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To cite this article: Allison C. Veronda, Christopher E. Kline & Leah A. Irish (2022) The impact of circadian timing on energy balance: an extension of the energy balance model, Health Psychology Review, 16:2, 161-203, DOI: [10.1080/17437199.2021.1968310](https://doi.org/10.1080/17437199.2021.1968310)

To link to this article: <https://doi.org/10.1080/17437199.2021.1968310>



Published online: 19 Aug 2021.



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The impact of circadian timing on energy balance: an extension of the energy balance model

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ABSTRACT

A significant proportion of the population is classified as having overweight or obesity. One framework which has attempted to explain biobehavioral mechanisms influencing the development of overweight and obesity is the energy balance model. According to this model, the body continually attempts to balance energy intake with energy expenditure. When energy intake and energy expenditure become imbalanced, there is an increase in homeostatic and allostatic pressure, generally to either increase energy intake or decrease energy expenditure, so as to restore energy homeostasis. Recent research has indicated that circadian aspects of energy intake and energy expenditure may influence energy balance. This paper provides a narrative review of existing evidence of the role of circadian timing on components of energy balance. Research on the timing of food intake, physical activity, and sleep indicates that unhealthy timing is likely to increase risk of weight gain. Public health guidelines focus on *how much* individuals eat and sleep, *what* foods are consumed, and the *type* and *frequency* of exercise, but the field of circadian science has begun to demonstrate that *when* these behaviors occur may also influence overweight and obesity prevention and treatment efforts.

ARTICLE HISTORY

Received 11 August 2020
Accepted 9 August 2021

KEYWORDS

Energy balance; timing of food intake; sleep timing; physical activity timing; obesity

Obesity is a significant public health concern: 42.4% United States adults have obesity (body mass index (BMI) ≥ 30.0 kg/m²) (Hales et al., 2020), and an additional 33% of adults are classified as having overweight (BMI of 25.0–29.9 kg/m²) (Flegal et al., 2016). Individuals who have overweight or obesity are at risk for numerous negative health consequences, including hypertension, type 2 diabetes, depression, and all-cause mortality (Flegal et al., 2013; Hruby & Hu, 2015). Given the array of adverse health effects associated with overweight and obesity, decades of research have sought to elucidate the biobehavioral factors influencing overweight and obesity development, which can then inform effective overweight and obesity prevention and treatment strategies.

The energy balance model is one such theoretical framework which has been developed to understand physiological and behavioral factors which lead to obesity. This model posits that the body continually attempts to maintain its fat stores through a coordinated balance between energy intake and energy expenditure (Schwartz et al., 2003; Woods et al., 1998). While there is some evidence of a more dynamic process involved in energy balance (Manore et al., 2017), a balance between energy intake and energy expenditure is the foundation of the energy balance model at its most basic level. When the body detects that energy intake and energy expenditure are unbalanced, this sets off a coordinated network of physiological and behavioral changes to restore

balance. These physiological and behavioral changes consist of both homeostatic and allostatic processes (McEwen & Wingfield, 2010). Homeostatic processes allow the body to maintain homeostasis, i.e., relatively constant levels of physiological factors necessary for sustaining life, such as body temperature and blood pH. Alternatively, allostatic processes involve allostasis, defined as stability through change. Allostatic processes can thus involve a larger magnitude of changes that help the body adapt to unpredictable changes, such as increased cortisol levels. Figure 1 provides an overview of the ways in which the body imparts homeostatic and allostatic pressure to either increase energy intake or decrease energy expenditures so as to restore energy balance, i.e., to ensure energy intake and energy expenditure are balanced (Schwartz et al., 2003).

Various physiological, psychological, and behavioral factors are involved in maintaining energy balance through their role in energy intake. Physiological factors which contribute to energy intake include leptin, ghrelin, and insulin, and psychological factors include hunger, appetite, and satiety. Leptin is a hormone released by adipose tissue which signals the hypothalamus to stop energy intake. Ghrelin is a hormone primarily released by the stomach, which signals the hypothalamus to increase appetite, encouraging energy intake. Insulin is a pancreatic hormone that plays a vital role in maintaining blood glucose levels. The amount of glucose in blood rises after food intake. This increase in blood glucose triggers the release of insulin, which allows cells to either convert glucose into energy or store it for later use, thereby keeping blood glucose levels stable. A behavioral factor which contributes to energy intake is food intake. Major classes of nutrients which may be consumed during food intake are carbohydrates, fats, and proteins. Carbohydrates and fats provide the body with energy, and protein is important for the growth and repair of bodily tissues. Both physiological and behavioral changes may occur to increase or decrease energy intake (for reviews, see Hall et al., 2012; Hill et al., 2013; Keeseey & Powley, 2008; Lenard & Berthoud, 2008; Schwartz et al., 2003). Physiological changes that may occur to increase energy intake include decreases in leptin and increases in ghrelin levels, decreases in insulin, increases in hunger and appetite, and decreases in satiety, and a behavioral change aimed at increasing energy intake is increased food intake (Schwartz et al., 2003). It should also be acknowledged that food choice, which is not under biological or homeostatic and allostatic control, also plays a role in determining food and macronutrient intake. When there is homeostatic and allostatic pressure to reduce energy intake, reciprocal biological and physiological processes typically occur (e.g., increases in leptin levels, decreased food intake).

Similarly, physiological and behavioral factors are involved in maintaining energy balance through their role in energy expenditure. Physiological components of energy expenditure include respiratory quotient, resting metabolic rate, and the thermic effect of food. The body's respiratory quotient is the ratio of the volume of CO₂ produced by the body to the volume of O₂ used by the body. Resting

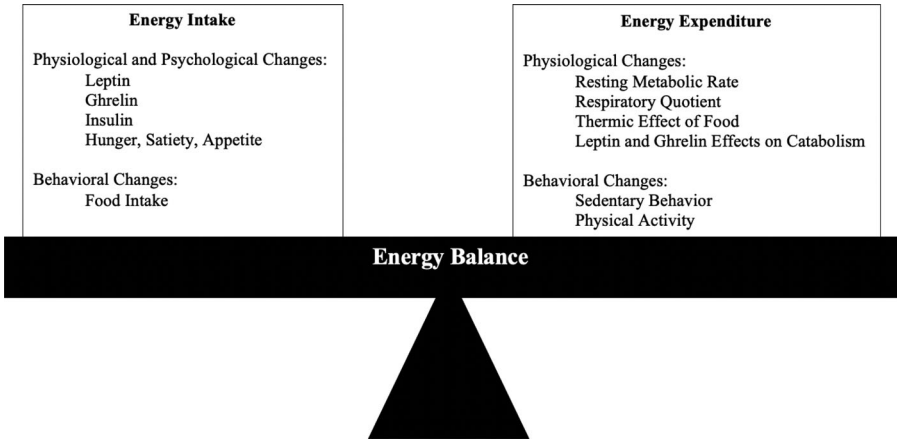


Figure 1. Diagram of energy balance model depicting physiological, behavioral, and psychological changes aimed at balancing energy intake and energy expenditure.

metabolic rate is the largest proportion of energy expenditure; this term refers to the rate at which the body uses energy when it is at rest. The thermic effect of food refers to the energy required to ingest, digest, absorb, and store energy intake. Behavioral aspects of energy expenditure sedentary behavior and physical activity. Sedentary behavior is defined as any waking behavior that is characterized by low energy expenditure (i.e., ≤ 1.5 metabolic equivalents) performed while in a seated or lying posture (e.g., reading, watching television) (Tremblay et al., 2017). Physical activity, on the other hand, is any bodily movement that increases energy expenditure; it is commonly subcategorized into light, moderate, or vigorous physical activity based upon the perceived effort and energy expended. Thus, physiological and behavioral changes may also occur to either increase or decrease energy expenditure in response to homeostatic and allostatic pressure (for reviews, see Hall et al., 2012; Hill et al., 2013; Keeseey & Powley, 2008; Lenard & Berthoud, 2008; Schwartz et al., 2003). Physiological adaptations to decrease energy expenditure may include an increased respiratory quotient, alowered resting metabolic rate, and decreased thermic effect of food, while behavioral changes aimed at decreasing energy expenditure consist of increased sedentary behavior and decreased time spent in moderate to vigorous physical activity. Opposite behavioral and biological changes generally occur in response to homeostatic and allostatic pressures to increase energy expenditure (e.g., increased resting metabolic rate, decreased sedentary behavior).

Despite this sophisticated system of homeostatic and allostatic processes, energy imbalances do occur over time, and these imbalances alter body weight as well as health. If, over time, energy expenditure exceeds energy intake (i.e., negative energy balance), individuals lose weight. Alternatively, if energy intake chronically exceeds energy expenditure (i.e., positive energy balance), individuals gain weight. Likely because of the evolutionary advantage of engaging in behaviors that prevent starvation, this system tends to favor weight gain in the modern obesogenic environment, in which individuals are eating, sleeping, working, and socializing throughout the 24-h day (Greenway, 2015; Schwartz et al., 2003). Thus, the advent of this 24-h society has indicated that *when* behaviors occur may also be important to consider in relation to energy balance, health, and obesity risk.

Recent research seems to indicate that circadian aspects of energy intake and energy expenditure influence energy balance. To date, reviews have focused on links between genetic components of the circadian system and metabolism (e.g., Bass & Takahashi, 2010; Hurley et al., 2016; Kim et al., 2019; Lekkas & Paschos, 2019). Other reviews have examined links between metabolic processes, circadian processes, and individual behaviors related to energy balance (Chaput et al., 2020; Longo & Panda, 2016; Manoogian & Panda, 2017; Melkani & Panda, 2017; Serin & Acar Tek, 2019) while neglecting other behaviors which likely contribute to energy balance. This paper will provide a narrative review and critical analysis of existing evidence of the role of circadian timing of food intake, physical activity, and sleep behaviors on components of energy balance. In particular, this paper will examine homeostatic and allostatic processes that allow the body to adapt in an effort to restore balance. Thus, our paper builds upon existing reviews by incorporating relationships between the circadian timing of three key behaviors (i.e., food intake, physical activity, sleep) and energy balance, while also discussing evidence of allostatic and homeostatic pressures that promote energy balance.

A literature search was conducted in Google Scholar to identify relevant empirical articles using various combinations of search terms such as: *chrononutrition, energy balance, circadian timing, food intake, sleep/wake timing, meal timing, physical activity timing, exercise timing, morning meals, breakfast eating, breakfast skipping, time-restricted feeding, time-restricted eating, evening meals, evening eating, night eating, body mass index, obesity, body weight, weight loss, energy intake, energy expenditure, weight gain, morning exercise, morning physical activity, evening exercise, evening physical activity, glucose, insulin, insulin resistance, social jetlag, shift work, morning shift, delayed bedtime, evening shift, overnight shift, fasting, eating window, metabolism, caloric intake, and metabolic hormones*. References of retrieved articles and studies that were in the 'Cited By' list in Google Scholar were then screened to identify additional relevant studies. Included studies were those which examined at least one of the focal behaviors (i.e., timing of food intake, timing of physical activity, sleep/wake timing) and relationships between the behavior and components of energy balance (see Table 1 for characteristics of

Table 1. Characteristics of original research studies cited in review.

