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REVIEW

Physiological effects of food availability times in higher vertebrates

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ABSTRACT

Food availability is a crucial ecological determinant of population size and community structure, and controls various life-history traits in most, if not all, species. Food availability is not constant; there are daily and seasonal differences in food abundance. When coupled to appetite (urge to eat), this is expressed as the eating schedule of a species. Food availability times affect daily and seasonal physiology and behaviour of organisms both directly (by affecting metabolic homeostasis) and indirectly (by altering synchronization of endogenous rhythms). Restricted food availability times may, for example, constrain reproductive output by limiting the number or quality of offspring or the number of reproductive attempts, as has been observed for nesting frequency in birds. Consuming food at the wrong time of day reduces the reproductive ability of a seasonal breeder, and can result in quality–quantity trade-offs of offspring. The food availability pattern serves as a conditioning environment, and can shape the activity of the genome by influencing chromatin activation/silencing; however, the functional linkage of food availability times with epigenetic control of physiology is only beginning to emerge. This Review gives insights into how food availability times, affected by changes in eating schedules and/or by alterations in feeding environment or lifestyle, could have hitherto unknown consequences on the physiology and reproductive fitness of seasonally breeding vertebrates and those that reproduce year round.

KEY WORDS: Food restriction, Food abundance, Metabolism, Fitness, Reproduction

Introduction

Feeding (eating) is necessary for survival. It allows an animal to meet its daily energy requirements and provides substrates for metabolic homeostasis; there is increased food intake and, concurrently, decreased energy expenditure when energy levels are depleted (Galgani and Ravussin, 2008). Eating is controlled at two levels: endogenously, by recurring appetite (urge to eat), a strong biological signal that emanates from intense homeostatic regulatory mechanisms, and exogenously, by fluctuations in the availability of both the type and amount of food resources (Saper et al., 2002; Rogers and Brunstrom, 2016). Together, these tightly coupled control systems shape an animal's foraging pattern, which ensures that appetite-controlled feeding occurs when food is readily available. Animal species show significant variation in the time, frequency and duration of eating bouts. Many diurnal birds, for example, show periodic foraging during the daytime, because of the trade-offs associated with the costs of fasting and foraging (i.e. the time and energy involved in finding suitable food).

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Both fasting and feeding periods are accompanied by changes in physiology, such as variation in the circulating levels of metabolic hormones (e.g. thyroid hormones: thyroxin, T4; and triiodothyronine, T3) and metabolites (e.g. triglycerides) (McCue, 2010; Fokidis et al., 2011).

Daily patterns in feeding are achieved mainly by the endogenous circadian clock (or clocks; Schibler, 2006; Kumar, 2017), in which a set of core 'clock' genes interact in a transcriptional–translational feedback loop and produce a near-24 h rhythm (Box 1). The most critical features of a recurring circadian clock-regulated function (=rhythm) are its alignment between tissues and its relationship with the external environmental Zeitgebers (i.e. time cues; German: Zeit=time; geber=giver; e.g. daily cycles of light–dark, feeding–fasting, temperature, etc.; Aschoff, 1981; Kumar, 2017). The latter relationship underlies the synchronization of the clock to environmental cues, and forms the basis for a reliable prediction of the regular changes in the environment to make circadian clocks advantageous to organisms.

Although the light–dark cycle is the dominant Zeitgeber of the circadian rhythms set by the principal circadian clock of the suprachiasmatic nucleus (central clock), the clocks in other tissues (called peripheral clocks) can be sensitive to other zeitgebers, such as the feeding and fasting cycle (Kumar, 2017; Pickel and Sung, 2020). The differential responsiveness of tissue clocks to different environmental zeitgebers may induce misalignment amongst peripheral clocks. For example, a shift in the timing of food access or shift work alters the rhythm of feeding–fasting and affects the peripheral clocks in the gut and liver. As a result, there can be misalignment of circadian rhythms between peripheral and central clocks; if so, this is detrimental to the overall metabolic and reproductive health of an organism (Roenneberg and Merrow, 2016). Indeed, nocturnal rodents that eat during their active time at night become obese when they are forced into circadian rhythm desynchrony by eating into inactive daytime or by exposure to bright light at night, despite having similar calorie intake (Arble et al., 2009; Salgado-Delgado et al., 2010; Coomans et al., 2013). Similarly, providing access to food to nocturnal mice only during the light phase when they would otherwise be inactive led to a complete reversal of the phase of the clock genes in the liver, stomach, intestine, heart, pancreas and kidney, without affecting the phase in the suprachiasmatic nucleus (Damiola et al., 2000). Likewise, the rhythmicity in circadian clock gene expression imparts reproductive fitness (Xu et al., 2011), and the disruption of one or more core clock genes (e.g. *bmal1* and/or *clock*) can be detrimental to reproductive health and disrupt the reproductive cycle (Sellix, 2013; Miller and Takahashi, 2014).

In an ecological sense, food is said to be 'available' when all individuals of a population have consistent access to sufficient food to provide a nutritional diet, which provides enough energy and essential nutrients to sustain various physiological processes at an optimal level. Hence, a habitat sustains increasing population sizes up to the point where the total consumption by the population equals

Box 1. Circadian molecular clock: generalized

Animals adjust to daily and seasonal patterns in feeding in order to avoid mismatches between their feeding preferences and their energy requirements. This not only allows them to maintain homeostasis by keeping physiological parameters at a preferred level but also prevents any disturbance by facilitating the anticipation of changes in energy need. This is achieved mainly by the endogenous circadian clock (or clocks) that regulates biological processes at multiple levels and is expressed as a recurring daily rhythm at multiple levels, from the molecular level to physiology and behaviour, when synchronized with environmental time cues (Zeitgebers; Zeit=time, geber=giver) (Schibler, 2006; Kumar, 2017). Cell-autonomous circadian clocks are the ubiquitous time-tracking biological system evolved to enable organisms to anticipate changes in their environment.

The molecular gears constituting a circadian clock have been identified in a set of core 'clock' genes interacting in a transcriptional–translational feedback loop (left panel of figure) with activator or positive [formed by *clock* (*circadian locomotor output cycles kaput*) and *bmal1* (*brain* and *muscle arnt like protein 1* genes] and repressor or negative [formed by *per* (*Period*) and *cry* (*Cryptochrome*) genes] limbs. Additional molecular loops of nuclear

orphan receptor genes [*rors* (*retinoid-related orphan receptor*), *rorα*, *rorβ* and *rorγ*; and *rev-erbs* (*reverse transcript of erythroblastosis*) *rev-erbα* and *rev-ervβ*] and post-translational modifications also contribute to circadian time generation (Bell-Pedersen et al., 2005; Kumar and Sharma, 2018). Periodic feeding–no feeding cycles seem to enhance the robustness or amplitude of the circadian oscillators, affecting the activity of both activator and repressor limb genes. For example, the feeding-induced mTOR pathway phosphorylates casein kinase 1 (CK1) and glycogen synthase kinase 3 (GSK3), which affect the stability of the circadian clock component period (PER) via its phosphorylation (Zheng and Sehgal, 2010). Likewise, fasting-induced AMPK, which inhibits mTOR activity, phosphorylates cryptochrome (CRY) and promotes its degradation (Lamia et al., 2009). Additionally, the levels or activity of nicotinamide adenine dinucleotide (NAD) and sirtuins also fluctuates, and affect the circadian molecular clock in response to the prevailing food cycle (Asher et al., 2008; Masri and Sassone-Corsi, 2013). The alteration in the eating pattern also impacts 24 h oscillations of clock genes, suggesting the involvement of the circadian clock in energy homeostasis (right panel of figure; original data from Batra et al., 2019).

