

Morningness—Eveningness and Sociosexuality from a Life History Perspective

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MORNINGNESS-EVENINGNESS

Basic Aspects of Morningness– Eveningness

Many human biological processes are regulated by circadian rhythms, sometimes referred to as 'internal clocks'. These circadian rhythms apply to hormone concentrations, brain activity, heart rate, and body temperature. In humans and many other animals, a 'master clock' is attuned to a 24-hour cycle, and corresponds to sleep and wakefulness. The master clock in humans operates through the action of the suprachiasmatic nucleus (SCN) in the hypothalamus (Herzog et al., 1998). Although our circadian rhythms have been selected for based on a general pattern of light and dark, environmental factors can influence circadian rhythms, and rhythms can vary between people.

Morningness-eveningness - or chronotype - refers to the notion that individuals vary from one another in preferences for the timing of waking up and falling asleep, as well as for

diurnal peaks in activity and performance, such that some individuals tend to be more active, both cognitively and physiologically, in the morning, whereas others tend to be more active in the evening (Randler et al., 2016). Variation in morningness-eveningness tends to occur along a continuum, and the individuals at the two extremes of this continuum are often denoted as morning-types and evening-types, or 'early birds' and 'night owls'. Research has shown that approximately 40% of individuals are either morning- or evening-types, with the other 60% falling into a more neutral category (Adan et al., 2012). Propensities for being a morning- or an evening-type are significantly heritable (e.g., Hur, 2007; Hur et al., 1998; Vink et al., 2001) but age, sex, and environment are important as well.

Children are typically morning-oriented but evening orientation tends to increase in both males and females throughout adolescence (Randler, 2011; Roenneberg et al., 2004). Sex differences in morningness—eveninness also begin to appear in adolescence, with more males being represented in the eveningtype category than females (Randler, 2007). However, these sex differences disappear after women reach menopause, suggesting that that they may be functionally linked to reproduction and be regulated by reproductive physiology, at least in women (Adan et al., 2012). Early experience and environment can influence variation in morningness-eveningness. For example, individuals who spend their first few months of life in a short photoperiod (i.e., autumn and winter) tend to be morning-types, whereas those who spend their first few months in a long photoperiod (i.e., spring and summer) tend to be evening-types (Mongrain et al., 2006; Natale and Di Milia, 2011). Latitude has also been shown to have a strong effect on chronotype, with people at northern latitudes having significantly later midpoints of sleep (Natale et al., 2009). This effect is moderated by residency type, however, with larger towns being less affected by latitude (Borisenkov et al., 2012). Thus, it is probable that sunlight, and potentially artificial light as well, plays a role in the development and shaping of chronotype. However, this effect is not entirely clear, as evening-types tend to have been exposed to more sunlight post-birth, but less during life.

Measuring Morningness– Eveningness

Measurement methods for chronotype were first developed in the late 1970s. These methods include the Morningness-Eveningness Questionnaire (MEQ; Horne and Östberg, 1976), the Circadian Type Questionnaire (CTQ; Folkard et al., 1979), and the Diurnal Type Scale (DTS; Torsvall and Åkerstedt, 1980). The MEQ remains the most cited and most used technique today for assessing chronotype. It is a fairly reliable technique, with ~0.8 reliability coefficient across countries and ~0.9 across time for an individual (Adan et al., 2012). The MEQ uses 19 multiple-choice questions to generate a composite number that falls on a spectrum of eveningness (low) to morningness (high). However, the MEQ is somewhat

lengthy, and some items provide little discriminatory power. This led to the creation of the reduced MEQ (rMEQ; Adan and Almirall, 1991), which contains only five items.

One of the newest measures of chronotype is the Munich Chronotype Questionnaire (MCTQ; Roenneberg et al., 2003). The MCTQ determines chronotype by midpoint of sleep calculated on days off. It has been validated by the use of sleep logs, physiological parameters, and correlation with MEQ results (Roenneberg et al., 2003). The focus on midpoint of sleep and sleep on days off sets the MCTQ apart from its predecessors by collecting supplementary information in the questionnaire that may be useful for future comparisons.