Study Citation	Sample Species/Type	Sample Size (n)	Study Type	Rating of Control for Extraneous Variables	Key Extraneous Factors Controlled For	Key Extraneous Factors Not Controlled For	Study Aims/Protocol Designed to Distinguish Between Circadian Factors and Masking Effects?
<i>Circadian Timing of Food Intake and Energy Balance</i>							
Adamovich et al. (2014)	Wild-type and clock-disrupted male mice	4 per group	Experimental	High	Light/dark schedule; Feeding/fasting schedule; Energy intake	Locomotor activity	Yes
Andersson et al. (1996)	Men with obesity and normal weight men	86 men with obesity; 61 normal weight men	Observational	Low	Energy intake	Light/dark schedule; Sleep/wake schedule; Physical activity	No
Arble et al. (2009)	Male mice	6 per group	Experimental	High	Light/dark schedule; Feeding/fasting schedule; Energy intake; Locomotor activity	N/A	No
Bandín et al. (2015)	Women	32; 10 in one protocol and 22 in another protocol	Experimental	High	Feeding/fasting schedule; Sleep/wake schedule; Energy intake; Energy expenditure	Light/dark schedule; Body mass index ^a	No
Barnea et al. (2009)	Male mice	4 per group	Experimental	High	Light/dark schedule; Feeding/fasting schedule; Energy intake	Locomotor activity	Yes
Baron et al. (2011)	Adult humans	52	Observational	Moderate	Sleep/wake schedule	Light/dark schedule; Physical activity ^a	No
Barrington and Beresford (2019)	Adult humans	2389	Observational	Moderate	Physical activity	Light/dark schedule; Sleep/wake schedule	No
Betts et al. (2014)	Adults aged 21–60 living in southwest England	33; 12 men and 21 women	Experimental	High	Feeding/fasting schedule	Light/dark schedule; Sleep/wake schedule; Body mass index ^a	No
Bo et al. (2014)	Non-obese, non-diabetic middle-aged adult humans	1245	Observational	Moderate	Physical activity	Light/dark schedule; Sleep/wake schedule	No
Bolli et al. (1984)	Non-diabetic adult males	8	Observational	Moderate	Feeding/fasting schedule; Energy intake; Sleep/wake schedule; Physical activity	Light/dark schedule	No

Bray et al. (2010)	Male wild-type mice	Not provided	Experimental	High	Light/dark schedule; Feeding/fasting schedule	Physical activity ^a	No
Buonfiglio et al. (2018)	Male rats	35; 5–10 per group	Experimental	High	Light/dark schedule; Feeding/fasting schedule; Food intake	Locomotor activity	No
Carlson et al. (2007)	Healthy, normal-weight 40–50 year-old adults	15; 5 men and 10 women	Experimental	High	Feeding/fasting schedule; Energy intake	Light/dark schedule; Sleep/wake schedule; Physical activity	No
Chaix et al. (2014)	Male wild-type mice	392; mice randomly assigned into one of six feeding regimens with 8–32 mice per group	Experimental	High	Light/dark schedule; Feeding/fasting schedule; Energy intake	Physical activity ^a	No
Chow et al. (2020)	Adult humans with overweight or obesity	17 women and 3 men: 11 in time-restricted eating group; 9 in unrestricted eating group	Experimental	High	Feeding/fasting schedule; Body weight loss	Light/dark schedule; Energy intake; Sleep/wake schedule; Physical activity ^a	No
Chowdhury et al. (2016)	Adults aged 21–60 living in southwest England	23; 8 men and 15 women	Experimental	High	Feeding/fasting schedule	Sleep/wake schedule ^a ; Energy intake ^a ; Physical activity ^a ; Body mass index ^a	No
Corbalan-Tutau et al. (2012)	Normal-weight and obese women	20 normal-weight women and 50 women with obesity	Observational	Low	N/A	Light/dark schedule; Physical activity; Sleep/wake schedule ^a ; Feeding/fasting schedule ^a	No
Dattilo et al. (2010)	Healthy adults aged 19–45 years	24 men and 28 women	Observational	Low	Physical activity	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule	No
de Castro (2004)	Adult humans	375 men and 492 women	Observational	Low	N/A	Light/dark schedule; Sleep/wake schedule; Physical activity	No
de Castro (2007)	Adult humans	375 men and 492 women	Observational	Moderate	N/A	Light/dark schedule; Sleep/wake schedule; Physical activity; Body mass index ^a	No
de Castro (2009)	Adult humans	388 men and 621 women	Observational	Moderate	N/A	Light/dark schedule; Sleep/wake schedule; Physical activity	No

(Continued)

Table 1. Continued.

Study Citation	Sample Species/Type	Sample Size (n)	Study Type	Rating of Control for Extraneous Variables	Key Extraneous Factors Controlled For	Key Extraneous Factors Not Controlled For	Study Aims/Protocol Designed to Distinguish Between Circadian Factors and Masking Effects?
Delahaye et al. (2018)	Male mice	Total of 4 diet groups with 10–11 mice assigned to each group	Experimental	High	Light/dark schedule; Feeding/fasting schedule; Energy intake	Locomotor activity	No
Eckel-Mahan et al. (2013)	Mice	90; 45 per feeding group	Experimental	High	Light/dark schedule; Feeding/fasting schedule; Energy intake	Physical activity	Yes
Garaulet et al. (2013)	Adults with overweight and obesity	420	Observational	Low	N/A	Light/dark schedule; Sleep/wake schedule; Physical activity ^a ; Total energy expenditure ^a	No
Geliebter et al. (2014)	Adults with overweight	36; 12 participants per condition	Experimental	Moderate	Feeding/fasting schedule	Light/dark schedule; Sleep/wake schedule; Resting energy expenditure ^a	No
Gill and Panda (2015)	Healthy, non-shift-working adults	Baseline: 156; 65 men and 91 women Follow-up: 8; 5 men and 3 women	Baseline: Observational Follow-up: Experimental	Baseline: Low Follow-up: Low	Baseline: N/A Follow-up: N/A	Baseline: Physical activity Follow-up: Light/dark schedule; Feeding/fasting schedule; Sleep/wake schedule; Energy intake	No
Gluck et al. (2008)	Healthy non-diabetic Pima Indians and whites	117 Pima Indians and 43 whites	Experimental	Moderate	Light/dark schedule; Energy intake	Sleep/wake schedule; Physical activity	No
Goel et al. (2009)	Adult females	15 patients with night eating syndrome and 14 controls	Observational	Moderate	N/A	Feeding/fasting schedule; Energy intake ^a	No
Hara et al. (2001)	Male mice	4–10 per group	Experimental	High	Light/dark schedule; Feeding/fasting schedule	Energy intake; Locomotor activity ^a	Yes
Hatori et al. (2012)	Male mice	24	Experimental	High	Light/dark schedule; Feeding/fasting schedule; Energy intake	Locomotor activity ^a	No
Hirao et al. (2009)	<i>Per2::luciferase</i> knock-in mice	26	Experimental	High	Light/dark schedule; Feeding/fasting schedule; Energy intake	N/A	Yes

Hirao et al. (2010)	<i>Per2</i> ::luciferase knock-in mice	24 intact mice and 21 lesioned mice	Experimental	High	Light/dark schedule; Feeding/fasting schedule	N/A	Yes
Hutchison et al. (2019)	Adult men	15	Experimental	Moderate	Feeding/fasting schedule	Light/dark schedule; Sleep/wake schedule; Energy intake; Physical activity ^a	No
Itokawa et al. (2013)	<i>Per2</i> ::luciferase knock-in mice	3–10 mice were analyzed per study condition	Experimental	High	Light/dark schedule; Feeding/fasting schedule	Food anticipatory activity ^a	Yes
Jakubowicz et al. (2012)	Sedentary non-diabetic adult men and women with obesity	193; 96 assigned to high carbohydrate and protein-enriched breakfast diet and 97 assigned to low carbohydrate diet	Experimental	High	Energy intake	Light/dark schedule; Sleep/wake schedule; Physical activity ^a	No
Jakubowicz et al. (2013a)	Lean women with polycystic ovarian syndrome	60	Experimental	High	Feeding/fasting schedule; Energy intake	Light/dark schedule; Sleep/wake schedule; Physical activity ^a ; Body mass index ^a	No
Jakubowicz et al. (2013b)	Women with overweight or obesity	93; 46 assigned to breakfast meal plan protocol and 47 assigned to dinner meal plan protocol	Experimental	High	Feeding/fasting schedule; Energy intake	Light/dark schedule; Sleep/wake schedule; Physical activity ^a	No
Jamshed et al. (2019)	Overweight adults	11	Experimental	Moderate	Feeding/fasting schedule; Energy intake; Physical activity	Light/dark schedule; Sleep/wake schedule	No
Kahleova et al. (2017)	Members of Seventh-day Adventist churches in the United States and Canada aged ≥30 years	50,660	Observational	Moderate	Feeding/fasting schedule; Energy intake; Physical activity	Light/dark schedule; Sleep/wake schedule	No
Kant and Graubard (2015)	United States adults aged 20–74 years	62,298	Observational	Moderate	Body mass index ^a	Light/dark schedule; Feeding/fasting schedule; Sleep/wake schedule; Physical activity	No
Kant et al. (1997)	United States adults aged 25–74 years	2580 men and 4567 women	Observational	Moderate	Energy intake; Physical activity; Body mass index	Light/dark schedule; Sleep/wake schedule	No

(Continued)

Table 1. Continued.

Study Citation	Sample Species/Type	Sample Size (n)	Study Type	Rating of Control for Extraneous Variables	Key Extraneous Factors Controlled For	Key Extraneous Factors Not Controlled For	Study Aims/Protocol Designed to Distinguish Between Circadian Factors and Masking Effects?
Karatzi et al. (2017)	Greek primary school children	1912	Observational	Moderate	N/A	Light/dark schedule; Feeding/fasting schedule; Sleep/wake schedule	No
Kelly et al. (2020)	Healthy adults 50 years of age or older	6; 4 men and 2 women	Experimental	High	Feeding/fasting schedule; Energy intake	Light/dark schedule ^a ; Sleep/wake schedule ^a ; Energy intake ^a ; Physical activity ^a	No
Kohsaka et al. (2007)	Mice	12 mice fed regular chow and 10 mice fed high-fat diet	Experimental	High	Light/dark schedule	Feeding/fasting schedule; Locomotor activity ^a	Yes
Kuroda et al. (2012)	Homozygous <i>Per2::luciferase</i> knock-in mice	6 mice per condition	Experimental	High	Light/dark schedule; Feeding/fasting schedule; Energy intake	Food anticipatory activity ^a	Yes
Kutsuma et al. (2014)	Japanese adults aged 20–75 years	60,800; 38,123 men and 22,677 women	Observational	Moderate	N/A	Light/dark schedule; Feeding/fasting schedule; Sleep/wake schedule	No
la Fleur et al. (2001)	Male rats	44	Experimental	High	Light/dark schedule; Feeding/fasting schedule	Energy intake	No
Lamia et al. (2008)	Wild-type mice and mice with a liver-specific disruption of <i>Bmal1</i>	7–9 mice per genotype	Experimental	High	Light/dark schedule; Feeding/fasting schedule	Locomotor activity ^a ; Energy intake	Yes
Lax et al. (1998)	Adult male rats	32	Experimental	High	Light/dark schedule; Feeding/fasting schedule	Locomotor activity	Yes
LeCheminant et al. (2013)	Healthy young men	29	Experimental	High	Feeding/fasting schedule	Sleep/wake schedule; Physical activity	No
Leidy et al. (2007)	Adult women	38; 21 assigned to higher protein diet and 17 assigned to normal protein diet	Experimental	High	Energy intake	Sleep/wake schedule; Body mass index ^a ; Physical activity ^a	No
Lopez-Minguez et al. (2018)	Adult women with overweight or obesity	40; 20 homozygous risk non-allele carriers and 20 homozygous carriers for MTNR1B rs10830963	Experimental	High	Feeding/fasting schedule; Energy intake	Physical activity; Light/dark schedule; Sleep/wake schedule ^a	No