Eating at night affects the rhythm of daily clock genes in diurnal zebra finches
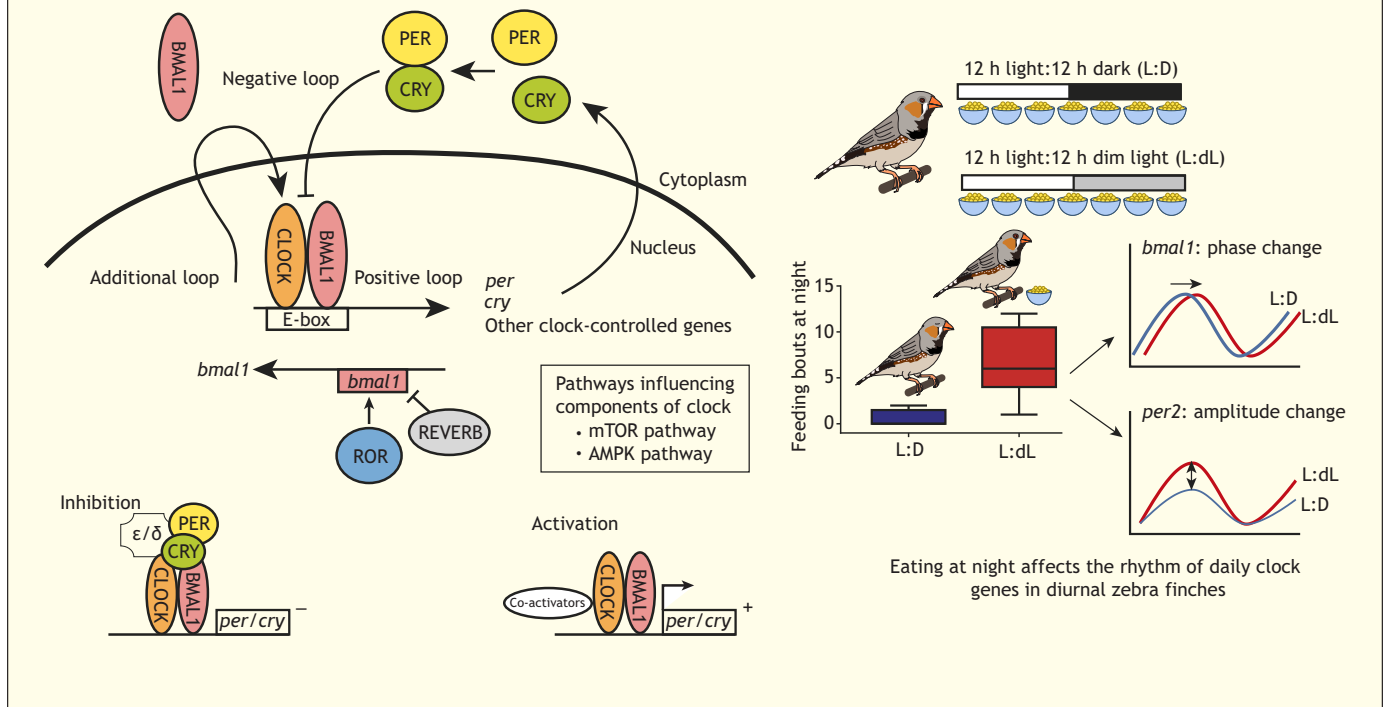
the production of food by the ecosystem. Notably, even among animals sharing the same ecosystem, there can be huge dietary diversity, as is expressed in variations in digestive and other physiological systems (Karasov et al., 2011).

In this article, we do not intend to review the literature on food and feeding behaviour, but rather we focus on findings related to the physiological effects of timed food availability in higher vertebrates, with a particular emphasis on birds. To begin, however, we present a brief discussion of the ecological and evolutionary aspects of feeding and related physiological features that are important for overall feeding physiology.

Ecology of food availability

The distribution of animal species in the wild is not random, but rather is such that the competition for acquiring food and feeding is minimized. Food availability acts as a limiting resource, and hence the spatial and temporal distribution of species is tightly coupled to

their foraging patterns. Daily access to food is also regulated by the predation risk while foraging, and by the risk of starvation; hence, there is a trade-off between starvation risk and the foraging cost that leads organisms to choose optimal food and foraging areas and/or eat available food (Bonter et al., 2013).

In addition to variations during the day, there are also seasonal differences in food availability. Food abundance varies significantly throughout the year, and seasonal food abundance is dependent to a large extent on changes in environmental factors such as day length, temperature or precipitation. For example, the abundance of insects is aligned with the breeding season and abundance of many birds, and is often positively linked to the amount of rainfall. Avian reproduction, in general, is timed such that energetically demanding processes like egg production and offspring feeding coincide with peak food availability times (Nagar and vanNoordwijk, 1995; vanNoordwijk et al., 1995; Hahn et al., 2005).

Correlated evolution of diet and physiological features

Animal physiology adapts to particular features of the diet; for example, there exists a positive relationship between dietary components (e.g. sugars, starch, protein and lipids) and enzymes/transporters necessary for their digestion and absorption in the gut (Karasov and Diamond, 1988; Karasov and Martinez del Rio, 2007). The overall phenotypic and functional plasticity of the gut depends on the diet; for example, herbivores tend to have digestive tracts that are larger in volume than those of similarly sized carnivores (Stevens and Hume, 1995; Karasov and Martínez del Rio, 2007). The correlated evolution of diet and digestive features is widespread among animals, as demonstrated by phylogenetic relationships of digestive enzymes based on feeding habits and dietary specializations (Bergerson and Wool, 1988; Martínez del Rio, 1990; Schondube and Martínez del Rio, 2004).

One aspect of digestive physiology that is increasingly recognized as being of great importance is the gut microbiome, which can show huge diversity between animals on different diets. Ley et al. (2008a,b) reported that among 54 mammalian species that they studied, the bacterial diversity was lowest, intermediate and highest in carnivores, omnivores and herbivores, respectively.

The best diet for a species (i.e. the one that results in optimal digestive performance) is influenced by the gut microbiome that the host harbours. This is suggested by the animal's own genome and its interaction with the environment, and the characterization of the diversity and inferred metabolic capacities of gut microbes (Hattori and Taylor, 2009). Gut microbiota are involved in the maturation and proliferation of intestinal cells and play an important role in regulating digestive physiology (Savage, 1977; Obata et al., 2020). However, like the host's physiology, the gut microbiome is flexible and shows changes in its composition and functions with dietary shifts. Turnbaugh et al. (2009) found that the phylogenetic composition of the microbiome was changed within 24 h when mice were switched from a plant-based, low-fat diet to a sugar- and fat-rich diet; however, no further changes occurred after approximately 7 days. However, it is not understood whether the microbiome changes have functional consequences for the digestive and metabolic performance of the host.

Physiological effects of food availability times

The concept of homeostasis (i.e. that set points or regulated values may change depending on ambient conditions or because of changing physiological conditions or demands; Jackson, 1987) becomes an important issue when an animal's access to food is limited or when they have preferred eating times during the day. Experimentally, this is investigated by using food-restriction protocols, based on how much food is available in terms of the energy content (calorie-restricted feeding, CRF) and/or when during the day food can be accessed (time-restricted feeding, TRF). Both protocols use *ad libitum* (i.e. at one's pleasure) feeding as a control (see Box 2).

Physiological responses to the feeding environment are important environmental drivers of developmental and phenotypic variations, and increasing evidence suggests that there are both direct and indirect effects of time-restricted food availability. Changes in food availability could have direct effects on the activity of the hypothalamus that, in turn, would affect multiple physiological pathways. At the same time, altered food availability could cause indirect effects via the internal biological clock (Hahn, 1995; Hau and Gwinner, 1996; Perfito et al., 2008; Singh et al., 2012). Below, we discuss what is known about the effects of the timing of food availability on various aspects of animal physiology.