Many biological markers, including temperature, cortisol, melatonin, and certain genetic variants, are associated with chronotype and are often used to assess measurement technique reliability. Morning-types have been shown to have a body temperature circadian phase that occurs about two hours earlier than the evening-types (Baehr et al., 2000; Kerkhof and Van Dongen, 1996). Morning-types also show stronger cortisol awakening responses (CAR) than eveningtypes (Griefahn and Robens, 2008; Randler and Schaal, 2010). Correspondingly, melatonin rhythms in morning-types occur about three hours earlier than in evening-types (Gibertini et al., 1999; Griefahn et al., 2002; Mongrain et al., 2004). Furthermore, it has been suggested that melatonin is the best marker for the circadian master clock (Arendt, 2006). In addition to circadian rhythms of temperature, cortisol, and melatonin, some genetic variants are associated with chronotype. Polymorphisms in certain genes, including CLOCK, PER1, and PER3, have been shown to correlate with chronotype (Adan et al., 2012) but these associations are not well understood.

Psychological and Behavioral Correlates of Morningness– Eveningness

Associations between morningnesseveningness and personality traits have been documented by a number of studies. Early studies used the Eysenck Personality Questionnaire (e.g., Matthews, 1988), whereas the Big Five Model has been used in more recent studies concerning chronotype (e.g., Tonetti et al., 2009). This model recognizes five main dimensions of personality: agreeableness, extraversion, conscientiousness, neuroticism, and openness (Costa and McCrae, 1992). Several other personality models have also been used to assess the relationship between chronotype and personality, including the Alternative Five-Factor Model, Temperament and Character Inventory, and the Milton Index of Personality Styles.

In general, it has been found that morning-types are more conscientious (Tsaousis, 2010), agreeable (DeYoung et al., 2007; Hogben et al., 2007; Randler, 2008), proactive (Randler, 2009), optimistic, and resilient (Antúnez et al., 2015). Evening-types tend to be more unconventional (Vollmer and Randler, 2012); more impulsive (Adan et al., 2010; Selvi et al., 2011); more into sensationseeking (Muro et al., 2011), novelty-seeking (Adan et al., 2010; Caci et al., 2004; Randler and Saliger, 2011), and risk-taking (Killgore, 2007; Maestripieri, 2014; Ponzi et al., 2014; Wang and Chartrand, 2015); display greater openness to experience, extraversion, lower agreeableness, lower conscientiousness (Randler, 2008; Randler et al., 2014; Tsaousis, 2010), and lower self-control (Digdon and Howell, 2008); are more emotionally unstable and prone to depression (Hidalgo et al., 2009; Randler, 2008; Selvi et al., 2011), and have higher levels of Dark Triad traits (i.e., narcissism, Machiavellianism, and psychopathy; Jonason et al., 2013).

It has been suggested that evening-types suffer from 'social jetlag', in that they frequently experience a mismatch between their preferred timing of diurnal activity and the demands of their environment (e.g., having to get up early for school or work; Wittmann et al., 2006). Social jetlag in evening-types may be associated with drowsiness, headaches, and difficulty in concentration, as well as low HDL cholesterol, greater insulin

resistance, and greater adiposity (Wong et al., 2015). These side effects may be due in part to - or are exacerbated by - attempts at coping with social jetlag, such as increased intake of sugary and caffeinated drinks (Foster, 2013). Morning-types may have an advantage in school due to social demands lining up with their chronotype. For example, if exams are taken in the morning, then morning-types may perform better than evening-types (Randler and Frech 2006; see also Borisenkov et al., 2010). Indeed, there is evidence that eveningness is generally associated with overall worse performance in school (see Tonetti et al., 2015, for a review). However, several lines of evidence indicate that eveningness is associated with higher performance on a number of different cognitive tasks. Roberts and Kyllonen (1999) showed that evening-types have greater working memory than morningtypes, even when the tasks were performed in the morning. Although the effect size was small (r = 0.08), Preckel et al. (2011) found in a meta-analysis that evening-types had significantly higher cognitive abilities than morning-types. Moreover, Piffer et al. (2014) found that evening-types had significantly greater GMAT scores (an admission test for Business Schools) than morning-types in both male and female business graduate students. Kanazawa and Perina (2009) have also shown that evening-types tend to have greater verbal intelligence than morning-types. In all of these studies, the effects are not due to differences in hours of sleep (this variable is usually controlled for in the analyses) but to chronotype itself. The reason why evening-types exhibit greater cognitive function remains unclear but Preckel et al. (2011) have suggested that evening-types may have developed greater problem-solving skills as a result of living in a social world that is out of sync with their chronotype.