Martens et al. (2020)	Healthy non-obese midlife and older adults	22	Experimental	High	N/A	Light/dark schedule; Sleep/wake schedule; Energy expenditure ^a	No
Masri et al. (2014)	Liver-specific SIRT6 knock-out mice, liver-specific SIRT1 knock-out mice, and wild-type mice	Not provided	Experimental	High	Light/dark schedule	Feeding/fasting schedule; Energy intake; Physical activity	Yes
McHill et al. (2017)	Young adults aged 18–22 years	110; 64 men and 46 women	Observational	Moderate	Light/dark schedule	Sleep/wake schedule; Energy intake ^a ; Physical activity ^a	No
McHill et al. (2019)	Young adults aged 18–22 years	106; 61 men and 45 women	Observational	Moderate	Light/dark schedule	Physical activity; Sleep/wake schedule ^a ;	No
Mills et al. (2011)	Midlife women	1099	Observational	Moderate	Physical activity	Light/dark schedule; Feeding/fasting schedule; Sleep/wake schedule	No
Moro et al. (2016)	Males with at least 5 years of experience in resistance training	34	Experimental	High	Feeding/fasting schedule; Energy intake; Physical activity	Light/dark schedule; Sleep/wake schedule	No
Oike et al. (2011)	BALB/cAn mice and Per2::Luciferase knock-in mice	3–8 mice per group	Experimental	High	Light/dark schedule	Locomotor activity	Yes
Okada et al. (2019)	Japanese women aged 40–74 years	19,687	Observational	Moderate	Physical activity	Light/dark schedule; Sleep/wake schedule	No
Parr et al. (2020)	Men with overweight or obesity	11	Experimental	High	Feeding/fasting schedule; Energy intake	Light/dark schedule; Sleep/wake schedule ^a ; Physical activity ^a	No
Przulj et al. (2021)	Adults with obesity	50	Experimental	Low	N/A	Light/dark schedule; Sleep/wake schedule; Physical activity; Feeding/fasting schedule ^a	No
Qin et al. (2003)	Medical students aged 20–23	7; 6 men and 1 woman	Experimental	Low	Feeding/fasting schedule; Sleep/wake schedule	Light/dark schedule; Physical activity; Energy intake	No
Rains et al. (2015)	Overweight premenopausal women	35	Experimental	High	Feeding/fasting schedule	Light/dark schedule; Sleep/wake schedule; Physical activity	No
Rangaraj et al. (2020)	Adults without diabetes, aged 21–50 years	44	Observational	Moderate	Sleep/wake schedule; Body mass index; Energy intake	Light/dark schedule	No

(Continued)

Table 1. Continued.

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Reid et al. (2014)	Adult men and women	59	Observational	Moderate	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake	N/A	No
Ruiz-Lozano et al. (2016)	Bariatric surgery patients	270; 57 men and 213 women	Observational	Low	N/A	Light/dark schedule; Sleep/wake schedule; Energy intake ^a ; Total energy expenditure ^a	No
Sajjad et al. (2014)	Male and female medical students	234; 122 men and 112 women	Observational	Low	N/A	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake	No
Saladin et al. (1995)	Rats	3–7 per group	Experimental	High	Light/dark schedule; Feeding/fasting schedule	Locomotor activity; Energy intake	No
Scheer et al. (2013)	Healthy adults without obesity	12; 6 men and 6 women	Experimental	Moderate	Light/dark schedule; Feeding/fasting schedule; Energy intake; Sleep/wake schedule; Physical activity	N/A	Yes
Schlundt et al. (1992)	Women with moderate obesity	52	Experimental	High	Energy intake	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule	No
Spaeth et al. (2014)	Healthy adults aged 21–50 years	44; 23 men and 21 women	Experimental	Moderate	Light/dark schedule; Sleep/wake schedule; Physical activity	Feeding/fasting schedule	No
Stokkan et al. (2001)	Rats	3–9 per group	Experimental	High	Light/dark schedule; Feeding/fasting schedule	N/A	Yes
Stote et al. (2007)	Healthy, normal-weight 40–50 year-old adults	15; 10 women and 5 men	Experimental	High	Feeding/fasting schedule; Energy intake	Light/dark schedule; Sleep/wake schedule; Physical activity ^a	No

Striegel-Moore et al. (2008)	United States adults aged 15–39 years	8250; 2068 exhibiting night eating syndrome and 6182 not exhibiting night eating syndrome	Observational	Low	N/A	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Physical activity	No
Tahara et al. (2011)	Male ICR mice and homozygous Per2 ^{luciferase} knock-in mice	3–6 mice per group	Experimental	High	Light/dark schedule; Feeding/fasting schedule	Locomotor activity	Yes
Tuomi et al. (2016)	Adult human islet cells; Melatonin-receptor knockout and wildtype mice	25 adults; 3–25 mice per group	Experimental	High	For mice: Feeding/fasting schedule	Light/dark schedule; Sleep/wake schedule; Physical activity/ Locomotor activity; Energy intake For humans: Feeding/fasting schedule	No
Van Cauter et al. (1989)	Healthy individuals without obesity	14; 7 males and 7 females	Experimental	Moderate	Light/dark schedule; Feeding/fasting schedule; Energy intake	Sleep/wake schedule; Physical activity	No
Versteeg et al. (2018)	Men with obesity and insulin resistance	23	Experimental	Moderate	Energy intake	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule ^a ; Physical activity	No
Vollmers et al. (2009)	Male wild-type mice and circadian clock-deficient mice	3–8 mice per group	Experimental	High	Light/dark schedule; Feeding/fasting schedule	Locomotor activity; Energy intake ^a	Yes
Westerterp-Plantenga et al. (1996)	Women with and without obesity	32; 16 with obesity and 16 without obesity	Experimental	Low	Feeding/fasting schedule; Physical activity	Light/dark schedule; Sleep/wake schedule	No
Wilkinson et al. (2020)	Adults with metabolic syndrome and a baseline mean eating window of ≥ 14 h/day	19	Experimental	Moderate	N/A	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake; Physical activity ^a	No
Circadian Timing of Physical Activity and Energy Balance							
Alizadeh et al. (2015)	Women with overweight	46	Experimental	Low	N/A	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule	No
Alizadeh et al. (2017)	Women with overweight	48; 25 in morning aerobic exercise and 23 in evening aerobic exercise	Experimental	Moderate	N/A	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule	No

(Continued)

Table 1. Continued.

Study Citation	Sample Species/Type	Sample Size (n)	Study Type	Rating of Control for Extraneous Variables	Key Extraneous Factors Controlled For	Key Extraneous Factors Not Controlled For	Study Aims/Protocol Designed to Distinguish Between Circadian Factors and Masking Effects?
Chomistek et al. (2016)	Women	7157	Observational	Moderate	Energy intake	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule	No
Dalbram et al. (2019)	Male mice, assigned to either a high – or low-fat diet and to either sedentary or voluntary wheel running conditions	96; 24 mice per group	Experimental	High	Light/dark schedule	Energy intake ^a	No
Di Blasio et al. (2010)	Sedentary post-menopausal women	29; 14 morning walkers and 15 early evening walkers	Experimental	Low	N/A	Light/dark schedule; Feeding/fasting schedule; Sleep/wake schedule	No
Haugen et al. (2003)	Healthy men and women aged 21–67 years	37; 12 men and 25 women	Experimental	Low	Feeding/fasting schedule	Light/dark schedule; Sleep/wake schedule	No
Keim et al. (1997)	Women	10	Experimental	High	Feeding/fasting schedule; Energy intake	Light/dark schedule; Sleep/wake schedule	No
Kelly et al. (2020)	Healthy adults 50 years of age or older	6; 4 men and 2 women	Experimental	High	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake	N/A	No
Kline et al. (2020)	Adults with overweight or obesity	125	Observational	Moderate	N/A	Light/dark schedule; Feeding/fasting schedule; Energy intake; Physical activity	No
Kräuchi and Wirz-Justice (1994)	Generally healthy male adults	7	Experimental	High	Light/dark schedule; Feeding/fasting schedule; Energy intake; Sleep/wake schedule	N/A	Yes
Larsen et al. (2019)	Inactive men with overweight	11	Experimental	Moderate	Feeding/fasting schedule	Light/dark schedule; Sleep/wake schedule; Energy intake	No
Maraki et al. (2005)	Healthy, normal-weight females aged 18–45	12	Experimental	Low	Feeding/fasting schedule	Light/dark schedule; Sleep/wake schedule	No
Marinac et al. (2019)	Adults	125	Observational	Moderate	Physical activity	Energy intake	No

Moholdt et al. (2021)	Adult males with overweight or obesity	24; 8 per exercise condition	Experimental	High	Feeding/fasting schedule; Energy intake; Physical activity	Light/dark schedule; Sleep/wake schedule	No
Morris et al. (2015)	Healthy adults	13	Experimental	High	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake	N/A	Yes
Romon et al. (1993)	Young men working a night shift	9	Experimental	High	Sleep/wake schedule; Feeding/fasting schedule; Energy intake	Light/dark schedule	No
Spengler et al. (2000)	Healthy adult males	10	Experimental	High	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake	N/A	Yes
van Moorsel et al. (2016)	Young lean Caucasian males	12	Experimental	High	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake	N/A	No
Willis et al. (2020)	Physically inactive young adults with overweight or obesity	88	Experimental	High	Physical activity	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake ^a	No
Zitting et al. (2018)	Healthy adults	13; 7 in forced desynchrony group and 6 in control group	Experimental	High	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake	N/A	Yes
An Integrated Approach to the Study of Energy Balance Booth et al. (2012)	Young adults with parental history of type 2 diabetes	48	Observational	Moderate	Body mass index	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake;	No
Calvin et al. (2013)	Sedentary, healthy and normal-weight adults aged 18–40	11 men and 6 women, with 5 of the men and 3 of the women randomly assigned to sleep deprivation condition	Experimental	High	Sleep/wake schedule	Light/dark schedule; Feeding/fasting schedule	No

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Table 1. Continued.

