



## Variation in sleep behaviour in free-living blue tits, *Cyanistes caeruleus*: effects of sex, age and environment

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Although sleep is fundamental for survival, not much is known about sleep behaviour in free-living animals and between-individual variation in sleep patterns has hardly been studied, except in humans. We analysed sleep behaviour in a free-living population of blue tits in southern Germany. We recorded individuals roosting in nestboxes between November and April using infrared-sensitive cameras. We investigated the following sleep parameters: time of entering and leaving the nestbox, sleep onset, awakening time, sleep duration, midpoint of sleep, latency to sleep and frequency and duration of nocturnal awakenings. Sleep onset, awakening time and sleep duration followed seasonal changes in daylength. Blue tits slept ca. 4.8 h longer in winter than in spring. During the night, birds woke up between 23 and 230 times, but this did not change seasonally. Local light conditions influenced awakening time: birds at brighter locations woke up earlier. Females slept on average 15 min longer per night than males and this sex difference became more pronounced in early spring. Although females spent a greater proportion of the night awake than males, they still slept more overall. First-year birds spent more time in the nestbox after waking up and left the nestbox later in the morning than older individuals. Repeatability estimates showed that individuals were consistent in their sleep behaviour over the 2-year study period. Our results indicate that sleep patterns are individual-specific traits in blue tits. We suggest that the observed sex difference in sleep duration is caused by sexual selection.

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Sleep is a widespread behaviour in the animal kingdom, being found in most if not all animals (Cirelli & Tononi 2008; Siegel 2008). It is generally defined as a rapidly reversible state of immobility and greatly reduced responsiveness (Siegel 2008). Animals spend a considerable proportion of each day and of their entire lifetime asleep (Zepelin et al. 1994). Daily sleep duration can vary tremendously among species. For example, elephants and horses apparently require only a few hours of sleep, whereas the armadillo, *Chaetophractus villosus*, opossum (*Didelphis* sp.) and some species of bats spend about three-quarters of a 24 h day sleeping (Van Twyver & Allison 1970; Meddis 1975; Zepelin et al. 1994; Affanni et al. 2001). In addition to interspecific variation in sleep requirements, there is also substantial variation in sleep duration among individuals of a single species. Individual variation in duration and other characteristics of sleep behaviour have only been studied in detail in humans (Webb & Agnew 1970; Webb & Friel 1971; Roenneberg et al.

2003; Dijk & von Schantz 2005; Buckelmuller et al. 2006) and are partly explained by effects of gender and age (Lindberg et al. 1997; Hume et al. 1998; Dijk et al. 2000; Jean-Louis et al. 2000; Van Cauter et al. 2000).

Because sleep is such a ubiquitous phenomenon, it most likely serves important adaptive functions. However, there is still considerable debate about what these functions are. The early hypothesis that sleep is simply a state animals adopt when they do not have anything else to do (Meddis 1975) is clearly untenable. Many studies have shown negative consequences for animals that were deprived of sleep. For example, sleep deprivation induced DNA damage in brain and blood cells in rats, *Rattus norvegicus* (Andersen et al. 2009) and negatively affected vigilance, mood and motor or cognitive performance in humans (Ferrara & De Gennaro 2001; Van Dongen et al. 2003). Sleep may have a restorative function for the brain (Tononi & Cirelli 2006; Mignot 2008) and it may be essential for memory consolidation (Solodkin et al. 1985; Walker & Stickgold 2006; Jackson et al. 2008; Mignot 2008). Sleep may also serve to conserve energy or to reduce exposure to predators (Meddis 1975; Zepelin et al. 1994; Lima & Rattenborg 2007), although this would also be accomplished through simple resting.

Despite the fact that sleep is ubiquitous and despite strong empirical evidence that sleep is important for an individual's

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health, sleep behaviour has received little attention in studies of animal behaviour and behavioural ecology. Most studies on sleep and its functions have been conducted in captivity on mammals, and there is an extensive literature covering sleep-related issues in humans. Studies on sleep in birds are mostly limited to captive birds, especially pigeons and chickens, and focus on physiological characteristics of sleep (Ookawa & Gotoh 1965; Berger & Walker 1972; Van Twyver & Allison 1972; Walker & Berger 1972; Ayala-Guerrero 1989; Ayala-Guerrero et al. 2003). These studies have found that birds show two distinct sleep states (slow-wave sleep, SWS and rapid-eye-movement sleep, REM) characterized by changes in brain activity remarkably similar to those in mammals (Rattenborg 2006; Rattenborg et al. 2009). Furthermore, previous studies have shown that at least some bird species are able to engage in unihemispheric sleep (blackbird, *Turdus merula*: Szymczak et al. 1996; mallard, *Anas platyrhynchos*: Rattenborg et al. 1999; domestic chicken, *Gallus gallus*: Bobbo et al. 2002, 2006a, b; Swainson's thrush, *Catharus ustulatus*: Fuchs et al. 2006).