In addition to differences in personality profiles and cognitive function, there are a host of behavioral differences between morningand evening-types. In general, evening-types engage in unhealthy or addictive behavior more often than morning-types, including increased smoking, drinking, and physical inactivity (Schaal et al., 2010; Urbán et al., 2011; Wittmann et al., 2010). Other differences in behavior are associated with evening-types' tendencies to engage in novelty-seeking, sensation-seeking, or risk-taking. In general, evening-types are generally found to be more unconventional whereas morning-types tend to be more traditional and conservative.

Until recently (Kanazawa and Perina, 2009; Piffer, 2010), investigations of the psychological, cognitive, and behavioral correlates of morningness and eveningness did not include any functional considerations concerning the possible adaptive value of these traits. New information about differences in sociosexuality associated with morningness and eveningness, however, has led to the formulation of specific functional hypotheses concerning these traits, as well as to some speculation about their possible evolutionary history. In this chapter, we argue that the functional/evolutionary significance of variation in chronotype is best understood if this trait is framed within evolutionary life history theory (LHT) and in relation to differences in sociosexuality between slow and fast life history individuals. In the next sections of this chapter, we illustrate some fundamental concepts in LHT, examine how LHT predicts interindividual variation in sociosexuality, and then review and discuss recent studies of morningness-eveningness and sociosexuality from an evolutionary perspective.

LIFE HISTORY THEORY AND SOCIOSEXUALITY

Fundamental Concepts of Life History Theory

LHT provides an evolutionary framework that examines how organisms allocate resources to activities that are relevant to their growth, survival, and reproduction in ways that maximize their fitness and based on their own characteristics and those of their environment (Del Giudice et al., 2015; Roff, 2002). One fundamental assumption of LHT is that organisms cannot capture and expend unlimited resources; therefore, investments of time and energy into one process or activity mean that investment into other processes must be reduced. Organisms that allocate resources in ways that maximize their fitness will out-compete those who allocate resources less optimally.

Individuals have two main paths to increasing fitness: investing in traits that improve survivorship and investing in traits that improve reproduction. Traits that enhance some aspects of fitness typically also have costs for other aspects of fitness, so that many traits have opposite effects on survival and reproduction, on present and future reproduction or survival, or on personal survival and reproduction and that of related individuals. However, a trade-off between two traits does not necessarily imply they must be negatively correlated because individuals with better genes or more resources can invest more in both processes than those with worse genes or fewer resources (Reznick et al., 2000). These trade-offs appear at all life stages and are relevant to a wide range of traits. The main fundamental life history trade-offs are those between growth/survival and reproduction, between current and future reproduction, between mating and parenting, and between quantity and quality of offspring (Del Giudice et al., 2015; Roff, 2002).

Allocation decisions made in relation to different trade-offs can be collectively referred to as life history strategies. Life history strategies are composed of combinations of co-adapted morphological, physiological, and behavioral traits (Flatt and Heyland, 2011). Demographic traits are also important, particularly age at maturity, age-specific fertility, and age-specific survival (Roff, 2002). Variation in life history strategies can occur at the level of species as well as at the level of individuals of the same species. In both cases, life history strategies may be broadly grouped

on a fast–slow continuum. Models of r–K selection divided species into those with early maturation, early reproduction, fast growth, short lifespan, high fertility, high quantity of offspring, and little investment in offspring quality (r-selected, or fast life history) and those with slow growth, late maturation, low fertility, and an emphasis on offspring quality rather than quantity (K-selected, or slow life history; Pianka, 1970).