Study Citation	Sample Species/Type	Sample Size (n)	Study Type	Rating of Control for Extraneous Variables	Key Extraneous Factors Controlled For	Key Extraneous Factors Not Controlled For	Study Aims/Protocol Designed to Distinguish Between Circadian Factors and Masking Effects?
Greer et al. (2013)	Healthy adults	23	Experimental	High	Sleep/wake schedule; Feeding/fasting schedule; Energy intake	Light/dark schedule; Physical activity	No
Kant and Graubard (2014)	American adults ≥ 20 years old	15,199	Observational	Moderate	N/A	Light/dark schedule; Sleep/wake schedule; Physical activity	No
Kim et al. (2011)	Women aged 35–74 years living in the United States or Puerto Rico	27,983	Observational	Moderate	Body mass index	Light/dark schedule; Sleep/wake schedule; Physical activity	No
Markwald et al. (2013)	Healthy adults	16; 8 men and 8 women	Experimental	High	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Physical activity	N/A	No
McHill et al. (2014)	Healthy adults	14; 6 men and 8 women	Experimental	High	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake	N/A	Yes
Nedeltcheva et al. (2010)	Overweight non-smoking adults	10	Experimental	High	Sleep/wake schedule; Feeding/fasting schedule; Energy intake	Light/dark schedule	No
Ravussin et al. (2019)	Adults with overweight	11	Experimental	High	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake	N/A	No
Sasaki et al. (2014)	Male mice	3–16 mice per condition	Experimental	High	Light/dark schedule	N/A	No
Schmid et al. (2009)	Healthy, normal-weight men	15	Experimental	Moderate	Light/dark schedule; Sleep/wake schedule	N/A	No
Spaeth et al. (2015)	Healthy adults	47; 36 in sleep restriction group and 11 in control group	Experimental	High	Light/dark schedule; Sleep/wake schedule; Physical activity	Feeding/fasting schedule; Energy intake	No

Spiegel et al. (2004)	Healthy men	12	Experimental	Moderate	Sleep/wake schedule; Feeding/fasting schedule; Energy intake; Physical activity	Light/dark schedule	No
St-Onge et al. (2012)	Healthy, normal-weight adults	30	Experimental	Moderate	Sleep/wake schedule; Feeding/fasting schedule; Energy intake	Light/dark schedule; Physical activity	No
Sutton et al. (2018)	Men with prediabetes	8	Experimental	High	Sleep/wake schedule; Feeding/fasting schedule; energy intake; Physical activity	Light/dark schedule	No
Taheri et al. (2004)	Wisconsin, USA, adults aged 30–60 years	1,024	Observational	Moderate	N/A	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake; Physical activity ^a	No
Tinsley et al. (2017)	Generally healthy, recreationally-active men	18	Experimental	Moderate	Feeding/fasting schedule; Physical activity	Light/dark schedule; Sleep/wake schedule; Energy intake	No
Van Proeyen et al. (2010)	Healthy males aged 18–25 years	28	Experimental	Moderate	Feeding/fasting schedule; Energy intake; Physical activity	Light/dark schedule; Sleep/wake schedule	No
Wong et al. (2015)	Adults without diabetes aged 30–54 years	224	Observational	Moderate	Energy intake; Physical activity	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule	No
<i>Circadian Timing of Sleep and Energy Balance</i>							
Alves et al. (2017)	Poultry-processing plant employees aged 18–60 years	423; 122 worked early- morning shift, 133 worked day shift, 168 worked night shift	Observational	Moderate	N/A	Light/dark schedule; Feeding/fasting schedule; Energy intake	No
Baron et al. (2011)	Adults with an evening or intermediate diurnal preference	52; 27 men and 25 women	Observational	Moderate	Sleep/wake schedule	Light/dark schedule; Physical activity ^a	No
Beebe et al. (2017)	Nurses working either a day or night shift	103	Observational	Moderate	N/A	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake	No

(Continued)

Table 1. Continued.

Study Citation	Sample Species/Type	Sample Size (n)	Study Type	Rating of Control for Extraneous Variables	Key Extraneous Factors Controlled For	Key Extraneous Factors Not Controlled For	Study Aims/Protocol Designed to Distinguish Between Circadian Factors and Masking Effects?
Cain et al. (2015)	Adults	16; 8 men and 8 women	Experimental	Low	Sleep/wake schedule;	Light/dark schedule; Feeding/fasting schedule; Physical activity	No
Centofanti et al. (2018)	Healthy adults	31; 13 men and 18 women	Experimental	Moderate	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake; Physical activity	N/A	No
Chaput et al. (2007)	Adults aged 21–64 years from the greater Quebec City area	740; 323 men and 417 women	Observational	Moderate	Physical activity	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake	No
Chaput et al. (2015)	Children aged 9–11 years from Australia, Brazil, Canada, China, Colombia, Finland, India, Kenya, Portugal, South Africa, the United Kingdom and the United States	5777	Observational	Moderate	Body mass index	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake	No
de Assis et al. (2003)	Garbage collectors working morning, afternoon, and night shifts	22 participants for each work shift	Observational	Moderate	N/A	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule	No
Duncan et al. (2016)	Australian adults	1317	Observational	Moderate	Body mass index	Light/dark schedule; Feeding/fasting schedule; Energy intake	No
Esquirol et al. (2009)	Males aged 39–60 years	198; 98 d workers and 100 rotating shift workers	Observational	Moderate	Physical activity	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule	No
Golley et al. (2013)	Children and adolescents aged 9–16 years	2200	Observational	Moderate	Physical activity	Light/dark schedule; Feeding/fasting schedule	No
Grant et al. (2017)	Healthy males	11; 4 assigned to eat at night and 7 assigned to not eat at night	Experimental	Moderate	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake; Physical activity	N/A	No

Hulsegge et al. (2016)	Adults aged 20–70 years	15092; 683 shift workers and 7173 d workers	Observational	Low	Physical activity; Body mass index	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule	No
Knutson et al. (1990)	Adult men	25; 12 shift workers and 13 d workers	Observational	Low	N/A	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule	No
Koopman et al. (2017)	Dutch adults aged 40–75 years	1585; 745 men and 840 women	Observational	Moderate	Feeding/fasting schedule; Physical activity; Body mass index	Light/dark schedule; Energy intake	No
Lennernäs et al. (1995)	Male industrial workers	96	Observational	Low	N/A	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Physical activity	No
Markwald et al. (2013)	Healthy adults	16; 8 men and 8 women	Experimental	High	Light/dark schedule; Sleep/wake schedule; Feeding/ fasting schedule; Energy intake	N/A	No
McHill et al. (2014)	Healthy adults	14; 6 men and 8 women	Experimental	High	Light/dark schedule; Sleep/wake schedule; Feeding/ fasting schedule; Energy intake	N/A	Yes
Mota et al. (2017)	Individuals with non- communicable chronic diseases (obesity, systemic arterial hypertension, type 2 diabetes mellitus or dyslipidemia) in Brazil	792	Observational	Moderate	Physical activity	Light/dark schedule; Feeding/fasting schedule; Energy intake	No
Mota et al. (2019)	Individuals with obesity-related chronic diseases in Brazil	792	Observational	Moderate	Physical activity; Body mass index	Light/dark schedule	No
Nakamura et al. (2018)	Japanese workers	2062 daytime workers and 302 shift workers	Observational	Moderate	N/A	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Feeding/ fasting schedule; Physical activity	No

(Continued)

Table 1. Continued.

Study Citation	Sample Species/Type	Sample Size (n)	Study Type	Rating of Control for Extraneous Variables	Key Extraneous Factors Controlled For	Key Extraneous Factors Not Controlled For	Study Aims/Protocol Designed to Distinguish Between Circadian Factors and Masking Effects?
Nooijen et al. (2018)	Swedish adults	12969; 5577 men and 7392 women	Observational	Moderate	N/A	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake	No
Olds et al. (2011)	Free-living Australian adolescents aged 9–16 years	2200	Observational	Moderate	N/A	Light/dark schedule; Feeding/fasting schedule; Energy intake	No
Parsons et al. (2015)	Individuals born between April 1972 and March 1973 in Dunedin, New Zealand, followed from birth until 38 years of age	1037	Observational	Moderate	N/A	Light/dark schedule; Feeding/fasting schedule; Energy intake; Physical activity	No
Pizinger et al. (2018)	Overweight adults	6; 4 men and 2 women	Experimental	High	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake; Body mass index	Physical activity	No
Polugrudov et al. (2017)	High school students and workers from the European North of Russia with normal weight	66	Experimental	Moderate	Feeding/fasting schedule; Energy intake; Physical activity; Body mass index	Light/dark schedule	No
Reinberg et al. (1979)	Healthy adult men	7	Observational	Low	N/A	Light/dark schedule; Physical activity	No
Roenneberg et al. (2012)	Individuals aged 16–65	64110	Observational	Moderate	N/A	Light/dark schedule; Feeding/fasting schedule; Energy intake; Physical activity	No
Roskoden et al. (2017)	Employees at a medical care center in Germany	46	Observational	Low	N/A	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule	No
Rutters et al. (2014)	Adults	145; 67 men and 78 women	Observational	Moderate	Feeding/fasting schedule	Light/dark schedule; Energy intake	No
Schechter et al. (2013)	Females aged 22–43 years with body mass index of 23.4–27.5 kg/m ²	10	Experimental	High	Sleep/wake schedule; Feeding/fasting schedule; Energy intake	Light/dark schedule	No

Schechter and St-Onge (2014)	Adults	22	Observational	Moderate	Body mass index	Light/dark schedule; Feeding/fasting schedule; Energy intake	No
Silva et al. (2016)	Undergraduate students in Brazil	204; 92 men and 112 women	Observational	Moderate	Body mass index	Light/dark schedule; Feeding/fasting schedule; Energy intake; Physical activity	No
Spaeth et al. (2013)	Healthy adults aged 22–50 years	225	Experimental	High	Light/dark schedule; Sleep/wake schedule; Physical activity	N/A	No
Taylor et al. (2016)	Non-shift working women aged 48–58 years	370	Observational	Moderate	Exercise	Light/dark schedule; Feeding/fasting schedule; Energy intake	No
Wakui et al. (2002)	Healthy females	9	Observational	Low	N/A	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake	No
Wittmann et al. (2006)	Humans aged 14–94 years	501; 198 men and 303 women	Observational	Moderate	N/A	Light/dark schedule; Sleep/wake schedule; Feeding/fasting schedule; Energy intake; Physical activity	No
Zerón-Rugério et al. (2019)	Young adults aged 18–25 years	534	Observational	Moderate	Physical activity	Light/dark schedule; Feeding/fasting schedule; Energy intake	No

Note: In order to be classified as a true circadian rhythm, a biological rhythm must meet three criteria: (1) rhythm is entrainable (i.e., reset by external stimuli); (2) rhythm exhibits temperature compensation; and (3) rhythm has an endogenous free-running period lasting approximately 24 h, independent of 'masking' effects by environmental and/or behavioral cycles. Diurnal rhythms cannot be classified as circadian unless these are confirmed to be endogenous and independent of masking effects, e.g., forced desynchrony or constant routine protocols for human research.

^aVariable was measured and explored in initial analyses by researchers and was indicated to be intentionally left out as a control variable for an empirical reason, e.g., variable did not differ between experimental groups.

original research studies cited in the present review). This search was limited to articles available in the English language.

The impact of circadian timing of food intake on energy balance

This section outlines literature on the circadian timing of food intake (i.e., chrononutrition) (Arble et al., 2009) and how it affects energy balance through physiological and behavioral changes that alter energy intake and energy expenditure. Key aspects of research are discussed, including late timing of food intake, early timing of food intake, and eating patterns across the 24-h day.

