, P. H. Sherrod). The significance of adding an additional phase to the model instead of assuming a linear relationship was assessed by an *F*-test [17]. In the 6LF group, a biphasic allometric regression model of log GEI with log body weight fitted the data significantly better than a linear regression model in both

broilers, *F*(2, 32) = 3.6, *p* < 0.05, and layers, *F*(2, 32) = 5.5, *p* < 0.01. In the 9LF group, this was only true for layers, *F*(2, 36) = 13, *p* < 0.005. In all other cases, a biphasic pattern did not significantly improve the fit compared to a normal linear regression model (*p* > 0.05; Fig. 4A). We are aware that some birds contribute multiple points to the analyses. However, our design does not permit correction for this.

GEI, after correction for body weight, varied significantly with photoperiod, *F*(4, 453) = 14, *p* < 0.001, and strain, *F*(1, 453) = 6.0, *p* < 0.025, with higher intakes at increasing photoperiods and in broilers (Fig. 4A). Photoperiod × body weight interaction significantly contributed to the explained variance, *F*(4, 453) = 11, *p* < 0.001, indicating that the allometric relationship between GEI and body weight differed per photoperiod: slopes between GEI and body weight were steeper in the 6LF and 9LF group. For an impression of the GEI levels for the different conditions, parallel slopes were assumed (0.53) for the individual regressions of GEI against body weight by assuming no photoperiod × body weight interaction. GEI level for 18LF broilers was 1.9, 2.4, 6.6, and 29% higher than for chicks of equal body weight in the 15LF, 12LF, 9LF, and 6LF group, respectively. In layers GEI was, for all conditions, on average 4.7% lower than in broilers of equal body weight.

Figure 5A compares the rate of energy intake (kJ·g⁻¹·h⁻¹) between photoperiods. The rate was calculated by dividing GEI by its corresponding body weight (Fig. 4A) and the number of feeding hours per 24 h. ANCOVA revealed that feeding rate per gram was influenced by photoperiod, *F*(4,

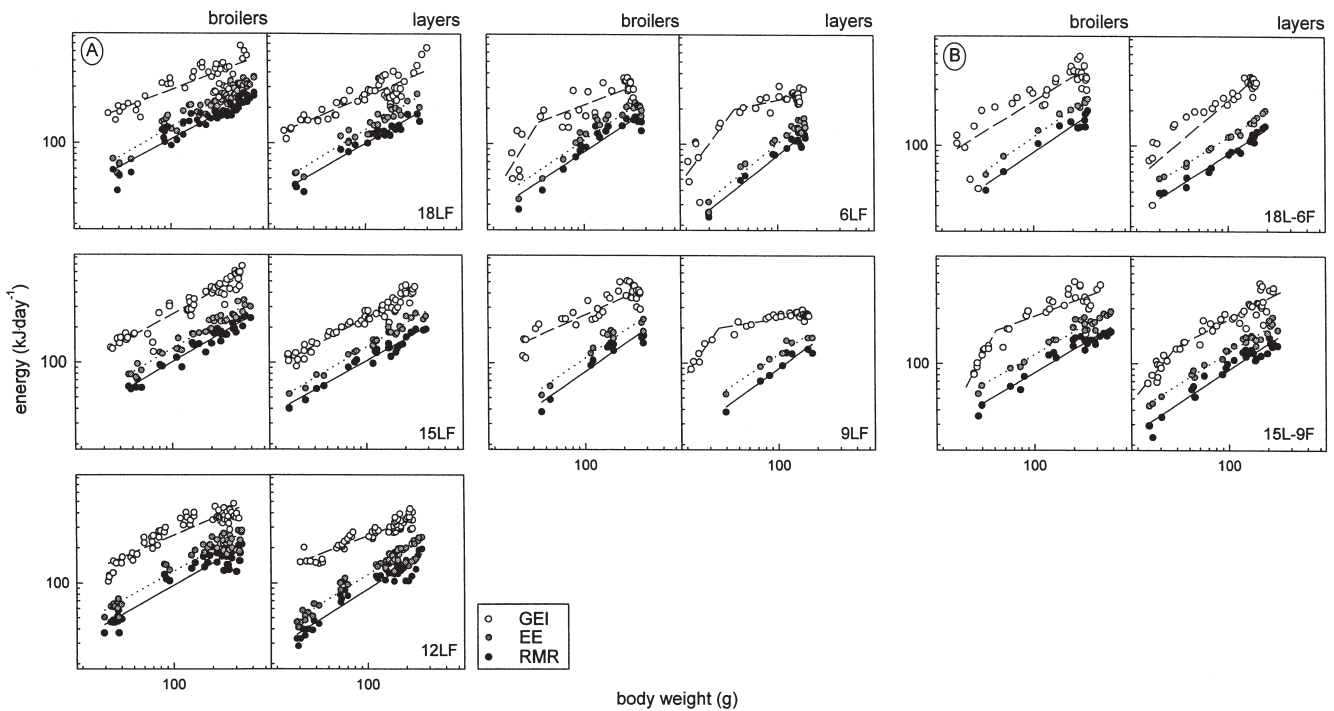


Fig. 4. Relationship between gross energy intake (GEI; kJ·day⁻¹), 24-h energy expenditure (EE; kJ·day⁻¹), and resting metabolic rate (RMR; kJ·day⁻¹), and body weight (g) in two strains of Japanese quail subjected to different photoperiods and food duration. For more details, see Fig. 1.

