



## Sources of intraspecific variation in sleep behaviour of wild great tits

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Ecologists have recently begun to recognize sleep as a behaviour that is important in animal ecology. The first steps have been taken to characterize sleep in free-living birds, but it is unclear to what extent these results can be generalized between species. To describe sleep behaviour in the wild, we videorecorded great tits, *Parus major*, in their roosting boxes during two consecutive winters and individuals in captivity for comparison. Here, we examined endogenous and exogenous correlates of sleep behaviour in free-living great tits and addressed the potential confounding issues of studying avian sleep in captivity. Like that in blue tits, *Cyanistes caeruleus*, sleep behaviour in great tits was strongly related to season, and was affected by sex, age and the environment. Although literature suggests relationships between sleep and risk-taking behaviours, possibly arising from stable differences in physiological state, sleep behaviour appeared to be plastic in great tits, and was not predicted by between-individual variation in exploratory tendencies. Captive tits initiated sleep later than wild individuals, even under natural photoperiodic conditions, suggesting that captivity alters timing and duration of sleep in great tits. Long-term repeatability in sleep behaviour was low for all variables, except morning latency (high repeatability) and evening box entry time, evening latency and frequency of awakenings (no detectable repeatability). Variation in sleep behaviour may largely represent within-individual differences in daily sleep requirements. Our study describes how different observable components of sleep are intercorrelated by providing evidence for significant within-individual correlations between sleep behaviours, which represent the integration of plasticity between traits. Consistent with low repeatability, low between-individual correlations suggest substantial behavioural plasticity in sleep, rather than a correlational structure leading to clear sleep 'syndromes'. Our study provides quantitative evidence for the factors producing phenotypic plasticity in behavioural sleep in an ecological context.

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Sleep and sleep-like behaviours are ubiquitous throughout the animal kingdom (Kryger, Roth, & Dement, 2011; Siegel, 2008). Studies on sleep and sleep deprivation indicate that sleep may function in cellular repair (Savage & West, 2007), memory consolidation, learning, synaptic plasticity (Stickgold & Walker, 2005), energy conservation (Siegel, 2005) and maintaining physical and cognitive performance (Koslowky & Babkoff, 1992). However, sleep is in many ways an underexplored phenomenon in the field of behavioural ecology (Lesku et al., 2012; Scriba, Rattenborg, Dreiss, Vyssotski, & Roulin, 2014; Steinmeyer, Mueller, & Kempenaers, 2013). Sleep may be evolutionarily homologous across the animal kingdom (Rattenborg, Martinez-

Gonzalez, & Lesku, 2009). Like mammals, birds exhibit both slow wave and rapid eye movement sleep (Campbell & Tobler, 1984), and may have evolved convergent electrophysiological characteristics in sleep states, but it is not yet clear whether sleep performs the same functions between taxa as many constitutional and ecological correlates differ when studied at the interspecific level (Lesku, Roth, Amlaner, & Lima, 2006). Thus, expanding the scope of sleep research to include field-based studies of diverse species will provide greater insight into the evolution and function of sleep across species.

There is enormous variation in sleep behaviour both between (Lesku et al., 2006; Lesku, Roth, Rattenborg, Amlaner, & Lima, 2009; Zepelin, Siegel, & Tobler, 2005) and within species (Rattenborg et al., 2008; Steinmeyer, Schielzeth, Mueller, & Kempenaers, 2010; Stuber et al., 2014) which may reflect differences in the functions of sleep, differences in selective pressures on sleep, ecological constraints on the patterns of sleep or differences in the

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effects of captivity on sleep. Variation in sleep across the animal kingdom has been partly attributed to differences in geographical location, precocial versus altricial development, size (Elgar, Pagel, & Harvey, 1988, 1990) and internal state (Davis, Darrow, & Menaker, 1983; Hagenauer & Lee, 2013; Randler, 2011; Spruyt, Molfese, & Gozal, 2011), but it is unclear to what extent these relationships exist in the wild. We examined the contributions of exogenous (i.e. the external environment; e.g. local light and temperature) and endogenous (e.g. sex, age, behavioural type) factors as sources for intraspecific individual differences in avian sleep behaviour in the wild. Furthermore, it is unclear to what extent endogenous ultradian rhythms in behaviourally defined sleep–wake cycles contribute to sleep patterns in the wild. Humans typically alternate between nonrapid eye movement and rapid eye movement sleep in approximately 90 min cycles, completing this endogenous cycle four to six times during the night (Hirshkowitz, 2004). A similar rhythm, behaviourally measured as nocturnal awakenings, occurs in free-living blue tits, *Cyanistes caeruleus* (Mueller, Steinmeyer, & Kempenaers, 2012). Describing the sources of variation in individuals' sleep behaviour under natural conditions is necessary to begin to elucidate the underlying physiological or genetic mechanisms.