The timing of food intake across the 24-h day has been linked to components of energy balance in past research. A landmark study on chrononutrition was conducted by Arble et al. (2009) in which nocturnal mice were fed a high-fat diet either during the typical inactive phase of the 24-h day (i.e., 'wrong' time of day), or during the typical active phase of the 24-h day (i.e., 'right' time of day). Extraordinarily, even though energy intake and energy expenditure did not differ between study conditions, the mice fed during the 'wrong' time of day gained significantly more weight than the mice fed during the 'right' time of day. Most notably, the rodent study conducted by Arble et al. (2009) laid the foundation for the potential role of chrononutrition in energy balance. These findings have been replicated in mice by other researchers (Chaix et al., 2014; Hatori et al., 2012). This line of research has begun to be applied in human samples, though differences in study design somewhat preclude direct comparisons. In correlational studies of humans, eating the main meal late in the 24-h day (i.e., at the 'wrong' time of day), as opposed to eating an earlier main meal, was associated with less weight loss in individuals who had obesity, even when energy intake and energy expenditure were not different between study groups (Garaulet et al., 2013; Ruiz-Lozano et al., 2016). More recent animal research has shown that even if caloric intake is greater in a high-fat diet condition compared to a normal chow condition, the restriction of food intake to typical waking hours may still prevent weight gain and decrease adiposity; however, it may not protect against inflammation (Delahaye et al., 2018). This research has highlighted an important distinction between studies which hold caloric intake constant across conditions (e.g., Garaulet et al., 2013; Ruiz-Lozano et al., 2016) and those that do not hold caloric intake constant (Delahaye et al., 2018); due to this discrepancy, additional research is necessary to fully understand the relationships between caloric intake, timing of food intake, and energy balance. As few chrononutrition studies have reported data on energy expenditure, the existing evidence has focused on the quantity and quality of energy intake in relation to circadian timing.

Late timing of food intake

Overall, late timing of food intake in particular may be associated with increased energy intake. In their examination of Americans' diurnal eating patterns, Gill and Panda (2015) found that almost 40% of participants' total daily energy intake was consumed after 6:00pm. This was deemed to be potentially problematic, as late meal intake was generally indicative of excessive total daily energy intake (i.e., contributing to a positive energy balance). Similar associations between eating later in the day and a greater energy intake have been reported by other researchers (Gluck et al., 2008; Reid et al., 2014), with men especially likely to engage in late-night eating (Spaeth et al., 2014). This increase in energy intake has also been linked to a positive energy balance, though the direction of this association remains unclear. While calorie consumption after 8:00pm has been linked to greater BMI (Baron et al., 2011), individuals who have obesity may be more likely to engage in energy intake later in the day (Andersson & Rossner, 1996; Corbalan-Tutau et al., 2012; McHill et al., 2017; McHill et al., 2019; for exception, see Mills et al., 2011). Conversely, restricting

nighttime energy intake (e.g., no energy intake from 7:00pm to 6:00am) may lead to a reduction in total daily energy intake (LeCheminant et al., 2013).

One factor which may be linked to increased homeostatic and allostatic pressure to engage in energy intake at night is a change in appetite for certain macronutrients throughout the 24-h day. Both humans and rats have an increased preference for high-fat foods at dinnertime compared to breakfast (Lax et al., 1998; Westerterp-Plantenga et al., 1996); preference for high-carbohydrate foods may also increase late at night (Gallant et al., 2014). This increase in the homeostatic and allostatic pressure of appetite for certain nutrients may be problematic for energy balance, because foods consumed late at night typically are low in satiety (de Castro, 2004; de Castro, 2007; de Castro, 2009), may contain high amounts of sodium (Striegel-Moore et al., 2008) or carbohydrates (McHill et al., 2019), and may simply be less healthy (Barrington & Beresford, 2019); these so-called 'empty calories' may lead individuals to consume additional snacks or drinks in an attempt to be satiated. Based on experimental work in mice, an increased appetite for high-fat foods at night may exert homeostatic and allostatic pressure to increase the likelihood of weight gain: compared to mice who consumed a high-fat diet near the beginning of the active phase, consumption of a high-fat diet near the end of the active phase was associated with markers of poor metabolic health such as weight gain and glucose intolerance, though total daily energy intake was identical between groups (Bray et al., 2010).

These effects of late-night eating on energy balance may also be due to melatonin, a hormone regulated by the central circadian clock that is released by the pineal gland at nighttime. Though melatonin may alter homeostatic and allostatic pressure in a variety of ways related to energy intake, melatonin seems to exert the greatest effects on insulin. During the day, i.e., when melatonin is low, insulin sensitivity is increased (Reutrakul & Van Cauter, 2014), whereas at night, i.e., when melatonin is high, insulin resistance is more likely (for reviews, see Cipolla-Neto et al., 2014; Owino et al., 2019). Additional research has shown that melatonin may suppress insulin release (Tuomi et al., 2016) and contribute to impaired glucose tolerance (Lopez-Minguez et al., 2018; Van Cauter et al., 1989), both of which have been related to obesity (Ferrannini & Camastra, 1998). Melatonin is considered a key regulator of leptin, as leptin also peaks late at night and decreases during the day (Saladin et al., 1995). Without melatonin, leptin signaling becomes impaired, potentially leading to leptin resistance over time (Buonfiglio et al., 2018). Thus, these physiological alterations in leptin, glucose, and ghrelin may increase homeostatic and allostatic pressure to engage in energy intake at night and could account for findings linking melatonin signaling to obesity (for review, see Cipolla-Neto et al., 2014). For example, energy intake close to melatonin onset has been associated with increased body fat and BMI (McHill et al., 2017). Taken together, individuals may be predisposed to engage in energy intake late at night due to increased preference for energy-dense foods, and melatonin may alter homeostatic and allostatic pressures such as insulin sensitivity and glucose tolerance when late-night energy intake occurs, contributing to a positive energy balance. Not all research to date has supported this relationship, however. Research in humans has highlighted some contrasting findings, such that higher concentrations of melatonin are linked to better glucose control (for review, see Garaulet et al., 2020). Garaulet et al. (2020) hypothesize that the timing of the body's melatonin cycle relative to the feeding/fasting cycle may account for these inconsistent findings; i.e., increased melatonin during the feeding cycle is linked to impaired glucose tolerance but increased melatonin during the fasting cycle may be beneficial for the body.

Early timing of food intake

Research has also examined how energy intake early in the day may affect energy balance. The first eating event of the day (i.e., breakfast) perhaps has the largest impact on the body's metabolic processes for the rest of the day. This is likely because the first eating event occurring after the overnight fasting period (i.e., nocturnal sleep; suggested to be a minimum of 10-12 h (International Standards

Organisation, 2010)) sets the phase of the body's liver clock (Hirao et al., 2010). The liver clock refers to a set of genetic feedback loops within cells of the liver that function as a self-sustained time-keeper to ensure vital metabolic processes (e.g., carbohydrate metabolism) occur at the 'right' time of day, and to help the liver and body maintain homeostasis through the varying physiological and behavioral time cues throughout the 24-hour day (for review, see Reinke & Asher, 2016). Thus, alterations to the timing of this first eating event may alter the timing of numerous metabolic processes, such as glucose homeostasis (Bolli et al., 1984; la Fleur et al., 2001; Lamia et al., 2008) and lipid metabolism (Adamovich et al., 2014; Masri et al., 2014) (for reviews, see Adamovich et al., 2015; Poggiogalle et al., 2018), while also altering the timing of other eating events.

Breakfast skipping may also alter homeostatic and allostatic pressures. Individuals who skip breakfast, for instance, may be more likely to engage in more mid-day snacking (Sajjad et al., 2014) or consume lunch earlier (Kant & Graubard, 2015) compared to those who eat breakfast. Though breakfast skipping – and, by extension, an earlier lunchtime – could hypothetically contribute to an earlier evening meal time, Nakajima (2018) have suggested that breakfast skipping is actually tied to a delayed eating schedule. Some evidence for this association has come from studies of night eating. Given that one criterion for night eating syndrome is lack of appetite in the morning following food intake late at night (Allison et al., 2010), nighttime eating may not only alter the phase of the body's liver clock (Kuroda et al., 2012), but also decrease the homeostatic and allostatic pressure of appetite and delay the timing of individuals' first eating event of the day, thus likely being linked to a delayed eating schedule throughout the 24-h day (Allison et al., 2005; Goel et al., 2009; O'Reardon et al., 2005). This association between late-night eating and skipping breakfast has also been observed in non-clinical samples (Karatzi et al., 2017; Kutsuma et al., 2014; Okada et al., 2019). In an effort to tease apart causal factors, experimental research has suggested that this relationship between breakfast skipping and late-night eating may be due in part to a daily endogenous peak in general hunger in the evening (i.e., 8:00pm) and a nadir in the morning (i.e., 8:00am) (Scheer et al., 2013), which would increase homeostatic and allostatic pressure to engage in late-night eating and decrease homeostatic and allostatic pressure to engage in energy intake in the morning. However, additional research is necessary to determine directionality of the association between late-night eating and breakfast skipping.

In addition, research has examined the effect of consumption of certain nutrients at breakfast on homeostatic and allostatic pressures tied to energy intake. For instance, a breakfast rich in protein has been associated with both initial and longer-term feelings of fullness and satiety, and reduced levels of the appetite-stimulating hormone ghrelin (de Castro, 2007; Leidy et al., 2007; Rains et al., 2015); a high-carbohydrate and protein breakfast may have similar effects on appetite and satiety (Jakubowicz et al., 2012). However, studies of the effect of breakfast skipping on body weight are inconsistent (for review, see St-Onge et al., 2017). For instance, a foundational clinical trial by Schlundt et al. (1992) demonstrated that a *change* in breakfast consumption behaviors (i.e., habitual breakfast skippers beginning to eat breakfast and habitual breakfast eaters beginning to skip breakfast) led to greater weight loss compared to those who maintained breakfast consumption behaviors, rather than an individual's breakfast behavioral pattern in and of itself. Other studies have reported no effects of breakfast skipping on body weight, compared to breakfast consumption in individuals with overweight and obesity (Chowdhury et al., 2016), and in individuals at a healthy weight (Betts et al., 2014). Other research has indicated greater weight loss due to breakfast skipping, although skipping breakfast did result in higher cholesterol levels in the blood (Geliebter et al., 2014). St-Onge (2017) and colleagues suggest that minimal effects of breakfast consumption on weight loss efforts may be due to compensatory behaviors throughout the rest of the 24-hour day; further work is warranted to understand this complex relationship.

Evidence has also indicated that the consumption of certain nutrients can alter the timing of various metabolic processes and the phase of the liver clock (Hara et al., 2001; Stokkan et al., 2001; Vollmers et al., 2009). For instance, a high-fat diet can greatly distort daily rhythms of leptin and insulin (Kohsaka et al., 2007), leading to a high degree of variability in leptin and insulin levels

during both the light and dark cycles. A high-fat diet may also blunt daily patterns of lipid metabolism (Eckel-Mahan et al., 2013; Kohsaka et al., 2007). A diet high in fat may also delay adiponectin signaling in the liver (Barnea et al., 2009), thereby altering the body's glucose levels (Combs & Marliss, 2014; Gamberi et al., 2018). These physiological changes can increase homeostatic and allostatic pressure to engage in energy intake and lead to erratic eating behaviors that encourage a positive energy balance, such as increased energy intake during the 'wrong' time of day (Kohsaka et al., 2007). Conversely, a diet of carbohydrates and protein allows for stabilization of the phase of the liver clock (Hirao et al., 2009); therefore, these nutrients may enable synchronization of metabolic processes to optimize health and functioning. Insulin (Tahara et al., 2011), glucose and amino acids (Oike et al., 2011), and rapidly digested starches (Itokawa et al., 2013) may also be important for regulating the timing of the liver clock.