> **Box 2. Calorie-restricted feeding (CRF) versus time-restricted feeding (TRF): confounding effects?**
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> Food-dependent effects are investigated by using the CRF and TRF protocols. In CRF, food availability is restricted in terms of 'how much' the caloric intake is while an animal is feeding. Here, the food ration typically contains 60–80% of calories compared with *ad lib.* feeding; hence CRF enforces a reduction in the total energy intake. TRF, in contrast, restricts food intake in terms of 'when' during the day food is accessible. Here, the eating window is generally of 4–12 h day^{-1}, but allows *ad lib.* food consumption (Acosta-Rodriguez et al., 2017); hence, TRF per se does not enforce a reduction in the energy intake, unless an animal needs intermittent feeding and/or cannot store the food when available.
>
> Both CRF and TRF protocols have been used to demonstrate the beneficial effects of food restriction (Harper et al., 2006; Ottinger et al., 2005). With adjusted essential minerals and vitamins as in a balanced diet, CRF enhances both reproductive activity and reproductive life span in turkey hens (*Meleagris gallopavo*; Renema et al., 1995). TRF and CRF may not co-exist. For example, yellow-rumped warblers (*Setophaga coronate*) adapted to daily 7 h TRF by increasing their food intake by 50% without a change in digestive efficiency or the mean retention time (McWilliams and Karasov, 1998). Likewise, total food intake (also in terms of energy from seeds) did not differ between zebra finches (*Taeniopygia guttata*) fed *ad lib.* and for only 4 h per day when birds ate and stored food in their crop (Prabhat et al., 2020). Furthermore, nocturnal mice subjected to *ad lib.* and 8 h TRF at night had equivalent caloric intake; importantly, unlike *ad lib.* controls, mice on TRF with a high-fat diet were neither obese nor showed obesity-related metabolic disorders (Hatori et al., 2012).
>
> Nonetheless, a confounding effect of TRF with CRF cannot be discounted completely if access to food was shorter in time than required for an animal to consume and fulfil its energy needs; then, TRF might inadvertently enforce a CRF regimen. More detailed investigations are needed to elucidate the limits of TRF, and its differential effects from CRF.

Effects on circadian rhythms

Many vertebrates show a daily rhythm in feeding, as they do in their activity (rest and sleep–wake patterns) (Kumar and Gwinner, 2005; Kumar, 2017). The feeding–no feeding (or feeding–fasting) and activity–rest periods overlap when animals are exposed to normal light–dark cycles, suggesting that these circadian clock-controlled functions are causally linked. In support of this, studies have shown that 24 h feeding–fasting cycles have a synchronizing effect on daily activity–rest cycles in several bird species, including non-migratory house sparrows (*Passer domesticus*; Hau and Gwinner, 1996) and Indian weaverbirds (*Ploceus philippinus*; Rani et al., 2009) held under both periodic (light–dark, LD) and constant (LL) light environments.

Various experiments have shown the effects of 24 h food presence:food absence (P:A) cycles in the development of the migratory phenotype (body fattening and *Zugunruhe*, or migratory restlessness, which in captive birds is akin to migratory flight when they are disallowed from migrating) in migratory songbirds. For example, there was an increase in nocturnal melatonin secretion and a reduction in *Zugunruhe* following food reintroduction after food deprivation for 2 days in blackcaps (*Sylvia atricapilla*); fasting and refeeding were considered to be simulating migratory flight and stopover, respectively (Fusani and Gwinner, 2004, 2005). Further, food availability times can act as a Zeitgeber; for example, food access from hour 2 to hour 11 seems to synchronize *Zugunruhe* in blackheaded buntings held under constant dim light (Fig. 1A).

Twice a year, migratory diurnal songbirds fly at night over distances of several hundred kilometres. These birds show interesting seasonal differences in phase coupling between

A Food availability time synchronizes daily *Zugunruhe*
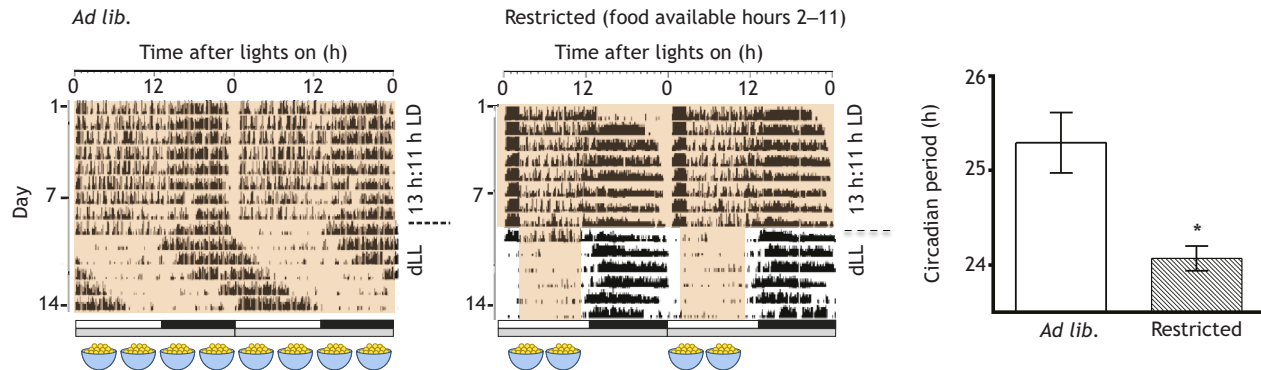
B Food availability time affects duration and amplitude of *Zugunruhe*
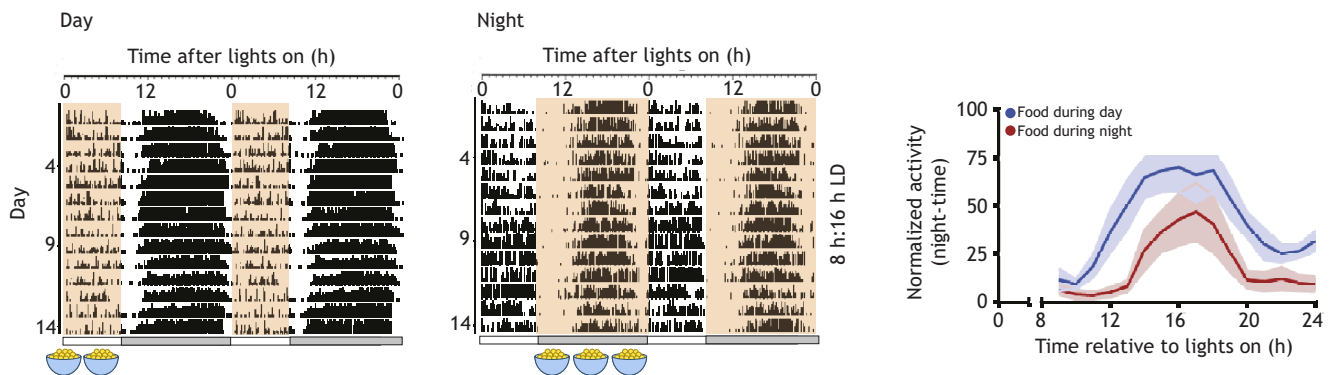