Life history strategies vary as a function of age-specific rates of extrinsic mortality or extrinsic morbidity-mortality, including unavoidable causes of disability and decay that limit reproductive capacity (Del Giudice et al., 2015; Ellis et al., 2009). The degree of unpredictable environmental variation and the overall availability of resources are also relevant variables for determining optimal allocation trade-offs. For example, high extrinsic mortality in adulthood selects for typically fast life history traits, particularly early maturation, reproduction, and senescence, and concentration of reproductive effort in a short window of time, whereas high extrinsic mortality in juveniles also selects for early maturation but spreads reproductive effort over a longer window of time (Kirkwood and Rose, 1991). Similarly, variability in rates of adult mortality select for quick maturation and a concentration of reproductive effort, whereas stable adult mortality conditions but unstable pre-reproductive conditions select for iteroparity (Murphy, 1968). More generally, high extrinsic mortality in juveniles and adults reduces the relative payoff of investment in embodied capital (Kaplan, 1996).

Sexual selection may alter the fundamental life history trade-offs experienced by males and females. As a result of these differences, males and females may pursue divergent life history strategies (Kruger and Nesse, 2006; Magwere et al., 2004). Patterns of sexual selection within a species may have profound effects on differences between sexes in vital demographic traits, including time of maturation, timing of reproductive effort, and senescence. Characteristics of the environment can

account for variation in life history strategies both between and within sexes. Populations in highly variable environments may evolve a generalist strategy that performs adequately in a wide range of circumstances, or generate stochastic variation in life history strategy among offspring to increase phenotypic diversity and the likelihood that at least some offspring have optimal strategies for the environment (Ellis et al., 2009; Starrfelt and Kokko, 2012). In situations where the environment provides predictive cues, there may be selection for plasticity in life history traits, such that perception of specific cues triggers changes in traits relevant to life history (Stearns and Koella, 1986). These processes may thus produce variation in life history strategy at the individual level as well as at the population level (Belsky et al., 1991). Individual variation may also arise through genotypic factors, whether through variation in average level of a trait or degree of plasticity (Del Giudice et al., 2015).

Life History Theory and Interindividual Variation in Sociosexuality

In human research, sociosexuality refers to an individual's willingness to engage in sexual relations without closeness or commitment (Gangestad and Simpson, 1990; Jackson and Kirkpatrick, 2007). Interindividual variation in sociosexuality is typically measured in terms of restricted or unrestricted sociosexual behavior or attitudes (and, in some cases, also desires). Restricted sociosexuality typically includes monogamous sexual and relationship orientation, low number of sexual partners, and low levels of sexual activity, whereas unrestricted sociosexuality includes promiscuous sexual relationships, high number of sexual partners, and high levels of sexual activity (Gangestad and Simpson, 1990; Jackson and Kirkpatrick, 2007). Such variation in sociosexuality is relevant to differences in mating strategies; more unrestricted sociosexuality

would be beneficial for a more short-term mating strategy that emphasizes many uncommitted matings and limited parental investment (Gangestad and Simpson, 2000).

Although uncommitted and committed mating strategies have been conceptualized as opposite ends of a continuum (Gangestad and Simpson, 1990; Simpson and Gangestad, 1991), research suggests that individuals are flexible enough to simultaneously pursue short- and long-term strategies to different degrees (Buss and Schmitt, 1993; Fisher, 1998; Havlicek et al., 2005; Jackson and Kirkpatrick, 2007; Webster and Bryan, 2007). Furthermore, the relationship between sociosexual preferences and behavior is often confounded by environmental differences in opportunities for short- or long-term mating (Bailey et al., 1994). Therefore, it makes sense to consider committed and uncommitted sociosexuality, and sociosexual preferences and behaviors, on different scales (Jackson and Kirkpatrick, 2007). Jackson and Kirkpatrick (2007) propose three subscales of sociosexuality: long-term mating, shortterm mating, and previous sexual behavior.