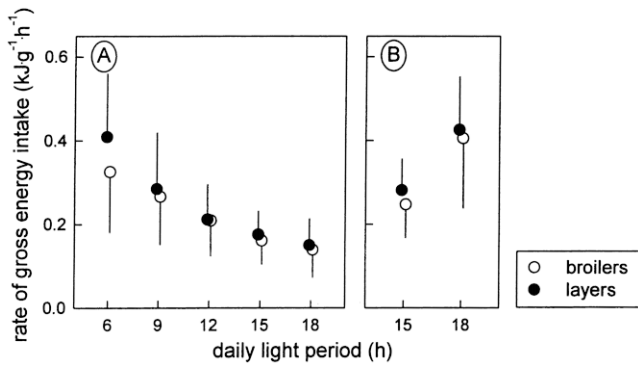


Fig. 5. Mean (\pm SD) rate of gross energy intake ($\text{kJ}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$) as a function of daily light period (h) in Japanese quail subjected to different photoperiods and food duration. For more details, see Fig. 1.

454) = 70, $p < 0.001$, and strain, $F(1, 454) = 5.8$, $p < 0.025$, with higher feeding rates at decreasing photoperiods and in layers (9.6% higher compared to broilers). The interaction term was not significant.

3.3. Energy expenditure

In Fig. 4A the 24-h energy expenditure (EE; $\text{kJ}\cdot\text{day}^{-1}$) and resting metabolic rate (RMR; $\text{kJ}\cdot\text{day}^{-1}$) are plotted as a function of body weight for the different conditions and strains. Linear regression models were fitted, because of no indications that a biphasic pattern between metabolic rate and body weight improved the fit (Fig. 4A). Also here some birds contribute multiple points to the analyses.

EE, $F(4, 289) = 8.6$, $p < 0.001$, and RMR, $F(4, 289) = 8.0$, $p < 0.001$, varied significantly with photoperiod, after correction for body weight, with higher metabolic rates at increasing photoperiods. Strain did not significantly affect EE and RMR. Only photoperiod \times body weight interaction was significant for both EE, $F(4, 289) = 5.7$, $p < 0.001$, and RMR, $F(4, 289) = 5.5$, $p < 0.001$, indicating that the slopes of the regressions between metabolic rate and body weight differed between treatments: slopes were steeper at shorter photoperiods (Fig. 4A). For an impression of the EE and RMR levels for the different conditions, we assumed parallel slopes (both 0.68) for the individual regressions of EE and RMR against body weight by assuming no photoperiod \times body weight interaction. EE level for 18LF chicks was -0.2 , 9.1, 14, and 24% higher than for chicks of equal body weight in the 15LF, 12LF, 9LF, and 6LF groups, respectively. The corresponding figures for RMR were -0.4 , 9.5, 14, and 20%.

3.4. Respiratory quotient

The mean 24-h RQ, after correction for body weight by incorporating this term as a covariate in ANCOVA, varied significantly with photoperiod, $F(4, 262) = 20$, $p < 0.001$ (Table 1). The relationship with body weight was negative (slope -0.00011 g^{-1} , $p < 0.01$), indicating a decrease in RQ when birds became heavier. No interaction term con-

tributed significantly to the explained variance. Because no effect of strain on 24-h RQ was detected, the mean 24-h RQ was compared between conditions irrespective of strain (Fig. 6A).

The RQ at the end of the dark period, after correction for body weight, varied significantly with photoperiod, $F(4, 243) = 5.4$, $p < 0.001$: RQ increased with longer photoperiods (Table 1, Fig. 6A). Photoperiod \times body weight interaction significantly increased the explained variance, $F(4, 243) = 15$, $p < 0.001$, due to a significant positive relationship between RQ and body weight in both the 9LF, $F(1, 17) = 4.9$, $p < 0.05$, and 18LF group, $F(1, 80) = 33$, $p < 0.001$. Neither strain nor other interaction terms significantly increased the explained variance.

For a better insight in how the variations in metabolic rate and RQ as a function of photoperiod are generated, we plotted for the two most extreme photoperiods (6LF and 18LF) the 24-h rhythms in metabolic rate (O_2 consumption, VO_2 ; $\text{liters}\cdot\text{h}^{-1}$) and RQ (Fig. 7). For this we used for both photoperiods the data of five broilers of around 100 g (6LF: 87 to 129 g, 18LF: 89 to 112 g). This weight is reached when rates of body weight gain are highest (Figs. 1A and 3A), and therefore, the largest effects of photoperiod can be expected. In both groups O_2 consumption levels were highly synchronized to the light–dark schedule: levels were high during the light period and decreased after lights-off (Fig. 7). Chicks of the 6LF group showed a tendency to higher O_2 levels during the light phase than 18LF birds. On the other hand, O_2 levels during the dark phase in the 6LF group were biased to lower values than in the 18LF group. The 6LF group showed a rise in O_2 consumption about 2 h prior to lights on, which was not shown by the 18LF group (Fig. 7). RQ was also highly synchronized to the light schedule with high values during the light phase and lower values during the dark phase (Fig. 7). The decrease in RQ after lights off was quick in the 18LF group, whereas 6LF chicks were able to maintain a rather high RQ during the first part of the dark

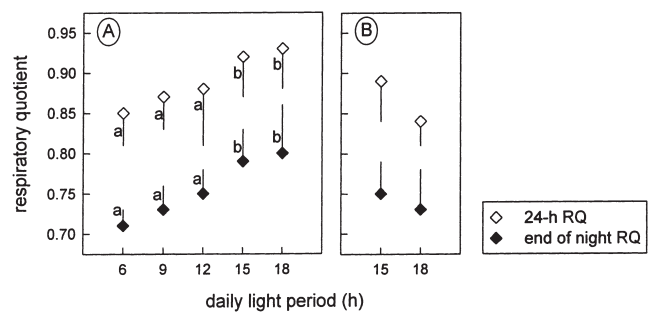


Fig. 6. Mean (\pm SD) 24-h and end-of-night RQ in relation to daily light period (h) in Japanese quail subjected to different photoperiods and food duration. For more details, see Fig. 1. Numbers within left panel (A) with the same number are not significantly (Tukey, $p > 0.05$) different from each other.