Fig. 1. Effects of food availability times on daily activity behaviour of migratory blackheaded buntings. (A) Double plot of 24 h activity–rest pattern of birds initially exposed to 13 h of light and 11 h of dark (13 h:11 h LD) and subsequently released into constant dim illumination (dLL). Peaks on the plot represent periods of activity. Birds were fed *ad lib.* (left) or given food for 9 h during the light period (hours 2–11, hour 0=lights on; middle) when they were released into dLL. Note the synchronization of photostimulated *Zugunruhe* (nocturnal migratory restlessness) under dLL in birds under restricted feeding but not in the *ad lib.* food group, as also shown by the circadian period (time interval between activity onset of two consecutive days) of the locomotor rhythm (right). Bars represent mean (±s.e.m.) circadian period (*ad lib.* fed versus food-restricted group; n=8). (B) Double plot of 24 h activity–rest pattern of birds exposed to 8 h:16 h LD with a low-amplitude light–dark cycle (light=25 lx; dark=5 lx), which was stimulatory. The food was available either during the day (left) or during the night (middle). There was an effect on the amplitude and duration of *Zugunruhe* (right). Data are mean (±s.e.m., n=6) normalized activity counts at night (*Zugunruhe*) from hour 8 to hour 24 of food availability during the day and night. Bars underneath the actogram represent the light and dark period; food cups and orange highlighting represent the food availability times. The graphs were plotted using original data from Rani et al. (2006; top left) and Singh et al. (2012; top right and bottom).

feeding and activity behaviour: during the non-migratory season, there is complete phase overlap of feeding and activity periods that are restricted mainly to the light; in contrast, feeding and *Zugunruhe* periods of birds during the migratory season are opposite in their phase profiles (Daan and Aschoff, 1975). A laboratory study investigated the relationship between feeding and activity behaviour in migratory blackheaded buntings, in which daily feeding patterns are generally inseparable from the LD cycles; as in most day-active species, the onset and end of feeding coincides with lights-on and lights-off times, respectively, of the LD cycle (Singh et al., 2012; Fig. 1). When the food availability was manipulated such that it overlapped either with the light or dark period of the LD cycle, there was a reduction in both the duration and amount of *Zugunruhe* when food was available at night but not when it was available during the day (Fig. 1B), when food effects were not discernible (Singh et al., 2012). This suggests that there is a hierarchy of environmental agents involved in the synchronization of circadian behaviour; food cycles act as a synchronizer in the absence of a dominant natural LD cycle. Besides the effect on the timing and duration of *Zugunruhe*, the resynchronization of circadian behavioural (activity–rest)

rhythms to food availability cycles can have implications for the survival of birds. For example, when buntings were presented food at night alone, four out of the eight birds that were resynchronized to food cycles in about 6–9 days by delaying their *Zugunruhe* onsets did not survive, whereas the other four birds that were resynchronized in about 11–14 days by advancing their *Zugunruhe* offsets survived through the experiment (Singh et al., 2012).

In another study, European starlings (*Sturnus vulgaris*) were exposed to a continuously lengthening or shortening LD Zeitgeber (i.e. changing cycle length, *T*). This induced alterations in the phase relationships of circadian clock-controlled activity, feeding and melatonin secretion cycles, because of differences in the rate of their entrainment to consistently varying *T*. The rhythms first broke loose from the LD Zeitgeber, then became out of phase, and finally ran free when *T* exceeded the entrainment limit of the circadian oscillators, suggesting a tight coupling of circadian oscillators governing behavioural rhythms in starlings (Kumar et al., 2007). Interestingly, the daily melatonin secretion pattern seemed to be more closely linked to feeding than to locomotion

rhythm (Kumar et al., 2000). Periodic feeding–no feeding cycles seem to enhance the robustness or amplitude of the circadian oscillators, as shown by the activity of the activator and repressor components of the circadian molecular clock (Longo and Panda, 2016; Box 1).

Effects on metabolism

The digestive system (including the liver) is physiologically expensive; it accounts for about 20–25% of daily energy expenditure (Martin and Fuhrman, 1955; Cant et al., 1996; Konarzewski and Diamond, 1995; Piersma, 2002). Natural selection has, therefore, ensured an apparent economy of design in the features of the digestive system – as discussed above, these are matched to food availability and the digestive system's quality to facilitate enzymatic and absorptive capacities that are modestly in excess of their corresponding loads (Diamond, 1991, 1993; Karasov and Martínez del Rio, 2007). Notably, many seasonally breeding animals, particularly avian migrants, switch from one diet type to another throughout their annual life history.

Independent of the quality of constituents (e.g. percentage of carbohydrate, protein, fat), the quantity (total calories) and timing of food consumption are crucial for the maintenance of good metabolic health. Hence, apart from what and how much one eats, the time when one eats has important physiological effects; for example, even when provided with identical meal size, the post-prandial rise in glucose after dinner is twice that of its post-breakfast levels (vanCauter et al., 1997). Hence, the anabolic and catabolic phases of body metabolism in healthy individuals alternate and coincide with the feeding and fasting periods, respectively. In contrast, irregular and frequent feeding bouts disturb the fasting state, and most likely maintain fed-state physiology throughout the day. Clearly, therefore, TRF allows the regular daily fasting period to induce a normal counter-regulatory metabolic state (opposite actions of the set of regulatory mechanisms) and imparts pleiotropic benefits (Panda, 2016). For example, the secretion of glucagon counter-balances the actions of insulin, which is secreted from the pancreatic beta-cells in response to increased blood glucose levels (Sprague and Arbelàez, 2011). TRF prevents obesity without reducing food intake or increasing activity in mice (Hatori et al., 2012; Chaix et al., 2014, 2019). In humans, night-eating syndrome (where an individual eats most of their daily calorie intake late at night) is associated with obesity (O'Reardon et al., 2004).

Eating at the 'wrong time' of day can negatively affect metabolism even when animals are exposed to a TRF paradigm. For example, TRF for 4 h in the afternoon of a 12 h day (i.e. feeding during hours 8–12 of the 12 h lights-on period) affects hepatic metabolism in zebra finches exposed to 12 h:12 h regimes with illuminated light and dark periods (12 h light of ∼150 lx; 12 h dark of ∼5 lux) (Batra et al., 2019). Nocturnal eating enhances mid-night blood glucose levels and reduces peripheral T4 levels, indicating reduced metabolism rate in zebra finches (Batra et al., 2019). Similar effects are found when food availability is unpredictable (i.e. during food restriction), which leads to increased baseline corticosterone (CORT) levels in mountain chickadees (*Poecile gambeli*; Pravosudov et al., 2001) and zebra finches (*Taeniopygia guttata*; Marasco et al., 2015).

Food-induced effects can be discerned in the liver, which is crucial in maintaining energy (metabolic) homeostasis. There is significant cellular lipid accumulation in response to food-induced impaired metabolism in both mammals and birds (Mehlem et al., 2013; Batra et al., 2019). Transcriptional assays of genes associated with glucose and fat metabolism (e.g. *g6pc*, *foxo1*, *sirt1*) also support this (Fonken et al., 2010; Opperhuizen et al., 2017; Batra et al., 2019). The alteration in the eating pattern also impacts 24 h oscillations of clock genes, suggesting the involvement of the circadian clock in energy homeostasis (Damiola et al., 2000; Yang et al., 2009; Marcheva et al., 2010; Shimba et al., 2011; Cho et al., 2012; Batra et al., 2019; Box 1). In fact, the circadian clock is intrinsically related to metabolic homeostasis (Lamia et al., 2008; Turek et al., 2005); the disruption of circadian rhythm can cause dyslipidaemia, which is characterized by abnormal levels of cholesterol and other lipids (Rudic et al., 2004). Although we know that these changes in gene expression occur, we cannot conclude whether (i) the effects are post-transcriptional or involve post-translational modifications of gene-encoded proteins (Jensen-Urstad and Semenkovich, 2012), and/or (ii) these effects are the cumulative response of multiple genetic pathways regulating metabolism and energy homeostasis (Batra et al., 2019).

Effects on reproduction

Abundant food availability is a crucial factor for the optimization of breeding schedules in small seasonally breeding vertebrates. Matching breeding to periods when food is abundant means that these animals have mature gonads and mate at the time when the chance of survival of their offspring (reproductive performance) is at its maximum. Here, we briefly review the effects of food availability on gonadal growth and development, as many species reproduce seasonally or show reproductive skewness to a season of the year. We also consider the effects of food availability on the overall reproductive performance of a species having reproductively mature gonads all through the year during adulthood.