LHT provides a powerful tool for considering the adaptive value of variation in sociosexuality (Belsky et al., 1991; Del Giudice, 2009). As sociosexuality measures preferences and behaviors related to short- and longterm mating strategies, it is inherently linked to life history trade-offs between mating and parenting activity. Thus, it is possible to use LHT to make predictions about connections between sociosexuality and life history traits. Sociosexuality might also be relevant to divergence in life history strategy between sexes, as there are different costs and benefits to short-term and long-term mating strategies for males and females. Finally, sociosexuality appears to be connected to the concept of embodied capital; self-perceived mate value, which is connected to physical condition, is related to psychological and behavioral orientation toward short-term mating among men and to previous sexual behavior among women (Jackson and Kirkpatrick, 2007).

Physical traits relevant to life history (e.g., birth weight) are also linked with sociosexuality. For example, lower birth weight typically corresponds to traits typical of faster life history strategies such that individuals with lower birth weight have a greater propensity toward short-term mating on average (Frederick, 2012). Sociosexuality also appears to be linked to endocrine function, as cortisol and testosterone concentrations and reactivity may mediate links between individuals' stable characteristics, their environment, and their sociosexuality (Puts et al., 2015; Wilson et al., 2015). In fact, the endocrine system provides a means of coordinating responses to the environment across a wide range of systems, from psychology to immunity to reproduction (Del Giudice et al., 2015). Finally, a number of personality traits are linked to sociosexuality across diverse cultures (Holtzman and Strube, 2013; Schmitt, 2008). In the rest of this chapter, we present and illustrate the hypothesis that differences in sociosexuality between morning- and evening-types may represent the expression of slow and fast life history strategies, respectively (Ponzi et al., 2015a). We begin by illustrating some possible scenarios for the evolution of morningnesseveningness in the human lineage.

MORNINGNESS-EVENINGNESS, LIFE HISTORY, AND SOCIOSEXUALITY

The Evolution of Eveningness as a Sexually Selected Trait

Since humans evolved from diurnal primate ancestors, morningness was probably the ancestral evolutionary condition for our species. Thus, hypotheses concerning the evolution of chronotype should mainly address the evolution of eveningness, under the assumption that this trait evolved relatively recently in the human lineage. Piffer (2010) was the first to propose a hypothetical scenario for

the evolution of eveningness in which this trait is specifically linked to sociosexuality and mating-related fitness benefits (see Kanazawa and Perina, 2009, for a different evolutionary hypothesis, focusing on eveningness-related intelligence). In this scenario, increased safety from predation and other ecological dangers during early human evolution may have increased opportunities to engage in social and mating activities in the late evening hours, when adults are less burdened by work or child-rearing. Individuals – both male and female – with a new genetic predisposition for eveningness presumably benefited more from these new social and mating opportunities, particularly if these individuals were not permanently pair-bonded, or if they were pair-bonded but engaged in extra-pair mating. In this scenario, evening-type males had a higher reproductive success than morning-type males, thus a genetic predisposition for eveningness gradually became more and more prevalent in the male population (morning-type males, however, continued to reproduce successfully, e.g., in the context of long-term pair-bonds with faithful morningtype females). Finally, since eveningness increased the fitness of men more than the fitness of women, eveningness became a sexually dimorphic trait, being more prevalent in men than in women (see Maestripieri, 2014; Putilov, 2014, for further elaboration of this hypothesis).

Piffer (2010) also speculated that eveningness may be a sexually selected indicator of genotypic and phenotypic quality, which includes good sleep and good health (see also Putilov, 2014; Randler et al., 2012b). The basis for this speculation lies in the fact that evening-types are at odds with the social schedule, and thus experience energetically negative effects. It has also been suggested that eveningness is an honest signal since mating and social activities often occur in the evening, when evening-types are at their peak performance. Of course, it is also possible that it is a mixture of a handicap and

honest signal. In either case, it seems likely that eveningness evolved somewhat recently in response to more modern social schedules (Jankowski et al., 2014a).