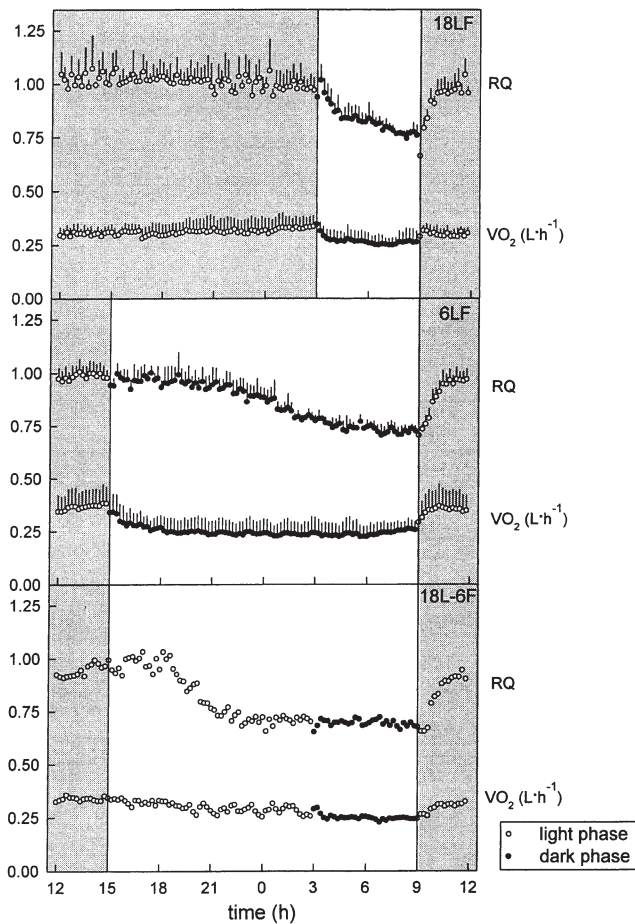


Fig. 7. The 24-h rhythms in O_2 consumption (VO_2 ; liters \cdot h $^{-1}$) and RQ for Japanese quail subjected to 18L:6D (18LF) or 6L:18D (6LF) with ad lib food during the whole light period, or 18L:6D with ad lib food during the first 6 h of the light period (18-6F). The shaded areas indicate periods of food availability. Values for the 18LF and 6LF are means, and bars indicate SDs. The values for the 18L-6F group are from one bird.

period. The RQ started to decline about 6 h after lights-off (Fig. 7). The RQ reached its lowest level after about 12 h of darkness in the 6LF group, while 18LF birds had not reached that level by the end of the dark phase.

3.5. Sexual maturity

Reaching sexual maturity was dependent on experimental condition in both strains (Table 2). Age and body weight at which the first egg was laid and egg mass of all eggs laid during the experiment were only tested for the layers: the numbers were too small for the broilers (Table 2).

3.6. Experiment 2: Food duration

To test if the effect of photoperiod on body weight gain, as found in Experiment 1, was mediated solely by the effect of photoperiod on food availability, a second experiment was conducted. In this experiment, chicks were exposed to long photoperiods (18L:6D or 15L:9D) with ad lib food during a limited part of the light period (first 6 or 9 h, re-

spectively): 18L-6F and 15L-9F, respectively. In this way these groups could be compared with the groups of Experiment 1 that were either exposed to the same photoperiod (18LF and 15LF, respectively) or the same food availability (6LF and 9LF, respectively).

3.7. Weight gain

In Fig. 1 we included with the results of Experiment 1 body weight against age for chicks subjected to limited food availability during a long photoperiod. The pattern of weight gain of these chicks showed the greatest resemblance to that of birds with the same food availability: both groups ceased to grow after food restriction was introduced at 7 days of age, and increased weight again from 9 days of age onwards (Fig. 1). This effect was clearest in the 18L-6F group, as in the 6LF group. Comparing the total body weight increase, irrespective of sex, with the groups subjected to either the same photoperiod or food availability revealed that weight increase in both strains of the 18L-6F group was significantly lower than the increase in chicks with the same light schedule (18LF), and did not differ from birds with the same food availability (6LF; Table 1 and Fig. 2). In the 15L-9F group weight increase in both strains could not be distinguished from the increase in either the 15LF or 9LF group (Table 1 and Fig. 2). The pattern of weight gain rate of the groups with limited access to food during a long light period was again more like the groups with the same food duration than like those with the same photoperiod (Fig. 3).

3.8. Gross energy intake

GEI for the groups with limited access to food during a long light period is plotted as a function of body weight at the right side of Fig. 4 (Fig. 4B). As in Experiment 1, biphasic regression models were fitted of log GEI with log body weight. Only in the 15L-9F group a biphasic allometric regression model fitted the data significantly better than a linear regression model [broilers: $F(2, 33) = 4.8, p < 0.05$; layers: $F(2, 44) = 3.4, p < 0.05$; Fig. 4B].

GEI, after correction for body weight, varied significantly with food duration when comparing chicks with restricted food availability during a long light period with birds of Experiment 1 that were subjected to the same photoperiod [15-h light phase: $F(1, 185) = 13, p < 0.001$; 18-h light period: $F(1, 159) = 9.0, p < 0.005$]; intakes were higher in birds exposed to longer feeding hours. Only treatment \times body weight interaction significantly increased the explained variance when comparing the two 18-h light period groups, $F(1, 159) = 8.3, p < 0.005$: slope between GEI and body weight was steeper for the 18L-6F group (Fig. 4). Because this interaction was not significant when comparing the two 15-h light period groups, parallel slopes (0.65) were assumed for the individual regressions of GEI against body weight. The resulting intercepts indicated that the GEI level for 15LF chicks was 9.8% higher than for 15L-9F