Gonadal maturation

Increasing evidence from seasonally reproducing animals (birds in particular) has shown that food supply regulates the onset of breeding by its effects on gonadal maturation and, in females, on mating and time of egg laying. For example, there is delayed and/or sub-optimal photo-induced gonadal maturation in European starlings (*Sturnus vulgaris*) subjected to TRF in which access to food was gradually reduced from 6 h to only 2 h by the end of a 9 week experiment (Meijer, 1991). Similarly, plasma testosterone levels were decreased in adult male zebra finches after 4, 6 and 10 h of fasting as compared with those in *ad lib.* feeding controls (Lynn et al., 2010). Gonadal maturation was also compromised in Abert's towhees (*Melozone aberti*) when they received 70% of their individual average *ad lib.* food consumption (Davies et al., 2015). Consistent with TRF-induced negative effects, the introduction of a protein-supplemented diet causes an advance in date and enhances breeding success (i.e. egg-laying frequency, clutch size, hatchling success, brood size and number of fledglings) in songbirds, including resident Florida scrub jay (*Aphelocoma coerulescens*; Reynolds et al., 2003), partial migratory blue tit (*Cyanistes caeruleus*; Robb et al., 2008) and migratory black-throated blue warbler (*Setophaga caerulescens*; Kaiser et al., 2014).

Restricted food availability (RFA) effects on photoperiodic induction of gonadal recrudescence

The duration and/or time of day of food availability can affect the photoperiodic induction of body fattening and weight gain, and gonadal maturation, as shown from experiments on migratory blackheaded buntings (Kumar et al., 2001). In one experiment that tested the duration of the effect of RFA aligned with lights-off time during 16 h days, birds showed a significantly reduced

photoperiodic response when food was available for 4 h compared with that of those with access to food for 8 h or those fed *ad lib*. Here, food intake was similar in birds given food for 4 and 8 h, but was lower than in those fed *ad lib*. However, in a separate experiment that examined TRF effects, birds supplied with food for 5 h in the evening (hours 11–16, hour 0=lights on), but not in the morning (hours 0–5), showed a nearly 50% reduction in the photoperiodic induction of body fattening and testes maturation during 16 h days, although there was no difference in food intake (Fig. 2A; Kumar et al., 2001). A similar effect on long day-induced testicular growth was found in non-migratory house sparrows, *Passer domesticus* (Bhardwaj and Anushi, 2004).

Carry-over of RFA effects into subsequent breeding season

The availability of food can have carry-over effects, where past constraints on food supply can influence reproductive events in the subsequent breeding season. In a landscape-scale experiment, Robb et al. (2008) showed that blue tits fed in winter for 6 weeks with a supplementary peanut diet of the kind commonly used by the general public for feeding birds laid eggs an average of 2.5 days earlier than controls without the supplementary feeding; this suggested a better body condition of females provided with winter feeding. In addition, broiler hens that were fed twice a day also laid more eggs than those fed only once a day (Spradley et al., 2008).
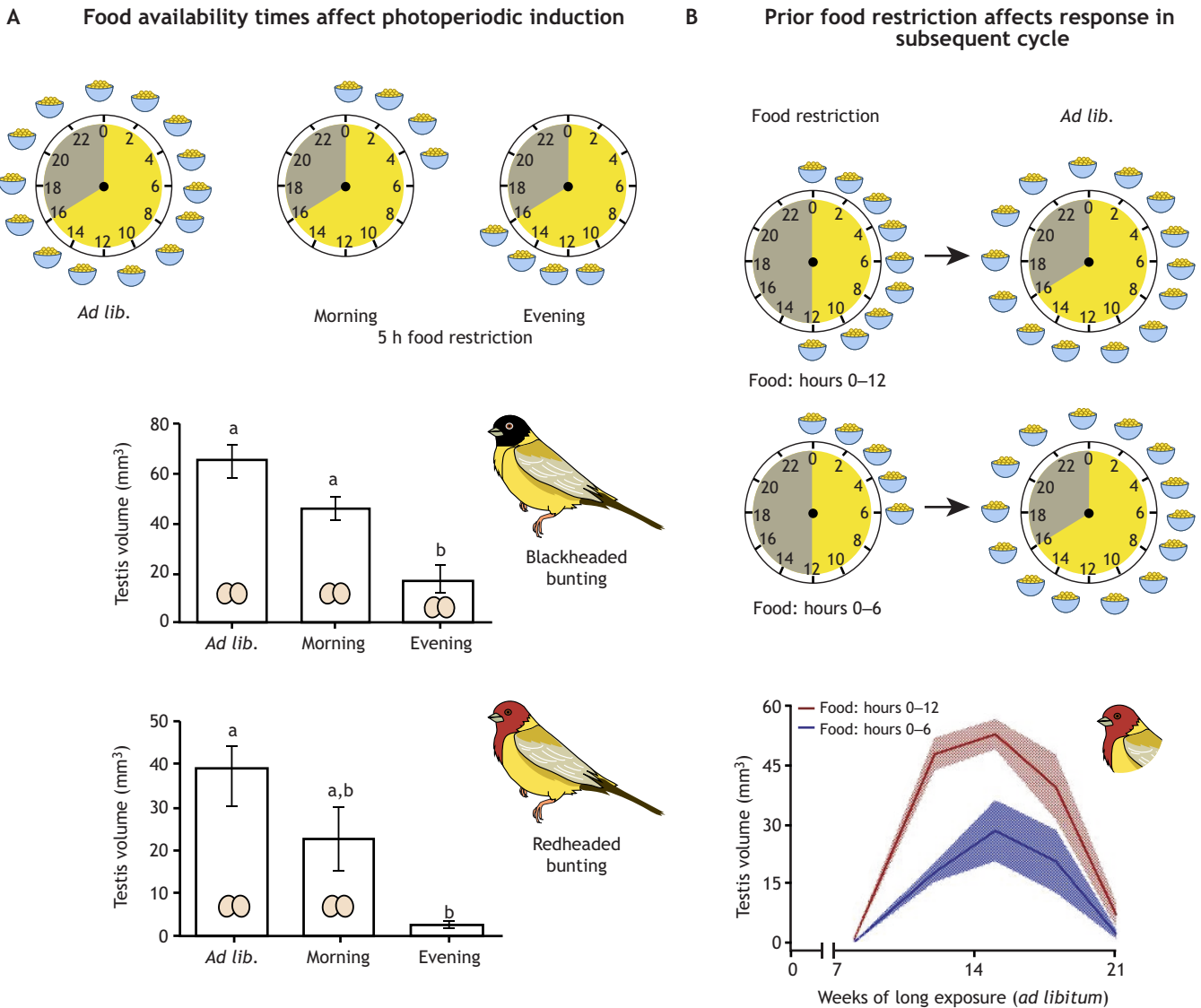

Fig. 2. Effects of food availability times on testis response in seasonal breeding migratory buntings. (A) Top: blackheaded buntings and redheaded buntings were exposed to a 16 h photoperiod (16 h:8 h LD) with *ad lib.* or 5 h restricted (morning: hours 0–5, evening: hours 11–16; hour 0=lights on) food, represented by food cups in the upper panel. Middle and bottom: mean (±s.e.m., *n*=6) testis volume in blackheaded and redheaded buntings. Different lowercase letters represent significant differences between groups. Note the reduced testis growth in the group with access to 5 h food in the evening. (B) Top: redheaded buntings were first exposed for 8 weeks to 12 h:12 h LD at low (non-stimulatory) light intensity. Concurrently, food was available for 12 h (hours 0–12) or 6 h (hours 0–6). Subsequently, birds were subjected for another 13 weeks to stimulatory 16 h:8 h L:D with food availability restored to *ad lib*. Bottom: mean (±s.e.m., *n*=6 per group) testis volume after 7, 14 and 21 weeks of long days. Note a significant effect of prior exposure to restricted feeding on the subsequent testicular growth cycle. Graphs were plotted using original data from Kumar et al. (2001) (blackheaded bunting) and Budki et al. (2009) (redheaded bunting).