Based on his hypotheses, Piffer (2010) predicted that evening-type men would report a higher number of mating partners than morning-type men. Consistent with these predictions, Piffer (2011) reported that evening-type Italian men had significantly more sexual partners than morning-type men. Gunawardane et al. (2011) then analyzed chronotype and number of sexual partners in Sri Lanka and Italy and found that, in both instances, evening-type men reported significantly more sexual partners than morning-type men. In a follow-up study, Randler et al. (2012b) found that, in male German students, eveningness was associated with higher mating success (defined as a greater number of sexual partners in the lifespan, sexual partners mated with others, and extra-pair sexual partners during committed relationships), even when controlling for age, extraversion, and propensity for staying out late.

Morningness and Eveningness as Life History Traits

Piffer's (2010) evolutionary hypothesis was later re-framed in terms of LHT by Ponzi et al. (2015a). In this view, the behavioral and personality differences between morningand evening-types are expressions of different life history strategies: slow life history strategies for morning-types and fast life history strategies for evening-types. Consistent with this hypothesis, morningnesseveningness assessed with the rMEQ was found to be correlated with a composite measure of life history, the mini-K (Figueredo et al., 2005), so that morning-types tended to show a slower life history than evening-types (Ponzi et al., 2015a). Furthermore, in the same study, evening-types scored higher on present fatalism subscale of the Zimbardo

Time Perspective Inventory (ZTPI), whereas morning-types scored higher on the future orientation subscale of the ZTPI. Therefore, consistent with a life history perspective, evening-types are more present-oriented whereas morning-types are more futureoriented. In another study involving Polish students, morningness was positively correlated with the past-negative and presentfatalisms subscores of the ZTPI, whereas eveningness was positively correlated with the past-positive dimension (Stolarski et al., 2013). It has also been reported that morningtypes scored lower on the Deviation from Balanced Time Perspective (DBTP) scale, so that they tended to have a more balanced, or closer to 'optimal', time perspective across scales (Stolarski et al., 2011; Stolarski et al., 2013). Associations between chronotype and ZTPI subscales, as well as between chronotype and the Delayed Gratification Inventory (DGI), were also found in samples of New Zealand students and Germans of various ages (Milfont and Schwarzenthal, 2014). The effects of morningness-eveningness on future orientation and DGI were mediated by selfcontrol, as morning-types have greater selfcontrol and impulse inhibition than evening-types (Milfont and Schwarzenthal, 2014). Further support for links between chronotype and time perspective comes from samples with larger age ranges (Díaz-Morales et al., 2008; Nowack and van der Meer, 2013). However, there is some evidence that relationships between time perspective and chronotype may shift with age and interact with sex. In a sample of Germans of various ages, morningness was associated with future time perspective among men of all ages and women under 30, but there was no such relationship among women over 30 (Nowack and van der Meer, 2013). Since present- verus future-orientation is a key difference between fast and slow life history strategies, the reported associations between time perspective and chronotype are consistent with the hypothesis that variation in chronotype reflects variation in life history.

Morningness–Eveningness and Sociosexuality

The most important prediction of the hypothesis that morningness and eveningness are life history traits is that they should be associated with differences in sociosexuality that are characteristic of slow and fast life history strategies, respectively. Therefore, morning-and evening-types should exhibit restricted and unrestricted sociosexuality, respectively.

Some recent studies have provided evidence in support of this hypothesis. Jankowski et al. (2014b) examined the relationship between morningness-eveningness and three aspects of sociosexuality (sexual behavior, attitude, and desire) in male and female Polish adults. They reported that, when age was controlled for, greater eveningness was related to less restricted sociosexuality, particularly to greater acceptance of casual sex (attitude). Analysis of partial correlations done separately for females and males showed, however, that greater eveningness was related to less restricted orientation and its three facets only in females, whereas in males no relationship was found between eveningness and sociosexuality. In a related paper, Jankowski et al. (2014a) reported that chronotype had some influence on the timing for desire for sex, such that while all males and females desired sex in the evening, morning-type women were more similar to men in desiring sex also in the morning, while all evening-types desired sex later in the evening than morning-types. In a follow-up study with German students, Randler et al. (2016) reported that eveningness was associated with more unrestricted sociosexuality (both attitudes and desire, but not behavior) in both men and women.