Proportion of energy intake across the 24-h day

Rather than focusing primarily on the timing of the first or last eating event of the day, other research has looked to identify the role of other eating patterns in energy balance. The largest meal (i.e., meal in which individuals consume the greatest proportion of energy across the 24-h day), relative to other meals, may be one relevant eating pattern. For instance, Rangaraj et al. (2020) found that consuming a greater proportion of energy intake early in the day, as opposed to later in the day, was linked to increased insulin sensitivity. A study by Carlson et al. (2007) examined the effects of a single meal consumed within a window from 5:00pm to 9:00pm as opposed to the traditional three meals per day, over a two-month period. Though fasting levels of metabolic hormones such as leptin and ghrelin did not differ between conditions, the single-meal condition resulted in increased glucose levels, a delayed insulin response, and lowered glucose tolerance in the morning (Carlson et al., 2007). The single-meal condition also resulted in decreased feelings of fullness and increased perceptions of hunger (Stote et al., 2007). As described by Stote et al. (2007), this study protocol had a high rate of withdrawal (~30%), perhaps due to the fact that this type of eating schedule is difficult to sustain for many adults. As such, results should be interpreted with caution. Overall, however, these results are generally consistent with findings that many others have demonstrated: consuming the majority of energy intake earlier in the day (i.e., at breakfast or lunch) may be more beneficial for energy balance and metabolic health than consuming most calories at a later mealtime (Bandin et al., 2015; Bo et al., 2014; Chaix et al., 2019; Dattilo et al., 2010; Garaulet et al., 2013; Jakubowicz et al., 2013a; Jakubowicz et al., 2013b; Jamshed et al., 2019; Kahleova et al., 2017; Kelly et al., 2020; Qin et al., 2003; for exceptions, see Kant et al. (1997) and Versteeg et al. (2018)); for reviews, see Allison and Goel (2018) and Pellegrini et al. (2020). Because of these findings demonstrating a link between energy balance and the timing of energy intake, other studies have attempted to uncover relationships between the timing of energy intake and other health outcomes related to energy balance.

Eating window within the 24-h day

Another relevant eating pattern may be an individual's eating window (i.e., duration of time from first eating event of the day to last eating event of the day). As part of a larger study assessing diurnal eating patterns in American adults, Gill and Panda (2015) conducted a pilot study in a subsample of individuals with overweight. These adults were asked to restrict their eating window from over 14 h per day to 10-11 h per day for three months, with the researchers providing no recommendations on managing nutrition or caloric intake. Participants in this pilot study lost weight, reported greater energy levels and greater sleep satisfaction, and, in contrast to the aforementioned studies of mice, daily energy intake decreased by approximately 20%. The innovative work conducted by Gill and Panda (2015) showed that modifying the timing of energy intake may enable individuals to decrease their total daily energy intake, and this behavioral target may also serve as a novel

avenue for weight loss and health improvement efforts; consistent findings have been reported by others (Moro et al., 2016).

Recent work by Wilkinson et al. (2020) found that restricting one's eating window may not only assist in weight loss efforts, but also in reducing waist circumference and improving blood pressure and cholesterol levels. Another study, conducted by Parr et al. (2020), compared the effect of a restricted eating window (8 h per day) to a longer (15 h per day) eating window for 5 days. Results indicated that participants' nighttime glycemic control improved after adhering to the shorter eating window schedule, compared to the 15 h per day eating window schedule. Hutchison et al. (2019) reported that following a 9 h per day restricted eating window schedule for one week can improve glucose tolerance compared to baseline. An additional study suggested that, compared to an unrestricted eating schedule, an 8-h restricted eating window can decrease the frequency of eating events and reduce body weight and fat mass even when physical activity did not differ between conditions (Chow et al., 2020). Further work by Ravussin et al. (2019) has indicated that restricting the eating window to early in the day (i.e., 8:00am to 2:00pm) can reduce appetite, compared to a 12 h eating window (i.e., 8:00am to 8:00pm); similar findings have been reported in other work (Przulj et al., 2021). Such restriction of one's eating window has been shown to be a safe and feasible option for adults (Martens et al., 2020), and a recent meta-analysis suggests this is a promising strategy for improving metabolic health (Moon et al., 2020).

This area of research is developing rapidly, but many questions remain. One topic of inquiry relates to the effects of a nocturnal eating window, in which an individual fasts from sunrise to sunset (e.g., Ramadan fasting). Overall, evidence suggests that fasting during Ramadan is related to lower BMI and improved markers of metabolic health (for reviews, see Mindikoglu et al., 2017; Osman et al., 2020), though these positive effects may be short-lived (Fernando et al., 2019; Sadeghirad et al., 2014). Studies to date tend to be limited by short follow-up periods and heterogeneous Ramadan fasting practices around the world. Further research is needed to explicate these relationships and to determine whether these effects are primarily due to restricting energy intake to a specific window, or whether these benefits may simply illustrate the effect of reduced caloric intake. A recent review suggests that restricting the eating window and restricting caloric intake may actually have equivalent effects on body weight (Rynders et al., 2019). Given that a reduction in caloric intake was shown to accompany a restricted eating window schedule in a preliminary study (Gill & Panda, 2015), perhaps restricting one's eating window improves metabolic health primarily through a reduction in caloric intake and not through circadian mechanisms.

Taken together, this body of research indicates that the association between energy intake and energy expenditure may not simply be due to *what* and *how much* is eaten, and that improper timing of food intake may have a moderating effect on energy balance.

Impact of circadian timing of physical activity on energy balance

Research has also begun to examine the role of the timing of physical activity in energy balance. This section details the impact of the timing of physical activity on aspects of energy balance. It begins with a discussion of daily patterns of nonvolitional energy expenditure, then discusses the timing of physical activity and components of energy balance.

Daily patterns of nonvolitional energy expenditure

Early research on energy expenditure has examined daily patterns of the physiological components of energy expenditure (for review, see Shaw et al., 2019). Studies have demonstrated an endogenous circadian rhythm in resting metabolic rate (Spengler et al., 2000; Zitting et al., 2018) with resting metabolic rate increasing into the afternoon (Haugen et al., 2003) and peaking in the late evening (van Moorsel et al., 2016; Zitting et al., 2018). Romon and colleagues first reported a daily pattern of the thermic effect of food (Romon et al., 1993) while further research by Morris et al. (2015)

demonstrated the contribution of the circadian timing system in the thermic effect of food. Research has also suggested the presence of a daily rhythm in respiratory quotient. Kelly et al. (2020) utilized whole-room calorimetry to discover a diurnal pattern in respiratory quotient. Zitting et al. (2018) conducted a rigorous study which provided evidence for an unmasked circadian rhythm of respiratory quotient, though their study was limited by indirect calorimetry. Not all researchers have not found evidence of this daily pattern, however (Kräuchi & Wirz-Justice, 1994). Interestingly, Keim et al. (1997) have suggested that food intake patterns throughout the day may affect components of nonvolitional energy expenditure, such as respiratory quotient. Daily variations of other biological and behavioral factors associated with energy expenditure (e.g., physical activity) have also been demonstrated.

Timing of Physical activity and components of energy balance

In addition to physiological rhythms in energy expenditure processes, rhythms in volitional energy-expenditure behavior (i.e., physical activity) have also been shown to relate to energy homeostatic and allostatic processes, though findings have been somewhat mixed (Blankenship et al., 2021). Maraki et al. (2005) examined effects of a single exercise session, performed either in the morning or the evening, on appetite and energy intake. Exercise resulted in increased appetite and decreased satiety and fullness, without altering daily energy intake, with no differences between the morning and evening (Maraki et al., 2005). Another study found that a single session of exercise performed in the morning increased satiety more than an afternoon exercise session, but overall energy intake was not impacted (Alizadeh et al., 2015). Research by Larsen et al. (2019), however, indicated that the time of day (morning, afternoon, or evening) in which individuals engage in exercise may not have an effect on appetite and energy intake. The discrepancy in findings between these studies may be due in part to methodological differences in the time frame in which appetite was assessed. Maraki et al. (2005) measured appetite 45 min after participants completed aerobic exercise, after a cool down period, whereas Alizadeh et al. (2015) evaluated appetite immediately following exercise; further, Larsen et al. (2019) measured appetite up to 48 h after exercise was completed. Based on these findings, perhaps changes in appetite and satiety happen immediately following morning exercise, but these effects are less affected by exercise timing in the short-term, and then dissipate as time passes. A difference in the type of exercise and the intensity of exercise performed could also account for such a difference in results. Participants in the studies conducted by Maraki et al. (2005) and Alizadeh et al. (2015) engaged in aerobic exercise, but participants in Larsen et al.'s (2019) study completed high-intensity interval exercise. This is supported by a recent review by Manore et al. (2017) which concluded that higher-intensity exercise has a greater satiety effect and that specific exercises such as running may have greater effects on satiety. Additional work is necessary to determine impacts of various types of exercise on these homeostatic and allostatic processes, and to evaluate whether men and women differ in homeostatic and allostatic pressures in response to exercise.

Other studies involving long-term exercise have found mixed results in relation to weight outcomes as well. In a study of mice fed a high-fat diet, exercise late in the active part of the day protected against weight gain better than exercise performed early in the active part of the day (Dalbram et al., 2019). Surprisingly, the amount of energy intake was similar between study conditions, and the timing of exercise did not affect other homeostatic and allostatic pressures related to energy intake, such as insulin action or glucose homeostasis (Dalbram et al., 2019). The researchers posited that exercise late in the active phase may have protected against weight gain due to alterations in the timing of food intake (Dalbram et al., 2019), though the timing of food intake was not reported in this study. Additional research in human samples has provided conflicting findings. In a study of postmenopausal women, those who walked in the evening (i.e., before dinner, between 6:00 and 8:00pm) experienced a greater reduction in fat mass than women who walked in the morning (i.e., after breakfast, between 7:00 and 9:00am), as the evening walkers significantly

increased their energy intake in the morning compared to the morning walkers (Di Blasio et al., 2010). Conceivably these effects are due to the repeated acute impact of exercise on satiety levels among individuals who exercised prior to meals. These results contrast those from Alizadeh et al. (2017). In their study, women who completed 6 weeks of aerobic exercise training in the morning (i.e., between 8:00 and 10:00am) lost significantly more weight than women who exercised in the afternoon (i.e., between 2:00 and 4:00pm), due at least in part to a significant reduction in caloric intake over six weeks in the morning exercise group (Alizadeh et al., 2017). Similarly, in a 10-month supervised exercise intervention aimed at inducing weight loss, young adults who chose to perform the majority of their exercise sessions in the morning (i.e., between 7:00 and 11:59am) lost more weight than those who completed the majority of their exercise sessions in the afternoon/evening (i.e., between 3:00 and 7:00pm) (Willis et al., 2020).