Table 1. Effects of time-restricted food availability (TRF) on reproduction and offspring health of zebra finches (based on Mishra and Kumar, 2019)

Trait	Parameters measured	Direction of change relative to *ad libitum* fed birds	
		Food availability – morning	Food availability – evening
Reproduction	Initiation	↓	↓
	Mortality	–	↑
	Breeding success	↓	↓↓
	Mesotocin level	↓	↓
Offspring health	Egg quality	↓↓	↓
	Body mass	↓↓	↓
	Body size	↓↓	↓

Carry-over effects of RFA have also been tested in migratory redheaded buntings, which show a gonadal maturation–regression cycle under long days and then become photorefractory (i.e. they cease to show stimulatory effects of long days, akin to the post-breeding state of birds in the wild) (Budki et al., 2009). These photorefractory birds required several weeks of exposure to non-stimulatory photoperiods – similar to those that they would experience during the shortening late autumn and winter days – prior to the initiation of subsequent gonadal growth in late spring (Kumar, 1997). Here, buntings exposed for 8 weeks to 12 h:12 h LD at a daytime light intensity of ∼5 lx (i.e. non-stimulatory conditions), were subjected concurrently to a P:A of 6 h food present:18 h food absent (P:A 6:18) or 12 h food present:12 h food absent (P:A 12:12). Then, the birds were transferred to stimulatory 16 h:8 h LD conditions (light=400 lx; dark=0 lx) and fed *ad lib.* Food restriction during the photorefractory phase affected gonadal development in the subsequent growth phase of the annual breeding cycle. There was a slower recovery from the photorefractory state and an attenuated testis response under 16 h:8 h LD conditions in birds that were pre-treated with P:A 6:18, as compared with those pre-treated with P:A 12:12 (Fig. 2B; Budki et al., 2009). Because the number of calories that was consumed by birds was not determined in all these experiments, we cannot comment on whether the effects that were reported were due to TRF or to differences in the net energy available from the ingested food, akin to a situation when animals are subjected to a CRF regime.

Reproductive performance: the quality–quantity trade off
Breeding birds can respond in four possible ways to limited energy reserves and available resources: (1) parents can reduce egg size in order to produce more offspring and, in turn, an increased number of surviving young; (2) parents can invest additional energy in egg production to increase the number of surviving young, although the allocation of more energy would potentially reduce energy available for themselves or for post-egg developmental stages, affecting the survival probability of the young; (3) parents can delay egg production until they have more reserves stored; however, delaying egg production can result in fewer nesting attempts and increased mortality of young; (4) parents can avoid breeding completely during a breeding season when food supply is unfavourable, although this can be risky for species that may not have a high probability of breeding in the subsequent season. Irrespective of these four possible responses to limited resources, parents can differentially allocate available nutritional resources to eggs and hatchling feeding in order to maximize the fitness of their offspring when they are faced with nutritional deficits. The mother's nutritional state is particularly known to affect the size, number and macronutrient composition (e.g. protein and lipid content) of eggs laid (Reynolds et al., 2003).

In a recent study, Mishra and Kumar (2019) demonstrated the food-availability time-dependent trade-off of 'quantity' (offspring produced and/or survived) for 'quality' (offspring health) in continuously reproducing zebra finches. Indoor bred zebra finches were subjected for about a year to a TRF regime, in which they were provided with food for 4 h in the morning (hour 0–4 of lights on) or evening (hour 8–12 of lights on) of a 12 h light period. In comparison to controls on *ad lib.* food, the pairs on evening TRF showed a significant delay in the onset of breeding and produced fewer offspring; however, their eggs were of better quality and the offspring – although fewer in number – were larger in size and heavier. By contrast, when compared with *ad lib.* feeders, the pairs on morning TRF showed no effect on reproductive fecundity but had poor-quality eggs and lower-quality offspring; for example, the offspring were smaller in overall size, showed reduced skeletal growth and weighed less when they reached adulthood (Mishra and Kumar, 2019; Fig. 3, Table 1).

Neuroendocrine effects
The effects of food availability times on reproductive success reflect the activity of the reproductive (hypothalamic-pituitary–gonadal, HPG) axis, based on changes in circulating levels of luteinizing hormone (LH), follicle-stimulating hormone (FSH), oestradiol, testosterone and mesotocin (Onagbesan et al., 2006; Valle et al., 2015; Mishra and Kumar, 2019). In the absence of good evidence for how the timing of food availability possibly exerts its effects on the HPG axis, we propose that four mutually inclusive neuroendocrine pathways might be involved. First, food availability times might affect the hypothalamic peptide and enzyme pathways that are involved in photoperiodic activation of the pituitary–gonadal axis, assuming a common functional basis of reproductive axis activation across seasonal and non-seasonal species. These pathways might include sequential activation of gene switches comprising the thyroid hormone-responsive pathways (e.g. genes coding for types 2 and 3 deiodinases, DIO2 and DIO3, whose reciprocal switching alters local T3 concentration), gonadotropin releasing hormone (GnRH) secretion and gonadal maturation (Nakane and Yoshimura, 2014; Surbhi and Kumar, 2015). GnRH has two functional isoforms: GnRH-I (synthesized and secreted mainly from the hypothalamic preoptic area), which controls gonadal maturation, and GnRH-II (synthesized mainly in the midbrain region), which regulates reproductive behaviour (Maney et al., 1997). Concurrently, the gonadotropin-inhibiting hormone (GnIH; secreted from the hypothalamic paraventricular nucleus) influences gonadal maturation and reproductive behaviour by exerting opposing effects on GnRH-I and GnRH-II neurons (Ubuka et al., 2008). GnIH neurons show an increased activation in Pekin ducks (*Anas platyrhynchos domestica*) faced with food deprivation (Fraley et al., 2013). However, there is no association of TRF-induced reproductive effects on hypothalamic expression of

dio2 and *dio3* genes in zebra finches (Mishra and Kumar, 2019; Mishra et al., 2020a).

Second, TRF-induced differential reproductive performance might result from differential activation of hypothalamic pathways influenced by social facilitation and reproductive behaviour of breeding pairs. Mishra et al. (2020a) found a significant reduction in GnRH-II and increase in GnIH levels in the evening TRF, compared with the *ad lib.* fed group (see Mishra and Kumar, 2019). The lack of a GnRH-I response might indicate physiological adaptation to ensure a swift onset of reproduction between mates in response to GnRH-II-induced social facilitation in zebra finches; in addition, social context modulates the GnRH response in house sparrows (Stevenson et al., 2008).