Table 2

Number of animals laying at 71 days of age, total number of eggs laid during the experimental period, age and body weight at the first egg, and egg mass in broilers and layers of Japanese quail exposed to different photoperiods and food duration

	Laying animals (<i>n</i>)	Eggs (<i>n</i>)	Age (day)	Body weight (g)	Egg mass (g)
Experiment 1: photoperiod					
Broilers					
18LF ¹	4 (5) ²	66	52 ± 10	334 ± 20	11.8 ± 0.9 (62) ³
15LF	6 (7)	110	45 ± 3	318 ± 25	12.1 ± 1.1 (102)
12LF	1 (5)	1	71	330	13.6 (1)
9LF	0 (6)	—	—	—	—
6LF	0 (2)	—	—	—	—
Layers					
18LF	4 (4)	93	43 ± 3 ^{**}	229 ± 24 ^a	11.0 ± 1.4 (92) ^a
15LF	5 (5)	115	43 ± 5 ^a	214 ± 9 ^a	11.5 ± 2.0 (103) ^a
12LF	2 (3)	38	48 ± 1 ^a	226 ± 14 ^a	11.3 ± 0.9 (38) ^a
9LF	0 (3)	—	—	—	—
6LF	0 (8)	—	—	—	—
Experiment 2: food duration					
Broilers					
15L-9F	1 (5)	15	56	401	14.6 ± 0.9 (14)
18L-6F	1 (1)	2	69	241	10.4 ± 0.4 (2)
Layers					
15L-9F	7 (8)	127	48 ± 2A ^{**}	194 ± 25 ^a	11.3 ± 8.7 (110) ^a
18L-6F	7 (11)	84	56 ± 8 ^b	166 ± 11 ^b	9.4 ± 0.9 (78) ^b

Values are means ± SD.

¹For definitions, see the Materials and methods section.

²Numbers in brackets indicate total amount of females per group.

³Numbers in brackets indicate total amount of unbroken eggs.

*Numbers with the same letter within Experiment 1 are not significantly (Tukey, $p > 0.05$) different from each other.

**Numbers of the 15L-9F and 18L-6F group with the same letter as the groups with the same photoperiod in Experiment 1 are not significantly (t -test, $p > 0.05$) different from each other.

chicks of equal body weight. For none of the comparisons did strain increase the explained variance after correction for body weight.

Comparing GEI between the groups of both experiments with the same food availability, ANCOVA only revealed a significant photoperiod effect, after correction for body weight, when comparing the groups with a daily 6-h feeding period, $F(1, 133) = 6.8, p < 0.025$. None of the possible interaction terms significantly increased the explained variance. Therefore, parallel slopes (0.72) were assumed for the individual regression of GEI against body weight, and calculated that the GEI level for the 6LF chicks was 16% reduced compared to 18L-6F chicks of equal body weight. No difference in GEI between the two strains after correction for body weight was detected.

Energy intake rates (for calculation, see results Experiment 1) for both groups are plotted in the right panel of Fig. 5. In both strains the intake rates were highest in chicks subjected to daily feeding hours of 9 h or less, irrespective of photoperiod. In broilers, the intake rate was significantly higher in the 18L-6F group compared to the 6LF group (24%; Fig. 5).

3.9. Energy expenditure

For each treatment and strain linear regression models were fitted between metabolic rate and body weight, because there were no indications that a biphasic pattern be-

tween metabolic rate and body weight would improve the fits (Fig. 4B). For more details, see Experiment 1. Comparing EE between the groups of both experiments with the same photoperiod showed that, after correction for body weight, EE varied significantly with food duration [15-h light period: $F(1, 108) = 23, p < 0.001$; 18-h light period: $F(1, 117) = 6.3, p < 0.025$]: EE was higher in the groups with longer feeding hours (Fig. 4). Food duration × body weight interaction significantly increased the explained variance, $F(1, 117) = 4.1, p < 0.05$, when comparing the two 18-h light period groups: slope was steeper in the group with limited food availability (18L-6F). This interaction term did not improve the explained variance when comparing the two 15-h light period groups. Parallel slopes (0.67) were, therefore, assumed for the individual regressions of EE against body weight for this comparison. Intercepts showed that the EE level for the 15LF group was 9% higher than the level for 15L-9F chicks of equal body weight. For none of the comparisons did strain or other possible interaction terms significantly increase the explained variance. RMR also varied significantly with food duration after correction for body weight [15-h light period: $F(1, 108) = 46, p < 0.001$; 18-h light period: $F(1, 116) = 13.2, p < 0.001$]: RMR was higher in the groups with longer feeding hours (Fig. 4). Of the other possible effects, strain, $F(1, 116) = 5.1, p < 0.05$, and treatment × body weight interaction, $F(1, 116) = 870, p < 0.01$, significantly improved the explained variance in RMR when comparing the two 18-h light period groups: RMR level was

4% higher for broilers than layers of equal body weight, and slope of RMR against body weight was steeper in the 18L-6F group. Because photoperiod \times body weight interaction was not significant when comparing the two 15-h light period groups, parallel slopes (0.67) were assumed for the individual regressions of RMR against body weight. This yielded a 17% higher RMR level for 15LF chicks compared to 15L-9F chicks of equal body weight.

Comparing EE and RMR between the groups of both experiments with the same food availability, ANCOVA only revealed an effect of photoperiod on EE, after correction for body weight, when comparing the two groups with a daily 6-h feeding period, $F(1, 68) = 819, p < 0.001$. None of the other effects improved the explained variance in EE. Parallel slopes (0.79) were assumed for the individual regressions for EE against body weight, showing that EE level for 6LF chicks was 14% reduced compared to the level for 18L-6F chicks of equal body weight.