Ponzi et al. (2015a) investigated sociosexuality in US male college students and hypothesized that time perspective may be the psychological mechanism underlying the link between chronotype and sociosexuality. Specifically, they predicted that morningtypes are more long-term mating oriented and more sociosexually restricted because they are more future-oriented, whereas evening-types are more short-term mating oriented and less sociosexually restricted because they are more present-oriented. Ponzi et al. (2015a) reported that rMEQ scores were negatively correlated with short-term mating orientation, indicating that evening-types are oriented toward short-term mating. A mediation analysis revealed that time perspective was a significant mediator of the association between chronotype and sociosexuality: the future orientation of morning-types was associated with their longterm mating orientation and relatively low sexual experience, whereas the present orientation of evening-types was associated with their short-term mating orientation and greater sexual experience. The finding that morningtypes tend to be future-oriented whereas evening-types are more present-oriented was also replicated by Marvel-Coen et al. (in press). Finally, Ponzi et al. (2015b) reported that evening-type men are more competitive with other men in the context of mate competition than morning-type men are.

Although the best evidence that eveningtypes, especially males, pursue fast life history strategies is provided by measures of their unrestricted sociosexuality or mating competitiveness, evidence that morning-types follow slow life history strategies can be provided by aspects of their social behavior that are not necessarily linked to their sexuality or mating strategies. This evidence indicates that morning-types are more relationshiporiented, more cooperative, and better team players than evening-types. For example, Maestripieri (2014) reported that morningtypes, both male and female, were significantly more likely to be in a stable relationship than single when compared to evening-types. Furthermore, Marvel-Coen et al. (in press) showed that rMEQ scores were significantly negatively correlated with subjective social status, as measured by the MacArthur scale, such that morning-types, on average, considered themselves to have lower social status. In the same study, the cooperative tendencies of morning- and evening-types were examined in two experimental economic games, the Prisoner's Dilemma and the Ultimatum game. In the Prisoner's Dilemma, morning-type men were more likely to cooperate in the task than evening-type men, whereas the opposite was true for women. In the Ultimatum Game, morning-types, both men and women, tended to require a larger offer from their partner in order to accept, whereas evening-types were, on average, willing to accept smaller offers. The cooperative and competitive tendencies of morning- and evening-types need to be investigated more systematically before any firm conclusions can be drawn. Nevertheless, the existing evidence suggests that differences in cooperativeness and competitiveness between morning- and evening-types are consistent with their slow and fast life history profiles.

Mechanisms

In addition to time perspective, there may be other psychological and physiological mechanisms mediating the association between chronotype, sociosexuality, and other aspects of social preferences or social behavior. These other mechanisms include personality traits, the brain dopaminergic system, and hormones such as testosterone and cortisol.

Although Randler et al. (2012b) found that eveningness in males is associated with a higher number of sexual partners independent of extraversion, extraversion and other personality traits characteristic of evening-types probably contribute to their sociosexuality. In addition to extraversion - which is known to be associated with short-term mating orientation and greater sexual experience (Simpson and Gangestad, 1991; Wilson et al., 2015; Wright and Reise, 1997) – other behavioral and psychological traits that have been associated with eveningness, such as Machiavellianism, impulsiveness, risk-taking, and sensation seeking, are also associated with unrestricted sociosexuality and short-term mating orientation (e.g., Caci et al., 2004; Digdon and Howell, 2008; Jonason et al., 2013).