Third, food-induced effects from TRF might occur via changes in energy homeostasis, involving both reproductive and metabolic hypothalamic peptides. RFA causes a reduction of GnRH-II levels and negatively affects reproduction, whereas GnRH-II administration reverses these negative effects in musk shrews

(Kauffman et al., 2006). The food availability (or food deprivation) times can modulate GnRH-II levels, as shown by changes in hypothalamic GnRH-II-immunoreactivity and testicular GnIH levels in zebra finches (Lynn et al., 2015; Mishra et al., 2020a). Although it is possible that there is more than one end point (biological response) for food-induced effects, the overall hypothalamic reproductive peptide levels in response to altered food availability times correlate with earlier reported adverse effects of the imposed feeding regime on the reproductive health and performance in zebra finches (cf. Mishra and Kumar, 2019; Mishra et al., 2020a,b). Consistent with this, Mishra et al. (2020a) found negative and positive correlations of GnRH-II immunoreactivity with egg-laying latency and reproductive success (offspring per brood/pair), respectively. Besides reproductive peptides such as GnRH and GnIH, there are metabolic peptides that could influence HPG axis activity. For example, neuropeptide Y (NPY), an orexigenic compound (i.e. one that can increase appetite), can affect reproduction via direct effects on GnRH and/or GnIH
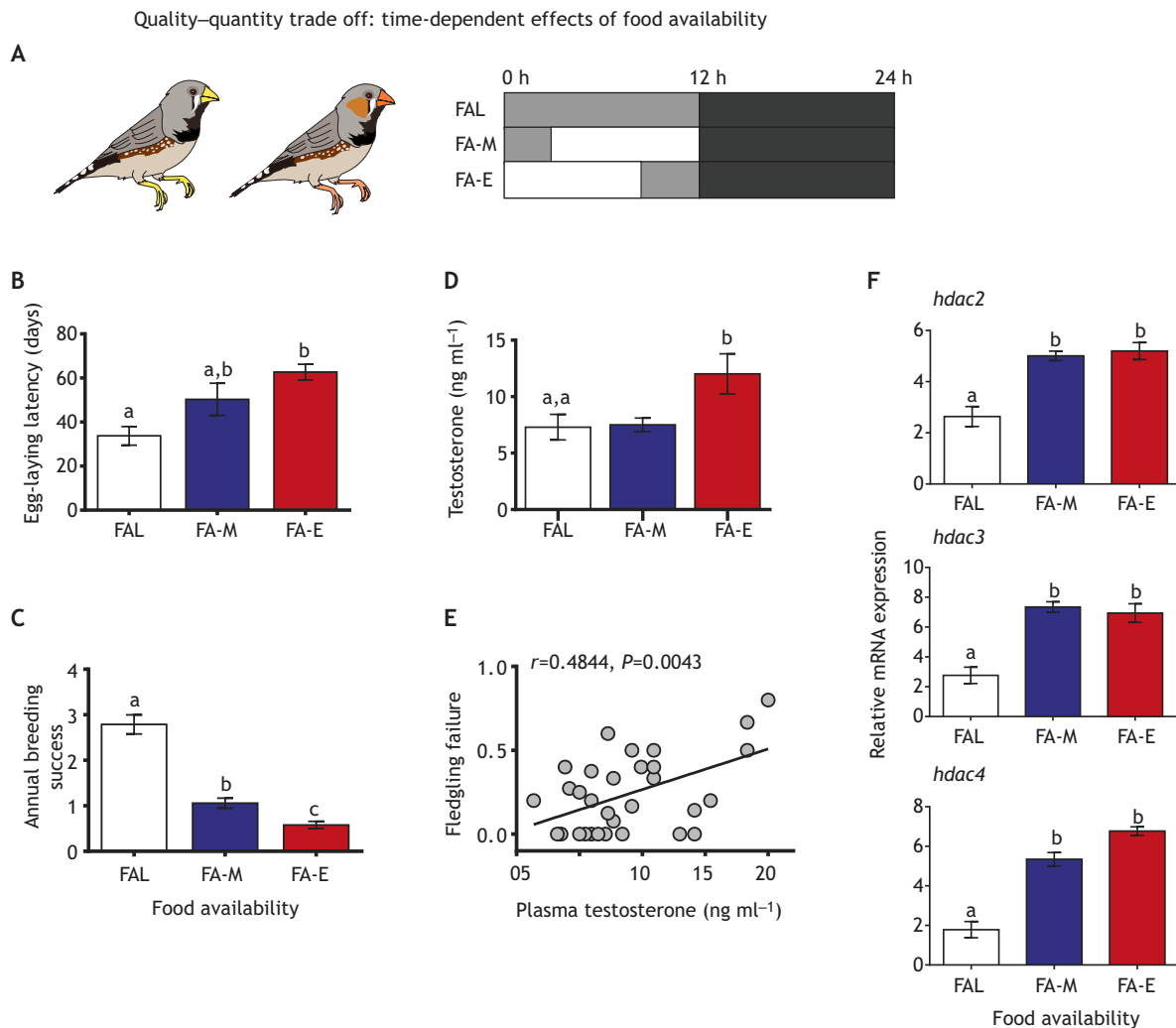

Fig. 3. Quality–quantity trade off: time-dependent effects of food availability. (A) Continuously breeding zebra finches were subjected to restricted food availability for 4 h either in the morning (hours 0–4, FA-M; hour 0=lights on) or evening (hours 8–12, FA-E), with controls on *ad libitum* food (FAL). The shaded area shows the food availability window for each group. Note a delayed initiation of breeding (B), reduced annual breeding success (C) and increased testosterone (only in evening-fed birds, D). (E) There was a positive relationship between plasma testosterone and fledgling failure rate. (F) High levels of *hdac* expression were observed in birds on food restriction. The breeding success was low in the FA-E group, whereas offspring health, measured in terms of the egg quality, body mass and body size, was affected in the FA-M group. The graphs were plotted using original data from Mishra and Kumar (2019, physiology) and Mishra et al. (2020c, gene expression).

(NPY fibres lie in close proximity to GnRH-I and GnIH neurons in the preoptic area; McConn et al., 2014; Surbhi et al., 2015) and/or indirect effects on feeding and energy homeostasis. Further, in association with NPY, CART (cocaine and amphetamine regulated transcript), which causes a reduction in appetite, was found to be involved in the regulation of energy balance in response to a fasting–refeeding paradigm (24 h of fasting was followed by 2, 6 or 10 h of free food access) in zebra finches (Singh et al., 2016). However, Mishra et al. (2020a) found no correlation between TRF and NPY or CART immunoreactivity in zebra finches on food access for 4 h in the morning and evening, with *ad lib.* fed controls under 12 h:12 h L:D. Differences in NPY and CART immunoreactivity between studies were perhaps caused by differences in starvation periods; unlike the birds in Singh et al. (2016), which experienced acute starvation for 24 h, birds were not completely starved during the long-term study of Mishra et al. (2020a; see also Mishra and Kumar, 2019).

Fourth, TRF-induced effects may involve dopamine (DA), which can affect sexual motivation. Midbrain DA levels influence sexual behaviour and parental care, which contributes significantly to reproductive success (Clarkson and Herbison, 2011; Klingerman et al., 2011; Hewlett et al., 2014). DA neurons project to both the preoptic area and the paraventricular nucleus, and DA activity affects GnRH synthesis and/or its effects on the downstream HPG axis (Clarkson and Herbison, 2011; Klingerman et al., 2011). Changes in levels of tyrosine hydroxylase (TH, a key enzyme in DA synthesis) have been commonly used as an indicator of brain DA activity (Durstewitz et al., 1998). Increased *th* mRNA levels were found in photostimulated migratory redheaded bunting exhibiting the spring migratory phenotype in captivity (Sharma et al., 2018). Interestingly, the negative and positive correlation of TH immunoreactivity with egg-laying latency and reproductive success (offspring per brood/pair), respectively, suggest that reproductive performance is related to hypothalamic TH immunoreactivity in zebra finches (Mishra et al., 2020a).

Epigenetic implications

The term 'epigenetics' refers to heritable changes in gene function without changing the DNA sequence (Goldberg et al., 2007). Epigenetic changes include chemical modifications of DNA and chromatin proteins, which affect DNA accessibility and regulate a wide range of DNA-templated processes, including gene expression. Epigenetic changes are different from changes in DNA sequence, as they are less stable and can be modified in response to various stimuli. Epigenetic mechanisms are increasingly studied and recognized as an important means of generating phenotypic diversity in response to changes in the surrounding environment (Bossdorf et al., 2008; Jablonka and Lamb, 2006; Verhoeven et al., 2016).