3.10. Respiratory quotient

Comparing mean 24-h RQ between the groups of both experiments with equal photoperiod revealed that, after correction for body weight, 24-h RQ varied significantly with food duration [15-h light period: $F(1, 80) = 14, p < 0.001$; 18-h light period: $F(1, 115) = 71, p < 0.001$]: RQ was higher in birds with longer feeding hours (Table 1 and Fig. 6). There was no difference in mean 24-h RQ when comparing the groups with equal food availability but different photoperiod. For none of the comparisons did strain or the interaction terms significantly increase the explained variance.

The RQ at the end of the dark phase, after correction for body weight, varied significantly with food duration when comparing the groups with equal photoperiod [15-h light period: $F(1, 81) = 18, p < 0.001$; 18-h light period: $F(1, 108) = 47, p < 0.01$]: RQ was higher in birds exposed to longer feeding hours (Table 1 and Fig. 6). The RQ at the end of the dark phase varied significantly with photoperiod when comparing the groups with equal food availability [6-h feeding period: $F(1, 63) = 23, p < 0.001$; 9-h feeding period: $F(1, 59) = 8, p < 0.01$]: RQ was higher in birds subjected to a longer photoperiod (Table 1 and Fig. 6). Neither strain nor the interaction terms significantly increased the explained variance in all comparisons.

As in Experiment 1, the 24-h rhythms in O_2 consumption ($\text{liter}\cdot\text{h}^{-1}$) and RQ were plotted of the group of Experiment 2 with the same photoperiod and food availability as the groups plotted in Fig. 7. For this, data were used of one broiler of about 100 g (comparable to Experiment 1). The O_2 level in this bird was synchronized to the light–dark schedule: levels remained high during the light period even though food was removed at 1500 h, and levels dropped during the dark period. As in the 6LF group this bird was able to maintain a high RQ level at the beginning of the fasting period. However, already after 4 h there was a pronounced decrease in RQ, and the lowest value was reached almost 3 h earlier than in the 6LF group (Fig. 7).

3.11. Sexual maturity

The time at which sexual maturity is reached was modulated by food availability (Table 2). Females of the 18L-6F group did reach sexual maturity despite food restriction, but at a later age and at a lower body weight. These birds also showed a tendency to produce smaller eggs. These effects were either absent or less clear in the 15L-9F group (Table 2).

4. Discussion

This experiment showed that photoperiod, by determining the period in which daily activity and feeding can occur, had major effects on body weight gain in young birds. Experiment 1 demonstrated that longer photoperiods are related with both higher energy intake and energy expenditure levels, resulting in larger weight gains. The photoperiod below which detrimental effects on weight gain were made visible was 9L:15D for both strains. Possibly, a 9-h light period is just long enough to compensate for a reduction in energy intake by an almost equivalent decrease in energy expenditure, resulting in weight gains comparable to values found at longer light periods. Experiment 2 showed that this effect of photoperiod on body weight gain is mainly due to the effect of photoperiod on food availability. Weight gain in birds with access to food during 6 h of an 18-h light period showed a pattern that was comparable to the group with the same food availability (6LF), but not with the same photoperiod (18LF). Photoperiod also significantly influenced sexual maturation, while food restriction seemed to delay, but not inhibit this process.

Net weight gain is the result of a positive balance between energy intake and energy expenditure. By manipulating photoperiod (Experiment 1), both daily energy intake and expenditure were influenced, with consequences for overall weight gain (Fig. 2). A reduction in photoperiod to 9L:15D or less affected body weight most during the first 2 days of the experiment (Fig. 1). During this period the birds lost weight or body weight remained the same. After that weight increased again, and during the third week of the experiment, no difference in average rate of weight gain was visible between the different photoperiods (Fig. 3). This recovery in body weight gain was mainly accomplished by adjustments in feeding behavior. Already on the second day of the experiment 6LF and 9LF birds started to exploit their crop as a temporary storage place for food. This food was mobilized when no food was present, as was evident from the maintenance of a high RQ during the first part of the dark period by the 6LF group (Fig. 7). In this way the birds managed to consume more food than would be expected on the basis of time reduction only, and were able to gain weight continuously after the initial drop in weight gain. They were, however, unable to increase their food intake to such an extent that they consumed the same amount or more as birds subjected to light periods of at least 12 h. Crop (and digestive tract) filling is a generally adopted feeding strategy by birds possess-

ing a crop that enables them to tide over prolonged fasting periods [1,2,5,14,28,41]. The effect of photoperiod on food intake found here was opposite to the effect of photoperiod on food intake as found in pigeons that were gradually transferred from a 12-h to a 3-h light period with only ad lib food during the light period: food intake increased when the birds were gradually subjected to shorter light periods [2]. These animals were, however, full grown, with lower feeding rates than the chicks investigated here. It is, therefore, possible that these birds did not experience a daily feeding period of only 3 h as time limited and were able to increase their food intake even during such a short period.

The effect of photoperiod on energy intake induced also diurnal fluctuations in metabolic status, as shown by the 24-h rhythms in RQ (Fig. 7). The mean 24-h RQ showed that birds subjected to 15L:9D and 18L:6D were mainly metabolizing carbohydrates (RQ > 0.9). These chicks maintained an overall positive energy balance, which allowed for continuous body weight increase. However, when photoperiod decreased to 12L:12D or less the mean 24-h RQ dropped below 0.9, indicating that birds relied for a larger part of the 24-h period on body reserves (fat) for energy (Fig. 7). In this postabsorptive state the energy balance becomes negative, resulting in either a cessation of weight gain or weight loss during a (large) part of the dark period. These birds show a discontinuous growth curve: body weight increase during the light phase, and part of the dark phase, alternates with a cessation of weight gain or weight loss during the rest of the dark period. Overall, birds were clearly in a net positive energy balance as they grew over the experimental period. The amplitude of weight gain and loss should become higher when the photoperiod decreases, with less overall weight gain. The mean RQ over the last half hour of the dark period confirmed this finding. Several studies in rats and birds have shown that the RQ drops dramatically at the end of a fasting period [2,19,31,40]. This drop in RQ results from the depletion of nutrients for fuel for energy metabolism, which leads to the catabolism of fat stores [31]. Our results showed that a daily feeding period of 12 h or less is too short to enable quail chicks to store enough food in their crop (and digestive tract) to prevent them from reaching a postabsorptive state during the next dark (fasting) period.