It should be noted that participants in the study by Di Blasio et al. (2010) were instructed to engage in exercise either after breakfast or before dinner. Thus, those individuals who exercised in the morning ate a meal and ended their nighttime fast prior to exercising, whereas those who exercised in the evening ate a meal after exercising. This difference in the timing of food intake patterns in relation to exercise could therefore have had a differential impact on the results of this exercise regimen. Alternatively, Alizadeh et al. (2017) and Willis et al. (2020) measured participants' natural food intake patterns but did not provide participants instructions on when to eat throughout the day in relation to exercise. Therefore, participants in those studies could have self-selected their own chrononutrition patterns, such as whether to exercise before or after an eating event. Willis et al. (2020) did report that the exercise groups did not differ in their proportion of energy intake consumed in the morning, afternoon, or evening, but Alizadeh et al. (2017) did not report patterns of energy intake across the day. These studies also may have been confounded by differences in caloric intake. Mice in Dalbram et al.'s (2019) and humans in Willis et al.'s (2020) various study conditions did not significantly differ in energy intake. However, morning walkers reduced their caloric intake in research by Alizadeh et al. (2017) and evening walkers in Di Blasio et al.'s (2010) study increased their caloric intake in the morning. Taken together, participants in each of these exercise intervention studies seemed to display different patterns of chrononutrition and caloric intake. These exercise patterns and study designs likely influenced and shifted participants' chrononutrition (e.g., eating window, first and last eating events of the day), and it is unclear whether the reported results are due to exercise timing or the timing and quantity of food intake. A recent randomized controlled trial assigned sedentary male participants with overweight or obesity to consume a high-fat diet for five days, with instructions to consume meals at scheduled times (7:30am, 1:00pm, and 7:30pm) (Moholdt et al., 2021). After the five days, participants continued consuming the high-fat diet but were also randomly assigned to an exercise condition (morning; evening; no exercise) for 5 days. Results indicated that five days of a high-fat diet led to changes in lipid and amino acid metabolism. Further, the evening exercise condition resulted in some reversal of these changes, such as decreases in fasting blood glucose, insulin, and LDL-cholesterol and triacylglycerol concentrations; these beneficial effects were not seen in the morning exercise and no exercise conditions (Moholdt et al., 2021). For this study, morning exercise occurred at 6:30am and evening exercise occurred at 6:30pm; many of the participants in the morning exercise condition had to alter their sleep timing to adhere to the exercise regimen. In addition, the morning exercise condition occurred after the overnight fast, while the evening exercise condition occurred after a 5.5 h fast. Perhaps these findings are due in part to these changes in sleep timing and differences in fasting duration. Because of these discrepancies, additional research should build off of work to date and continue to provide more consistent chrononutrition timing parameters to allow for a clearer evaluation of the isolated impact of exercise timing on body composition and weight loss.

Cross-sectional studies that have examined the association between physical activity patterns and body composition have, likewise, produced mixed results. In a sample of older women, those who performed a lower proportion of the day's total physical activity in the morning had greater odds for obesity compared to those who performed a greater proportion of their daily activity in the morning

(Chomistek et al., 2016). However, a separate study reported that the timing of physical activity was not related to BMI (Marinac et al., 2019). Findings from Marinac et al. (2019) may be attributable to the fact that participants slept for approximately seven hours per night on average; this sufficient sleep duration may therefore have protected participants from such negative health effects of unhealthy timing of other behaviors. It is unclear whether sleep duration played a role in the effect seen by Chomistek et al. (2016), as the researchers did not evaluate participants' sleep duration. In sum, the available research has provided some conflicting evidence of the role of physical activity timing on energy homeostatic processes and body weight, but additional work is needed to better understand this relationship.

An integrated approach to the study of energy balance

Whereas most of the work described above studied individual circadian influences on components of energy balance in isolation, newer research has begun to take a more integrated approach by examining effects of both timing of food intake and timing of physical activity, rather than focusing on just one of these circadian-related behaviors. For instance, work that previously demonstrated the independent beneficial qualities of food intake early in the day and restricting food intake to a distinct window has recently been examined as an integrated intervention. In a randomized crossover study by Sutton et al. (2018), men with prediabetes were assigned to either a restricted eating window condition with an early last meal (6-h eating window with dinner before 3:00PM) or a control condition (12-h eating window) for five weeks. Participants then switched conditions for another five weeks. Energy intake was equivalent across conditions, and no weight loss occurred; however, the early restricted eating window condition decreased homeostatic and allostatic pressures to engage in energy intake, such as improved insulin sensitivity and insulin levels and decreased appetite in the evening (Sutton et al., 2018). Other experimental work also showed an early time-restricted eating window resulted in reductions in appetite, without impacts on energy expenditure, compared to a control eating schedule (Ravussin et al., 2019).

An additional area of research has looked to incorporate promising results from chrononutrition with existing knowledge of physical activity. In mice fed an identical high-fat diet, eating a high-fat diet early in the active phase of the day and then exercising later resulted in increased energy expenditure, decreased respiratory quotient, a smaller increase in body fat, and less weight gain overall, compared to early exercise followed by later eating (Sasaki et al., 2014). Research has also examined the combined effects of fasting and exercise training on homeostatic and allostatic pressures. In one study, individuals who fasted prior to undergoing morning exercise training had improved glucose tolerance and insulin sensitivity compared to those who consumed energy before and during the exercise training (Van Proeyen et al., 2010). Tinsley et al. (2017) examined the effects of a restricted window of energy intake (4 h/day, 4 days/week) combined with resistance training three days per week. Compared to individuals who only completed the resistance training program, participants who completed both the resistance training and the restricted energy intake window displayed a greater degree of muscle endurance, and energy intake was reduced (Tinsley et al., 2017). This work indicates that a restricted window of energy intake, coupled with increased energy expenditure, has the potential to improve strength and enhance energy balance. Further work incorporating additional circadian factors will continue to improve our understanding of the complex relationships between energy balance-related homeostatic and allostatic pressures and weight outcomes.

One such circadian factor that has garnered significant attention as a topic of research is the sleep/wake cycle. Thus far, most of the evidence has focused on the impact of short sleep duration (i.e., sleep duration of less than 6 h/night) on energy balance. As a result of this research, a theoretical model has been proposed to explain the relationship between short sleep duration and energy balance.

In an updated iteration of the energy balance model, Penev (2012) postulated that insufficient sleep results in physiological changes that disrupt energy balance. Examples of physiological

changes related to insufficient sleep include altered leptin and ghrelin levels (Spiegel et al., 2004; Taheri et al., 2004), reduced insulin sensitivity (Wong et al., 2015), increased activation in brain areas associated with emotional responses, motivation, and reward (Greer et al., 2013; St-Onge et al., 2012), and decreased resting metabolic rate (Spaeth et al., 2015). According to Penev (2012), these physiological changes then lead to behavioral changes aimed at conserving energy or providing the body with energy. Behavioral adaptations can involve changes in energy expenditure, e.g., increased sedentary behavior and decreased time spent engaging in moderate-vigorous physical activity (Booth et al., 2012; Schmid et al., 2009). Behavioral adaptations may also involve changes in energy intake, e.g., increased caloric intake (Calvin et al., 2013); increased preference for high-fat, sugary, and salty foods (Kant & Graubard, 2014; Kim et al., 2011; Spiegel et al., 2004); increased hunger and appetite (Nedeltcheva et al., 2010; Spiegel et al., 2004); and increased snacking (Kim et al., 2011). Collectively, this body of research indicates that while short sleepers may have increased energy expenditure due to extended wakefulness (Markwald et al., 2013), these individuals may be more likely to overcompensate with energy intake beyond what is necessary to sustain this extended wakefulness (Al Khatib et al., 2017; for review, see St-Onge, 2013). Thus, chronic short sleepers may have difficulty maintaining a healthy energy balance (i.e., maintain weight) or losing weight through a negative energy balance; these homeostatic and allostatic pressures tend to favor a positive energy balance.

Epidemiological studies and meta-analyses have indeed supported a link between sleep duration and energy balance, as short sleep duration is associated with increased likelihood of obesity in children and adults (Cappuccio et al., 2008; Chen et al., 2008; Ogilvie & Patel, 2017). While sleep duration is likely quite meaningful for health and energy balance, recent evidence has indicated that sleep/wake timing may also be important. For instance, studies focused on shift work have shown that its practice (i.e., working during the night and sleeping during day) has not only been linked to increased appetite for unhealthy foods (Souza et al., 2019) and decreased energy expenditure (McHill et al., 2014), but also to increased risk of obesity (Sun et al., 2017). While Penev's (2012) extension of the energy balance model has broadened our consideration of biobehavioral factors throughout the 24-h day, the current model fails to consider the specific time of the 24-h day in which sleep occurs.

Impact of circadian timing of sleep on energy balance

This section focuses on the effects of sleep timing and how it impacts aspects of energy balance. Key behaviors related to sleep timing are discussed, including sleep timing in non-shift workers, social jetlag, and shift work.

Sleep timing in non-shift workers

Abnormal sleeping patterns among non-shift workers may influence energy balance. For instance, in a study of children and adolescents, individuals with a delayed sleep/wake schedule (i.e., later bedtime and wake time) had higher BMI and were more likely to have an unhealthy diet compared to those who went to bed and woke up earlier (Golley et al., 2013). In a sample of adults, Baron et al. (2011) reported that late sleepers, those individuals with a sleep midpoint (i.e., the time at the middle of the sleep interval) after 5:30am were more likely to have a delayed eating schedule, such that they tended to consume a later breakfast and more energy after dinner and after 8:00pm, compared to those with a sleep midpoint before 5:30am. Late sleeping was also linked to consumption of a less healthy diet compared to normal sleepers (Baron et al., 2011). Further, a delayed bedtime has been associated with increased intake of energy-dense foods (Golley et al., 2013) and greater caloric intake (Spaeth et al., 2013), perhaps because the energetic costs of this extended wakefulness may increase homeostatic and allostatic pressure for individuals to provide the body with energy.

The sleep/wake cycle is known to significantly influence the body's insulin and glucose levels throughout the 24-h day (Van Cauter & Copinschi, 2006). Thus, it seems plausible that delayed sleep timing may also exert physiological changes associated with increased energy intake. However, it has been difficult to distinguish the effects of delayed sleep timing on metabolism from those due to insufficient sleep, as bedtime delay or wake time advancements are often accompanied by insufficient sleep (e.g., Chaput et al., 2007; Markwald et al., 2013; Spaeth et al., 2013). In an effort to test this more thoroughly, results from a pilot study by Pizinger et al. (2018) indicated that these negative effects of altered sleep timing on insulin sensitivity and glucose tolerance are seen only when accompanied by insufficient sleep. More research is therefore needed to determine the independent effects of altered sleep timing on physiological components of energy intake.

Later timing of sleep can also alter behavioral changes related to energy expenditure. For instance, Schechter and St-Onge (2014) reported that delayed sleep timing was associated with less time spent engaging in moderate to vigorous physical activity and more time spent in sedentary behavior. In addition, compared to adolescents with an early bedtime and rise time, adolescents with a late bedtime and rise time engaged in almost 30 min/day less moderate to vigorous physical activity (Olds et al., 2011). Similar findings were also discovered in a large multinational study of children: a later bedtime was positively associated with sedentary behavior and negatively associated with time spent in moderate to vigorous physical activity (Chaput et al., 2015). Overall, this indicates that among both children and adults, individuals may experience increased homeostatic and allostatic pressure to decrease energy expenditure in order to compensate for extended wakefulness.

Evidence to date has failed to examine the independent effects of sleep timing on physiological components of energy expenditure. Instead, laboratory research has shown that insufficient sleep, by way of a delayed bedtime and an earlier wake time, is associated with increased energy expenditure over the 24-h period (Markwald et al., 2013; Schechter et al., 2013); however, respiratory quotient may not be affected (Schechter et al., 2013). Though altered sleep timing and short sleep duration may require a greater amount of energy to allow one to sustain wakefulness, this body of research has consistently shown that opposing homeostatic and allostatic pressures are enacted which aim to provide the body with energy, and the amount of energy intake which occurs is beyond that which is required to maintain energy balance.

Another area of sleep timing which research is beginning to examine as a potential contributor to energy balance is the variability in one's sleep/wake schedule. Intra-individual variability in sleep/wake timing has been associated with components of energy balance, such as an unhealthy diet, more time spent engaging in sedentary behavior, and insufficient sleep (Duncan et al., 2016), as well as insulin resistance and BMI (Taylor et al., 2016; for review, see Bei et al., 2016). In addition, a recent longitudinal study by Kline et al. (2021) found that later sleep timing and more variable wake times were associated with less weight loss, among individuals enrolled in a 12-month behavioral weight loss intervention. Sleep/wake timing variability is a relatively novel area of research which should be explored in future work to further identify physiological and behavioral mechanisms which may influence metabolic outcomes.