Various factors, such as changes in food availability or ambient temperature, alter the local environment of a species and hence may lead to changes in the epigenetic patterns of genes to adjust to the new environment. Several studies have been carried out to understand the epigenetic mechanisms underlying the effects of dietary restriction, but the majority of these focus on caloric restriction. The functional linkage of TRF with epigenetic control of physiology and behaviour is only beginning to emerge. For example, in the mouse hippocampus, TRF significantly increased the concentration of beta-hydroxybutyrate, which inhibits the activity of the histone deacetylase (HDAC), and hence increased histone H3 acetylation (Landgrave-Gómez et al., 2016). In that study on a pilocarpine-induced seizure mouse model system, TRF induced an alteration in energy metabolism by modifications in chromatin structure, facilitating the transcription of genes that confer anticonvulsant activity, i.e. reduced the severity of epileptic fits (Landgrave-Gómez et al., 2016).

Among birds, when food is available either for 4 h during the morning or for 4 h during the evening, zebra finches show changes in the expression of genes involved in DNA methylation (*dnmts*, *tets*) and histone modification (*hat1*, *hdacs*) in the hypothalamus, liver and gonads of both male and female birds, although with tissue-specific and sex-dependent expression patterns (Mishra et al.,

Table 2. Effects of time-restricted feeding (TRF) on biological functions

Biological process/function	Species/tissue (reference)
Peripheral circadian clock:	Mice (Damiola et al., 2000)
The change in eating times alters 24 h oscillation of clock genes in liver	Zebra finch (Batra et al., 2019)
	Comprehensive review (Longo and Panda, 2016)
Regulation of metabolism:	Mice (Hatori et al., 2012)
TRF allows regular daily fasting period and prevents obesity without reducing food intake.	Mice (Chaix et al., 2014, 2019)
Reproductive axis and gonadal maturation:	Musk shrews (Kauffman et al., 2006)
(i) TRF reduces hypothalamic GnRH-II levels	Abert's towhees (Davies et al., 2015)
(ii) TRF leads to sub-optimal gonadal development	Zebra finch (Lynn et al., 2015; Mishra et al., 2020a)
	European starling (Meijer, 1991)
	Abert's towhees (Davies et al., 2015)
	Blackheaded bunting (Kumar et al., 2001)
	House sparrow (Bhardwaj and Anushi, 2004)
Reproductive performance and offspring health:	Zebra finch (Mishra and Kumar, 2019)
(i) Quality–quantity trade off observed when food was available either during morning or during evening hours only	
(ii) TRF (food available in morning only) leads to poor quality eggs, smaller overall size of offspring and reduced skeletal growth	
Epigenetic effects:	Mice (Landgrave-Gómez et al., 2016)
(i) TRF reduces HDAC activity and increases H3 acetylation	Zebra finch (Mishra et al., 2020c)
(ii) TRF alters expression of genes involved in DNA methylation [*dnmt*(*s*), *tet*(*s*)) and histone modification (*hat1* and *hdac*(*s*)]	
Carry-over effects on subsequent breeding season:	Redheaded bunting (Budki et al., 2009)
TRF during non-breeding season can compromise gonadal development in subsequent breeding season	

2020c). The overall hypothalamic and hepatic expression patterns of *hat1*, *hdac2*, *hdac3* and *hdac4* were similar but those of *dnmt(s)* and *tet(s)* are different between male and female zebra finches. More specifically, *hdac2*, *hdac3* and *hdac4* mRNA levels were increased in the hypothalamus when feeding time was restricted, irrespective of the timing of food restriction (Mishra et al., 2020c; Fig. 3F); however, hepatic *hat1* mRNA levels were increased only in the TRF-morning group. Although hypothalamic *tet(s)* was more highly expressed in TRF-evening males, hepatic *tet(s)* was more highly expressed in TRF-morning birds (*tet1*, only males). Gonadal expressions of genes involved in epigenetic modifications can vary and show sex-specific differences. For example, histone-modifying genes do not show TRF-dependent effects, except for the elevated testicular *hdac3* levels in response to TRF. Similarly, testicular *dnmt3b* and *tet2* mRNA levels were increased and decreased in TRF-morning and TRF-evening birds, respectively, whereas ovarian *dnmt1* and *tet2* mRNA levels were reduced in TRF-morning birds, and *tet1* mRNA levels were reduced in the TRF-evening birds (Mishra et al., 2020c). How these TRF-induced genetic effects relate to overall metabolic and reproductive health are unknown. This is a good area for further studies, as changes in the parental food environment can influence offspring phenotype, e.g. 4 week old chicks from mothers fed a low-protein diet had a significantly heavier body mass and pectoralis major muscle mass (Rao et al., 2009). Similarly, the female offspring of the F1 generation from a male parent fed on a high-fat diet showed altered expression of more than 600 genes associated with modified β cell functions (Ng et al., 2010).

Conclusions and perspective

Clearly, the timing of food availability (or food deprivation) has effects at multiple levels, including behaviour, metabolism, neuroendocrinology, reproduction and epigenetics (Table 2). Much of the evidence favours the idea that food that is available or eaten at the 'wrong time' of day negatively impacts metabolism and reproductive ability, and can result in a quality–quantity trade-off in the face of a limited feeding environment. However, the mechanistic basis of food-availability time-dependent effects remains unresolved. Based largely on TRF effects on metabolism and reproduction in selected species, the accumulated evidence centre on two main hypotheses. The first suggests that there is a direct effect of TRF on metabolism, because the cost to forage for and store sufficient food during a period of limited food availability reduces the energy available for physiological activities, including those related to reproduction (Maurer, 1996). If this is true, TRF should affect body mass and metabolic hormones (e.g. thyroxine, T4; CORT), which was not found to be the case in a study on zebra finch pairs in which birds exhibited reduced reproductive success but their body mass and T4 levels were not affected (Mishra and Kumar, 2019).

The second hypothesis suggests that there is an indirect effect of food availability; for example, via effects on the internal circadian clock (Box 1). The timing of food access acts as a circadian clock Zeitgeber, although its overall role is secondary to the light–dark cycle. Thus, a diurnal species forages during light hours, presumably as a result of photo-sensory limitations; its biological clock is synchronized to both light and food cues that remain well integrated during the whole day. Compared with this, there might be disruption in the coupling of light with food cues if food is absent during one or the other part of the day. We suggest that TRF-enforced changes disrupt the coupling of the daily feeding–fasting rhythm with that of the prevailing 24 h light–dark cycle. This subsequently affects clock-controlled behavioural and physiological functions. The adjustments to meal timing could be part of an adaptive strategy to reduce the disruption or misalignment in clocks comprising the circadian time-keeping system. Food availability times can, therefore, be used as a powerful Zeitgeber to disrupt or restore the synchrony of circadian rhythms underlying the physiology, behaviour and possibly higher order brain functions in animals and humans. This is an attractive proposition, but fails to account for homeostatic adjustments in terms of the behavioural and physiological effects that individuals might undergo in response to limited food availability, such as during TRF (Dall and Witter, 1998).

In spite of the limitations, both hypotheses are consistent with the overall idea that, in response to metabolic signals resulting from the prevailing feeding environment, animals modulate and optimize physiological processes underlying various biological events, including reproduction and breeding success. Mechanistically, this involves concurrent activation at multiple levels in both central (e.g. hippocampus, hypothalamus and midbrain) and peripheral (e.g. liver and muscle) tissues, which are involved in metabolic and energy homeostasis, behavioural motivation (e.g. desire to engage sexually) and the reproductive system (HPG axis). Taken together, it appears that food provisioning can potentially alter future reproductive performance and perhaps offspring quality; this could consequently affect the population dynamics of the species, an idea which remains to be investigated.

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