The 24-h energy expenditure (EE) and resting metabolic rate (RMR) were both positively correlated with photoperiod: longer photoperiods create more possibilities for locomotor and feeding activities, the main parameters determining metabolic rate. RMR was calculated as the lowest value of a 30-min running mean over the last 24 h of the energy measurement. This value is reached during the dark period in animals active during the light period. Comparing the 24-h O₂ consumption rhythms of the two most extreme photoperiods (6:18D and 18L:6D; Fig. 7) showed that a short photoperiod was associated with a high-amplitude cycle in metabolic rate: higher expenditure levels during the light phase and lower levels during the dark phase compared to 18LF

chicks, which resulted in lower RMR values in the 6LF group. Because of the long dark period, this high-amplitude in metabolic rate resulted in a lower EE: lower values during a long dark period more than compensated for higher levels during a short light period. Shorter dark periods, on the other hand, leave less time for the subsidence of after-effects of food intake and activity during the light phase, resulting in both higher RMR and EE levels. By incorporating the mean body weight for all ages (Fig. 1) into the regression models for both GEI and EE (Fig. 4), we estimated, via extrapolation, GEI and EE at every age (7–71 days) for all photoperiods. Subsequently, all results were added together to a total figure for both GEI and EE per photoperiod over the total experimental period (Fig. 8). In broilers, the effect of photoperiod on net energy balance is mainly achieved via changes in GEI: the decrease in GEI from 18L:6D to 6L:18D was 37%, while EE decreased with 33%. The corresponding values for layers were 22 and 34%, suggesting that birds that are not selected for high levels of food intake influence their net energy balance more by changing their expenditure levels. GEI appeared to reach its highest level at 15L:9D in broilers, and 12L:12D in layers. These variations in GEI and EE as a function of photoperiod suggest that 15L:9D is most beneficial for body weight gain in broilers, as was implied by the total weight gain (Fig. 2). In layers, it is less clear. The net energy balance seemed most positive at a 12-h light period, while total body weight increase was not highest at this point (Fig. 2).

Apart from a decrease in nocturnal metabolic rates and crop exploitation, a rise in O₂ consumption prior to lights on, as shown by 6LF chicks (Fig. 7), may also be considered as an adaptive strategy to deal with food restriction. Both mammals and birds when subjected to restricted feeding regimes

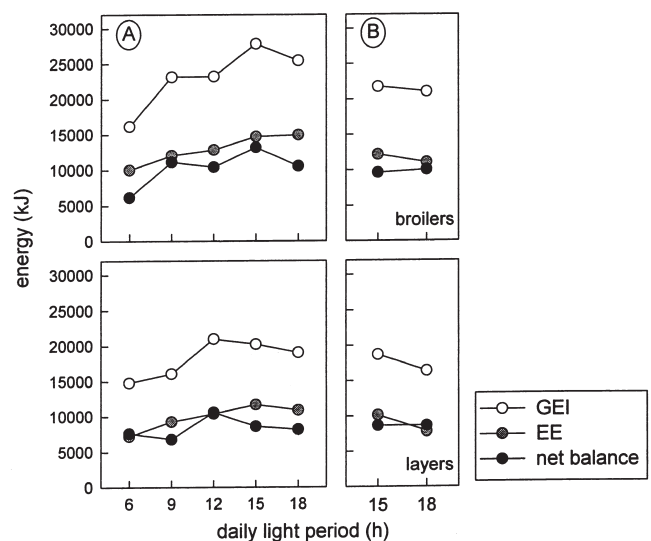


Fig. 8. Overall gross energy intake (GEI; kJ), 24-h energy expenditure (EE; kJ), and net balance (net balance; kJ) as a function of daily light period (h) in Japanese quail exposed to different photoperiods and food duration. For more details, see Fig. 1.

show increased levels of various response measures as feeding time approaches. Rats, for example, show increased levels of locomotor activity [22,26], and pigeons increase their levels of O₂ consumption and body temperature [2,31]. These increased levels may be an indicator for the activation of several processes in the body in anticipation of food arrival. For example, the anticipatory rise in O₂ consumption and body temperature prior to feeding may, apart from increased locomotor activity, be the result of increased enzyme and/or duodenal activity [8,34,36]. In this way, a high efficiency of food digestion may be accomplished. Possibly, the increase in metabolic rate prior to feeding in chicks subjected to long fasting periods is an indication of an increased readiness for food intake, resulting in a more efficient use of nutrients. Lower nocturnal energy levels during longer dark periods (Fig. 7) are possibly associated with lower body temperatures, as shown in pigeons [2,31]. This suggests that metabolic processes are turned down. Entering a new feeding period from a low metabolic position may reduce the efficiency with which food can be utilized during the following feeding period. To make optimal use of the feeding period the birds may raise metabolic processes preceding food access. We did not distinguish if this anticipatory rise in O₂ consumption was due to anticipation to light or feeding. However, in pigeons, the rise in O₂ consumption also appeared before a meal when this did not coincide with lights on, indicating that birds are able to anticipate feeding times irrespective of light [10].

Photoperiod also affected sexual development: 6LF and 9LF birds did not reach sexual maturity at 71 days of age. In quail, sexual development is known to depend on the length of the daily light period [4,10,15,27,39]: long photoperiods, from 12L:12D onwards [10], stimulate sexual maturation, while short photoperiods inhibit [4,10,15,27] or delay sexual maturation [39], depending on how long birds were followed. In this study short photoperiods inhibited sexual maturation. Female Japanese quail do reach sexual maturation when exposed to 6L:18D, but only at ages over 115 days [39]. Therefore, photoperiod may have delayed rather than prevented sexual development. Sexual maturity also influenced body weight gain in female chicks. Females that did not reach sexual maturity remained as small as males.