Social jetlag

An additional component of sleep timing which has been examined in relation to energy balance is social jetlag, i.e., misalignment between social and biological time (Wittmann et al., 2006). Because the timing of school and work constraints often hinder individuals' natural sleep/wake timing behaviors, people tend to fall asleep and wake up later on free days than they do on work or school days; this discrepancy between sleep/wake timing on work or school days and free days has been coined social jetlag (Wittmann et al., 2006). Social jetlag has been related to markers of metabolic dysfunction and obesity (Parsons et al., 2015; Roenneberg et al., 2012); however, older adults may not be as strongly affected, potentially due to fewer work obligations as individuals reach retirement

(Koopman et al., 2017). Subsequent research has attempted to uncover pathways underlying this relationship.

One way in which social jetlag may influence energy balance is through its effects on behavioral factors aimed at increasing energy intake. Social jetlag has been associated with increased total daily energy intake (Mota et al., 2019) and an increased likelihood of consuming an unhealthy diet (Mota et al., 2019; Silva et al., 2016; Zerón-Rugiero et al., 2019).

Research has also indicated that social jetlag can impart physiological changes that alter energy intake. In individuals with a metabolic-related chronic illness, social jetlag has been related to elevated fasting glucose levels (Mota et al., 2017). A recent study has suggested that the relationship between social jetlag and appetite may depend on the magnitude of social jetlag. Though energy intake was equivalent between comparison groups, Polugrudov et al. (2017) reported that normal-weight individuals with > 2 h of difference in sleep timing between work days and free days were hungrier after breakfast compared to those with ≤ 1 h of social jetlag; participants with > 2 h of social jetlag were also less satiated 2 h after consuming breakfast. Taken together, this work indicates that social jetlag may increase homeostatic and allostatic pressures to engage in energy intake.

Social jetlag may also influence energy balance through its effects on energy expenditure, though research on this topic is scarce. One observational study found that individuals with a ≥ 2 h difference in sleep timing between work or school days and free days were less physically active compared to those with less severe social jetlag (i.e., ≤ 60 min) (Rutters et al., 2014). Interestingly, social jetlag may occur in shift workers, and this combination has been shown to relate to less time spent engaging in moderate to vigorous physical activity and less energy expended through physical activity (Alves et al., 2017). However, given the limited number of studies examining this association, additional research is needed to fully understand how social jetlag may relate to energy expenditure.

Shift work

The study of shift work, which examines individuals who work, eat, and are active during the typical inactive portion of the 24-h day and sleep during the active portion of the day, may provide further insight into the relationships between sleep timing and energy balance. Shift work is increasingly common in the 24-h lifestyle of modern society; this work schedule has been associated with the development of numerous negative health consequences (e.g., Antunes et al., 2010; Van Dongen et al., 2011), as well as weight gain and obesity (Sun et al., 2017). Due to these relationships, research has begun to investigate potential mechanisms underlying this association. One pathway through which shift work may be linked to energy balance and health is through its relationships with homeostatic and allostatic pressure to engage in energy intake.

Studies have indicated that shift work may increase homeostatic and allostatic pressure to provide the body with energy through a couple of avenues. Shift work may increase appetite for energy-dense foods, i.e., high-fat and high-calorie foods (Cain et al., 2015; Souza et al., 2019) and also be tied to consumption of an unhealthy diet, such as one high in fat and sugar and low in fruit and vegetable intake (Knutson et al., 1990; Lowden et al., 2010; Nakamura et al., 2018; Peplonska et al., 2019; for exceptions, see Beebe et al., 2017; Hulsege et al., 2016) or increased snacking during the work shift (de Assis et al., 2003; Lennernäs et al., 1995; Reinberg et al., 1979). Such findings may be due to shift workers' increased homeostatic and allostatic pressure to engage in increased energy intake to stay awake and function during work. This pattern of eating during the night shift (i.e., typical inactive period of the 24-h day) has been linked to physiological changes which can impair metabolic health, such as a weakened glucose response (Centofanti et al., 2018) and reduced glucose metabolism (Grant et al., 2017).

Some cross-sectional research suggested that the negative health effects of shift work may be the result of greater total daily energy intake in shift workers (Hulsege et al., 2016; Nakamura et al., 2018), but additional evidence does not support this explanation. In a recent systematic review,

Cayanan et al. (2019) compared energy intake for night shift workers and non-night shift workers. Interestingly, researchers discovered that total energy intake and macronutrient intake were equivalent between shift workers and non-shift workers (Cayanan et al., 2019). Similar findings regarding energy intake were also reported in other studies and systematic reviews (Bonham et al., 2016; de Assis et al., 2003; Lennernäs et al., 1995; Souza et al., 2019). Though the relationship between shift work and energy balance is quite complex, overall research suggests that this abnormal sleep timing within the 24-h day may differentially affect energy balance by altering patterns of energy intake, perhaps by affecting how energy intake is metabolized by the body.

Research on energy expenditure and shift work has been sparse, with mixed findings reported. In an acute laboratory study of simulated shift work, McHill et al. (2014) demonstrated that just a few nights of shift work can lead to decreased total daily energy expenditure and a decreased thermic effect of food after a late dinner. Other research has shown contrasting effects of shift work on components of energy expenditure. For instance, in a study with objective measurements of physical activity via accelerometer, shift work was not associated with altered physical activity, compared to non-shift work (Roskoden et al., 2017). Additional research using objective assessments of physical activity showed no difference in total energy expenditure (Wakui et al., 2002) between shift workers and non-shift workers. However, Esquirol et al. (2009) used a questionnaire to estimate physical activity and discovered that shift workers displayed greater physical activity during work compared to non-shift workers. These findings may be due to the type of occupation typically utilized in shift work, as shift work is often more physically demanding than non-shift work positions. More time spent in occupational physical activity has been related to less time spent in leisure-time physical activity (Nooijen et al., 2018); this would likely contribute to the lack of difference in overall energy expenditure seen between shift workers and non-shift workers. Contradictory findings reported in these studies may also be a consequence of the method used to measure physical activity: researchers that utilized objective assessment methods (Roskoden et al., 2017; Wakui et al., 2002) found no difference in components of energy expenditure, but researchers that utilized self-report methods did find a difference between shift workers' and non-shift workers' physical activity. Further, Roskoden et al. (2017) and Wakui et al. (2002) were limited by small sample sizes. Additional analyses by Roskoden et al. (2017) compared shift-working nurses, non-shift-working nurses, and non-shift-working office workers. The researchers found that non-shift working nurses had a lower resting metabolic rate compared to shift-working nurses and non-shift-working office staff members. Roskoden et al. (2017) clarified that this result may be due to age effects on metabolism, as non-shift working nurse participants were older than the other two participant groups. Given the various energy expenditure assessment methods in these studies, additional research is needed to clarify patterns of physical activity and other components of energy expenditure among shift workers and to determine whether these relationships differ by the nature of the work (e.g., healthcare, call center, manufacturing plant).

In sum, research on sleep timing has indicated that abnormal sleep timing may increase homeostatic and allostatic pressure for individuals to increase energy intake, by altering appetitive hormones, appetite, and eating behaviors. A paucity of evidence exists regarding relationships between physical activity and sleep timing, but it seems plausible that individuals may face homeostatic and allostatic pressure to decrease energy expenditure in altered sleep timing conditions to conserve energy.

Conclusions and future directions

In conclusion, current evidence has indicated that the existing energy balance model does not consider a crucial contributor to energy balance: the timing of behaviors in the 24-h day. The timing of food intake, physical activity, and sleep may each influence energy balance by exerting changes in physiology and behavior, thereby altering homeostatic and allostatic pressure to either provide the

body with energy or conserve energy. Thus, expansion of the existing energy balance model may provide a more comprehensive approach to factors which impact energy balance and health.

The present review has identified relevant literature regarding the timing of behaviors in the 24-h day, but additional research is needed to fully understand how these behaviors affect components of energy expenditure and energy intake, and how these behaviors may affect the more dynamic and complex components of the energy balance model. Well-controlled studies which allow for assessment of the directionality of these relationships would be quite valuable. For example, research should attempt to identify whether late-night energy intake leads to an increased likelihood of breakfast skipping, or whether breakfast skipping leads to a delayed eating schedule.

In addition, it is important to recognize that a true circadian rhythm continues under constant conditions, i.e., when no environmental time cues are provided and when various 'masking' factors (e.g., physical activity, energy intake) are controlled. It is not always feasible to conduct studies under these very highly-controlled conditions, especially with research involving human subjects. However, more of this type of research is needed, as these studies allow for distinguishing between circadian rhythms and diurnal rhythms, and ensuring rhythms are independent of masking effects by behavioral and/or environmental cues.

The effectiveness of actually modifying the timing of food intake, physical activity, and sleep for weight loss should be further examined. While initial research has shown promising effects of restricting food intake to a certain time frame within the 24-h day, supplemental research is needed to determine whether this may serve as an effective tool for long-term weight loss or weight management. Studies could also be conducted to ascertain whether exercising in the morning, as opposed to the evening, may lead to increased weight loss, and to determine whether altering sleep timing can result in better weight loss or weight management. Perhaps research should also consider individuals' preferences for engaging in these behaviors as well, as this could strongly influence adherence to certain eating, exercise, or sleep schedules.

Finally, research is needed to determine whether the timing of food intake, physical activity, and sleep are variable or stable over time. Knowledge of longitudinal patterns is essential for future research and weight management efforts because this would inform the most relevant targets for intervention and to identify trait and state mechanisms related to chrononutrition. If the timing of eating, physical activity, and sleep are stable over time, this would confirm the approach presently being taken in the chrononutrition literature with interventions targeting the timing of food intake, but interventions may benefit further by also targeting the timing of physical activity and sleep. If the circadian timing of these behaviors is found to be variable over time, such findings might also suggest that circadian behavior-based interventions may be challenged by limited periods of effectiveness, and more intensive follow-up strategies could be important for maintaining energy balance and health.

As evidence continues to accumulate, this updated 'circadian' version of the energy balance model may be of use in clinical settings. Clinicians and researchers may consider healthy chrononutrition in the development of weight loss interventions; for example, individuals could simply be advised to stop energy intake after a certain time of day (e.g., 8:00pm), or to consume the majority of their calories early in the day. While the importance of adequate sleep duration in health and functioning has begun to be recognized by health care professionals, physicians and nurses should also consider sleep timing, especially if patients are involved in shift work or demonstrate variability in their sleep timing behaviors. After further research, health care professionals may also recommend engaging in exercise at a certain time of day. Future work might utilize this model to develop and test a range of weight management interventions to supplement and extend existing treatment options.

In sum, this area of research is continually evolving, with many new opportunities for further research. Existing evidence has indicated that the circadian timing of food intake, physical activity, and sleep may have substantial effects on energy intake and energy expenditure, but timing of behaviors in the 24-h day is largely ignored. Much of the current recommendations focus on *how much*

individuals eat and sleep, *what* foods are consumed, and the *type* and *frequency* of exercise, but emerging research suggests that the timing of these behaviors should also be prioritized in interventions. Targeting the timing of these behaviors in interventions may serve as a novel avenue to optimize obesity prevention and treatment efforts.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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