There is growing evidence that individuals within species display consistent differences in sleep behaviours (Randler, 2014). Typical examples include so-called 'lark' and 'owl' types, early or late chronotypes who show morning or evening preferences (Kerkhof & Van Dongen, 1996; Mongrain, Carrier, & Dumont, 2006; Putilov, 2008; Roenneberg et al., 2004; Wicht et al., 2014) or long- and short-duration sleep types (Allebrandt et al., 2010; Gottlieb, O'Connor, & Wilk, 2007; Steinmeyer et al., 2010). Because sleep–wake cycles are partly modulated by an endogenous circadian clock with heritable components, we might expect higher individual repeatability of sleep-related behaviours compared with most other behaviours that are indirectly related to biological rhythms. However, sleep is also regulated homeostatically, and thus may be less repeatable when environmental factors, such as temperature (Lehmann, Spoelstra, Visser, & Helm, 2012), can play a large role in shaping individual-specific sleep needs.

Accumulated evidence for the existence of consistent differences between individuals in behaviour has garnered the attention of ecologists who are interested in the adaptive nature of limited plasticity. Recent studies have gone even further in their exploration of plasticity to document behavioural correlations, within populations and species. Examples include individuals behaving along a proactive–reactive axis, or a 'fast' versus 'slow' pace of life continuum (Coppens, de Boer, & Koolhaas, 2010; Groothuis & Carere, 2005; Koolhaas et al., 1999), with 'fast' individuals being more aggressive, bold and exploratory than 'slow' individuals. Consistent individual differences in behaviours including sleep and exploratory tendencies might be explained by consistent individual differences in energy metabolism which can reflect daily energy expenditure (Mathot, Nicolaus, Araya-Ajoy, Dingemanse, & Kempenaers, 2015), levels of oxidative stress (Finkel & Holbrook, 2000) and food intake requirements (Biro & Stamps, 2010). The metabolic machinery necessary to support a fast pace of life may generate a positive relationship between metabolic needs and personality traits (Careau, Thomas, Humphries, & Reale, 2008). Indeed, evidence from the mammalian literature suggests relationships between amount or timing of sleep and risk-taking behaviours (humans: Killgore, 2007; McKenna, Dickinson, Orff, & Drummond, 2007; O'Brien & Mindell, 2005) or aggression (reviewed in Kamphuis, Meerlo, Koolhaas, & Lancel, 2012), although these data are equivocal. Consistent differences in metabolism along a low/high metabolism and fast/slow 'pace of life' continuum may be reflected in sleep needs. For instance, while high metabolic rate

may allow individuals to maintain high levels of activity and energy expenditure, it may also generate high levels of tissue damage via oxidative stress that must be repaired during sleep (Savage & West, 2007). Here, we asked whether an individual's initial exploration score, which reflects repeatable exploratory tendencies in our population (Stuber et al., 2013), and is repeatable and heritable in other great tit populations (Dingemanse, Both, Drent, Van Oers, & Van Noordwijk, 2002; Dingemanse, Bouwman, et al., 2012; Drent, van Oers, & van Noordwijk, 2003; Quinn, Patrick, Bouwhuis, Wilkin, & Sheldon, 2009), can predict the observed variation in sleep behaviours.

Animal behaviourists often record and study a wide array of interrelated behaviours during certain situations that together perform a specific function (Araya-Ajoy & Dingemanse, 2014). Researchers may record timing, duration and quality as components of a single sleep function. However, such observable behaviours are not necessarily independent of each other. Multiple sleep-related behaviours may all reflect an underlying latent, unobserved, biological process that we do not measure directly but can infer from observable variables (Araya-Ajoy & Dingemanse, 2014). Here, we investigated the correlations between multiple sleep behaviours to provide information on the existence of a single sleep trait or multiple underlying sleep-related traits that may generate behavioural variation.

In this study we (1) examined individual variation in nocturnal sleep behaviour in a free-living population of great tits, *Parus major*, (2) investigated correlations between sleep behaviour and putatively important endogenous and exogenous parameters that can affect variation in sleep behaviour within a species, (3) compared sleep variables obtained in the wild with those observed in captivity, (4) tested the repeatability of sleep variables and (5) examined potential sleep 'syndrome structure' by exploring bivariate correlations between different sleep variables. This study broadens our general understanding of sleep under ecological conditions and, by comparing it with sleep in wild blue tits (Steinmeyer et al., 2010), enabled us to examine whether the observed patterns can be generalized between Paridae species.

## METHODS

### Field Procedures

Sleep data for this study were collected from roosting great tits during the 2011–2012 and 2012–2013 winter seasons during December, February and March from 12 nestbox plots. The study sites were established in 2009 in southern Germany (Stuber et al., 2013) and consist of 9–12 ha forested plots with 50 nestboxes each. All birds recorded for sleep behaviour were previously captured and marked, as they are part of a larger, long-term study.

Each winter, we caught all great tits roosting at night in nestboxes and transported them to the laboratory within 1.5 h, where they were housed individually overnight. Food and water were provided ad libitum and human disturbance was minimal. On the following morning, all individuals underwent an exploration behaviour assay between 0800 and 1100 hours following standard protocols established for this species (Dingemanse et al., 2002). Briefly, birds were exposed to a novel environment and scored for exploratory tendency based on hopping and flying movements within the environment; so-called fast explorers have higher scores, indicating more movement, whereas slow explorers have low scores. Following the behavioural assay, we recorded standard morphometric measures, sexed and aged (yearling versus adult) the birds and implanted them with a PIT tag for individual identification (Nicolaus, Bouwman, & Dingemanse, 2008; Regierung von Oberbayern permit no. 55.2-1-54-2532-140-11). After processing,

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