Broilers grew faster than layers, irrespective of experimental condition (Figs. 2 and 3). Broilers, selected for high food intake, were expected to be more sensitive to reductions in photoperiod, and consequently, food availability, than layers. There was no evidence for a difference in sensitivity, as photoperiod \times strain interaction did not contribute to the explained variance in weight gain (Fig. 2). Broilers had higher GEI levels, even after correction for body weight. Because EE after correction for body weight did not differ between the strains, the higher GEI explains the higher rate of weight gain in broilers.

Experiment 1 showed that photoperiod had a major effect on body weight gain by influencing both energy intake and energy expenditure. To separate the effect of photoperiod from that of food duration, Experiment 2 was conducted. This

experiment showed that the effect of photoperiod on overall weight gain was mediated by the effect of photoperiod on food availability: overall weight gain in the 18L-6F group was equal to that of the group with the same food availability (6LF), and lower than that of the group with the same photoperiod (18LF) in Experiment 1. Also, the mean 24-h RQ seemed to indicate that the effect of photoperiod on body weight gain was realized via food availability: the overall 24-h digestive activity of 18L-6F chicks did not differ from that of 6LF birds. The way in which the same overall weight gain was achieved in these two groups showed that photoperiod did have an effect on energy intake and expenditure independent of food availability. Photoperiod, irrespective of food duration, induced both higher energy intake and expenditure levels, resulting in similar overall weight gains. The higher EE as a consequence of 12 h extra light without food may have induced higher energy intake levels by increasing energy requirements (Fig. 7). These effects of photoperiod on GEI and EE were not clear when comparing the 15L-9F group with the 9LF group. Birds subjected to a 9-h feeding period showed a normal weight gain curve (Fig. 1). Interestingly, exposure to an 18-h light period allowed birds to reach sexual maturity at lower body weights, despite restricted feeding regimes. The short-photoperiod response in sexual maturation is not mediated by the food restriction imposed by photoperiod. After maturation, the birds laid slightly smaller eggs, associated with their reduced body weight (Table 2).

In conclusion, the experiment showed that changes in feeding behavior and energy expenditure, in response to photoperiod and food availability manipulations, are part of a general strategy in chicks to maximize energy intake and minimize energy expenditure that enables them to gain weight continuously. When the daily light period, and consequently the feeding period, decreased to 9 h the reduction in energy intake could be compensated by a reduction in energy expenditure. When photoperiod was reduced further, the fasting period became too long to compensate the decrease in energy intake by a beneficial effect of a shorter light period on energy expenditure. These birds, therefore, showed retardation in weight gain compared to quail exposed to longer photoperiods.

Acknowledgment

This project was supported by grants from the Institute for Technical Sciences (STW, Grant GBI22.2743) and the Institute for Life Sciences (SLW, Grant 805.30.752), which are both funded by The Netherlands Organization for Scientific Research (NWO). Dr. F. R. Leenstra (Institute for Animal Science and Health, ID-DLO, The Netherlands) generously provided the food for the experiment.

References

- [1] Barash I, Nitsan Z, Nir I. Adaptation of light-bodied chicks to meal feeding: gastrointestinal tract and pancreatic enzymes. *Br Poult Sci* 1993;34:35–42.