Work on this is sparse but there have been some studies that have examined genetic factors at play in behavioral dispositions associated with eveningness and unrestricted sociosexuality. In particular, the dopamine receptor D4 (DRD4) and dopamine receptor D2 (DRD2) gene polymorphisms have been investigated as possible mediators of behavioral characteristics associated with chronotype. These studies have not linked chronotype directly with allelic variants, but have done so indirectly through linking them with behaviors that have independently been linked with eveningness. For example, Eisenberg et al. (2007b) found that individuals with the DRD2 A1 allele and the DRD4 long allele (7+ repeats) have increased impulsivity. A possible biological explanation for this is that individuals with DRD2 A1 have a greater sensitivity to reward, whereas those with the long allele of DRD4 exhibit decreased inhibition (Eisenberg et al., 2007b). Thus, individuals with both of these variants would display far greater impulsivity than individuals with only one or neither. Consistent with these findings, Dreber et al. (2009) found that men with the DRD4 long allele were significantly more likely to be risk-takers, particularly in a financial situation. Dreber et al. (2009) suggest that the biological explanation for this lies in the fact that the long allele is associated with decreased binding, thus individuals with this allele require more dopamine for a 'normal' response. This is particularly interesting considering the role dopaminergic pathways play in reward anticipation and motivation (Kelley, 2004; Kelley et al., 2005; Wise, 2002). Supplementing the connection between DRD4, sociosexuality, and chronotype, Eisenberg et al. (2007a) showed that young adults with the DRD4 long allele were also more likely to have had sex and reproduced earlier in life. These results corroborate findings from Zion et al. (2006) demonstrating that allelic variations of DRD4 are associated with sexual desire, arousal, and function.

Testosterone and cortisol can play potentially important roles as physiological mechanisms

underlying life history-relevant psychological and behavioral traits, including perhaps also morningness—eveningness. Randler et al. (2012a) reported that basal salivary testosterone was higher in evening-type men than in morning-type men and suggested that higher testosterone may be a proximate factor regulating the fast life history traits in evening-types. Other studies, however, failed to detect any significant differences in basal testosterone between morning- and evening-types, men or women (Marvel-Coen et al., in press; Ponzi et al., 2015a).

Randler and Schaal (2010) reported that morning-types had higher cortisol levels immediately after awakening than eveningtypes, whereas Maestripieri (2014) reported that afternoon cortisol concentrations were higher in evening- than in morning-types. Maestripieri (2014) also reported that basal cortisol was a significant predictor of risktaking in both men and women, and that the association between eveningness and higher risk-taking in women was mediated by cortisol; the cortisol profiles and risk-taking tendencies of evening-type females were more similar to those of males than to those of morning-type females. Other studies, however, did not report any significant differences in basal cortisol between morning- and evening-types, men or women (Marvel-Coen et al., in press; Ponzi et al., 2015a). Recently, Marvel-Coen et al. (in press) showed that morning-types had a greater increase in salivary cortisol in response to psychosocial stress than evening-types. In other work from the same lab, greater cortisol responses to psychosocial stress were associated with sociosexuality profiles characteristic of slow life histories, such as low sexual experience, low number of sexual partners, and low frequency of sexual behavior (Ponzi et al., 2016; Wilson et al., 2015). Taken together, these findings suggest that the variation in the activity of the brain dopaminergic system and of the hypothalamic-pituitary-adrenal (HPA) and hypothalamic-pituitary-gonadal (HPG) axes may explain some of the life

history-related differences in sociosexuality and other behavioral propensities between morning- and evening-types.

CONCLUSIONS

The functional significance of psychological, physiological, and behavioral differences between morning- and evening-types may be crucially linked to variation in sociosexuality associated with chronotype. Morning- and evening-types have a constellation of traits that are commonly associated with slow and fast life histories. The findings that variation in chronotype is significantly heritable, that sex differences in chronotype exist, and are most apparent in the time period between puberty and the onset of menopause in women, also strongly suggest that examining the mating strategies of morning- and evening-types can enhance our understanding of the evolution of morningness-eveningness and its functional significance. Further research on morningness-eveningness should test additional predictions of LHT, for example, with regard to the growth rates, timing of sexual maturation, and patterns of mating and parenting effort of morning- and eveningtypes, as well as further investigate the genetic, physiological, neurobiological, cognitive, emotional, and temperamental mechanisms underlying variation in morningnesseveningness both between the sexes and among individuals of the same sex.

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