- [2] Basco PS, Rashotte ME, Stephan FK. Photoperiod duration and energy balance in the pigeon. *Physiol Behav* 1996;60:151–9.
- [3] Boon P, Visser H, Daan S. Effect of photoperiod on body mass, and daily energy intake and energy expenditure in young rats. *Physiol Behav* 1997;62:913–9.
- [4] Brain PC, Onagbesan OM, Peddie MJ, Taylor TG. Changes in plasma concentrations of reproductive steroids in female Japanese quail (*Coturnix coturnix japonica*) raised on long or short photoperiods. *Gen Comp Endocrinol* 1988;69:174–80.
- [5] Buysse J, Adelsohn DS, Decuyper E, Scanes CG. Diurnal-nocturnal changes in food intake, gut storage of ingesta, food transit time and metabolism in growing broiler chickens: a model for temporal control of energy balance. *Br Poult Sci* 1993;34:699–709.
- [6] Charles RG, Robinson FE, Hardin RT, Yu MW, Feddes J, Classen HL. Growth, body composition, and plasma androgen concentration of male broiler chickens subjected to different regimens of photoperiod and light intensity. *Poult Sci* 1992;71:1595–605.
- [7] Classen HL, Riddell C, Robinson FE, Shand PJ, McCurdy AR. Effect of lighting treatment on the productivity, health, behaviour and sexual maturity of heavy male turkeys. *Br Poult Sci* 1994;35:215–25.
- [8] Comperatore CA, Stephan FK. Entrainment of duodenal activity to periodic feeding. *J Biol Rhythms* 1987;2:227–42.
- [9] Dunn IC, Sharp PJ. Photoperiodic requirements for LH release in juvenile broiler and egg-laying strains of domestic chickens fed ad libitum or restricted diets. *J Reprod Fertil* 1990;90:329–36.
- [10] Follett BK, Maung SL. Rate of testicular maturation, in relation to gonadotrophin and testosterone levels, in quail exposed to various artificial photoperiods and to natural daylengths. *J Endocrinol* 1978;78:267–80.
- [11] Gebhardt-Henrich SG, Marks HL. Heritabilities of growth curve parameters and age-specific expression of genetic variation under two different feeding regimes in Japanese quail (*Coturnix coturnix japonica*). *Genet Res Camb* 1993;62:45–55.
- [12] Gessaman JA, Nagy KA. Energy metabolism: errors in gas-exchange conversion factors. *Physiol Zool* 1988;61:507–13.
- [13] Hill RW. Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. *J Appl Physiol* 1972;33:261–3.
- [14] Jackson S, Duke GE. Intestine fullness influences feeding behavior and crop filling in the domestic turkey. *Physiol Behav* 1995;58:1027–34.
- [15] King VM, Bentley GE, Follett BK. A direct comparison of photoperiodic time measurement and the circadian system in European starlings and Japanese quail. *J Biol Rhythms* 1997;12:431–42.
- [16] Koops WJ, Grossman M. Multiphasic allometry. *Growth Dev Aging* 1993;57:183–92.
- [17] Kwakkel RP, Ducro BJ, Koops WJ. Multiphasic analysis of growth of the body and its chemical components in white leghorn pullets. *Poult Sci* 1993;72:1421–32.
- [18] Larkin LM, Moore BJ, Stern JS, Horwitz BA. Effect of photoperiod on body weight and food intake of obese and lean Zucker rats. *Life Sci* 1991;49:735–45.
- [19] Le Magnen J, Devos M. Metabolic correlates of the meal onset in the free food intake of rats. *Physiol Behav* 1970;5:805–14.
- [20] Lewis PD, Perry GC, Morris TR. Effect of constant and of changing photoperiods on age at first egg and related traits in pullets. *Br Poult Sci* 1996;37:885–94.
- [21] Macleod MG, Tullett SG, Jewitt TR. Circadian variation in the metabolic rate of growing chickens and laying hens of a broiler strain. *Br Poult Sci* 1980;21:155–9.
- [22] Mistlberger RE. Anticipatory activity rhythms under daily schedules of water access in the rat. *J Biol Rhythms* 1992;7:149–60.
- [23] Nagy TR, Negus NC. Energy acquisition and allocation in male collared lemmings (*Dicrostonyx groenlandicus*): effects of photoperiod, temperature, and diet quality. *Physiol Zool* 1993;66:537–60.
- [24] Negus NC, Berger PJ, Brown BW. Microtine population dynamics in a predictable environment. *Can J Zool* 1986;64:785–92.
- [25] Norusis MJ. SPSS/PC+ V3.0 for the IBM PC/XT/AT and PS/2. Chicago: SPSS Inc., 1988.
- [26] Ono M, Shibata S, Minamoto Y, Watanabe S. Effect of the noncompetitive *N*-methyl-D-aspartate (NMDA) receptor antagonist MK-801 on food-anticipatory activity rhythm in the rat. *Physiol Behav* 1996;59:585–9.
- [27] Oruwari BM, Brody T. Roles of age, body weight and composition in the initiation of sexual maturation of Japanese quail (*Coturnix coturnix japonica*). *Br Poult Sci* 1988;29:481–9.
- [28] Powers DR. Diurnal variation in mass, metabolic rate, and respiratory quotient in Anna's and Costa's Hummingbirds. *Physiol Zool* 1991;64:850–70.
- [29] Prabakaran R, Abdul-Mujeer K, Ahmed M, Thangavel A, Sundararasu V. Effect of photoperiod on the laying performance of Japanese quails. *J Vet Anim Sci* 1991;22:5–8.
- [30] Prabakaran R, Babu M, Sundararasu V. Effect of photoperiod on the growth performance of Japanese quails. *J Vet Anim Sci* 1991;22:9–11.
- [31] Rashotte ME, Basco PS, Henderson RP. Daily cycles in body temperature, metabolic rate, and substrate utilization in pigeons: influence of amount and timing of food consumption. *Physiol Behav* 1995;57:731–46.
- [32] Ricklefs RE. Patterns of growth rate in birds. II. Growth rate and mode of development. *Ibis* 1973;115:177–201.
- [33] Ricklefs RE. Growth rates of birds in the humid new world tropics. *Ibis* 1976;118:179–207.
- [34] Saito M, Murakami E, Nishida T, Fujisawa Y, Suda M. Circadian rhythms of digestive enzymes in the small intestine of the rat. II. Effects of fasting and refeeding. *J Biochem* 1976;80:563–8.
- [35] Schanbacher BD, Crouse JD. Photoperiodic regulation of growth: a photosensitive phase during light-dark cycle. *Am J Physiol* 1981;241:E1–5.
- [36] Schwartz DH, Hernandez L, Hoebel BG. Serotonin release in lateral and medial hypothalamus during feeding and its anticipation. *Brain Res Bull* 1990;25:797–802.
- [37] Siopes TD, Pyrzak R. Effect of intermittent lighting on the reproductive performance of first-year and recycled turkey hens. *Poult Sci* 1990;69:142–9.
- [38] Spears N, Clarke JR. Effect of male presence and of photoperiod on the sexual maturation of the field vole (*Microtus agrestis*). *J Reprod Fertil* 1986;78:231–8.
- [39] Stein GS, Bacon WL. Effect of photoperiod upon age and maintenance of sexual development in female *Coturnix coturnix japonica*. *Poult Sci* 1976;55:1214–8.
- [40] Sugano Y. Heat balance of rats acclimated to diurnal 2-hour feeding. *Physiol Behav* 1983;30:289–93.
- [41] Tiebout HM. Tests of a model of food passage rates in hummingbirds. *Auk* 1989;106:203–8.
- [42] Wade GN, Bartness TJ. Seasonal obesity in Syrian hamsters: effects of age, diet, photoperiod, and melatonin. *Am J Physiol* 1984;247:R328–34.
- [43] Wingfield JC, Hahn TP, Wada M, Schoech SJ. Effects of day length and temperature on gonadal development, body mass, and fat depots in white-crowned sparrows, *Zonotrichia leucophrys pugetensis*. *Gen Comp Endocrinol* 1997;107:44–62.