Only a handful of studies have considered behavioural aspects of sleep in birds. A few have investigated sleep and vigilance in relation to season or to the position of individuals within a flock (Lendrem 1983; Gauthier-Clerc et al. 2000; Dominguez 2003). One study investigated the influence of temperature on sleep behaviour in three passerine birds in captivity (Wellmann & Downs 2009). Another study experimentally investigated the effect of the presence of ectoparasitic hen fleas in nests of great tits, *Parus major*, on the total amount of sleep (Christie et al. 1996).

To our knowledge, individual variation in sleep behaviour has not yet been systematically studied in any free-living bird. Studies in the wild are important because sleep behaviour of animals observed in captivity may differ substantially from behaviour shown in the natural environment (Dunnett & Hinde 1953; Rattenborg et al. 2008). The general aim of our study was to investigate sleep behaviour in a natural population of blue tits. The blue tit is a widespread and common passerine bird in Europe and parts of northern Africa. In Germany, blue tits are year-round resident and inhabit deciduous and mixed woodlands, as well as parks and gardens. They breed in natural cavities, but readily accept artificial nestboxes. We made use of the fact that in winter blue tits regularly roost in nestboxes, which allowed us to monitor their night-time behaviour without disturbance.

The specific aims of this study were threefold: (1) to describe seasonal variation in several variables reflecting the timing and duration of sleep; (2) to test whether factors such as local light conditions, temperature, individual age and sex explain some of the within-season variation; and (3) to estimate the proportion of variation in sleep behaviour that is individual specific (individuality). Because most knowledge about interindividual variation in sleep behaviour comes from studies in humans, we discuss our findings in comparison to human sleep patterns.

## METHODS

### Study Site and General Field Procedures

The study was carried out during the winter seasons 2007–2008 and 2008–2009 in a population of blue tits in southern Germany (Westerholz, 48°08'N, 10°53'E). The study site (39 ha) is a natural reserve ('Naturwaldreservat') dominated by oak trees (*Quercus* sp.) and forms the northeastern tip of a larger mixed deciduous forest. In November–December 2006, we put up 277 nestboxes (12 × 15 cm and 25 cm high) with an entrance hole of 26 mm diameter, which excludes the larger great tit. Blue tits readily accepted nestboxes for roosting during winter and for breeding.

We caught blue tits inside the nestboxes during monthly checks at night in winter (November–February in both seasons) and once during nestling feeding (May–June in the breeding seasons 2007 and 2008). We determined age by comparing the coloration of primary and secondary coverts and classified individuals as either yearling or adult (Svensson 1992). We marked each bird with a numbered metal band of the German ringing scheme and with a unique combination of three plastic colour bands. We also took a 10–50 µl blood sample from the brachial vein for genetic analyses and implanted an RFID transponder (Biomark Inc., Boise, Idaho, U.S.A.) subcutaneously between the shoulder blades. This allowed us to determine the identity of individuals occupying a nestbox at night without disturbing the sleeping bird (see [Recording Sleep Behaviour](#)). Transponders were 8.5 mm long, 2.1 mm in diameter and weighed 0.067 g (0.6% of the average body mass of an adult blue tit). We did not encounter any problems during implantation and all birds behaved normally after release.

### Recording Sleep Behaviour

Every 4 weeks we checked all nestboxes at night for sleeping birds, using a handheld transponder reader (EUR 1000 Multi-Chip from EURO I.D., Weilerswist, Germany), which we moved around the outside of the nestbox. Our previous observations suggested that only rarely was a bird carrying a transponder missed using this technique. The following day, we installed infrared-sensitive cameras in all boxes where a roosting blue tit had been detected. We also cleaned nestboxes of faeces to attain higher movie quality. Cameras were programmed to record on two consecutive nights between an hour before sunset and an hour after sunrise. We refer to these two consecutive nights as a recording session. We recorded 13–37 individuals (median 27) per night. We never observed two birds in a nestbox at the same time.

The infrared-sensitive black-and-white cameras (S/W-Kamera modul 1 from Conrad Electronic, [www.conrad.de](http://www.conrad.de)) were attached to the nestbox lid. As a light source, we placed six LEDs emitting infrared light (peak wavelength 940 nm) invisible to the blue tit eye (Hart et al. 2000; Hart 2001) around each camera objective. We connected each camera to a digital recorder (Abus, TV8450) that saved the recording on a 2GB SD card. Power for all electrical devices was supplied by lead–acid batteries (Panasonic, LC-R067R2P). To obtain information about the microclimate at a nestbox, we fixed a Hobo Data Logger (Onset Computer Corporation, Bourne, MS, U.S.A.) just above each nestbox. The sensitive electrodes of the loggers pointed in the direction of the entrance hole and recorded light intensity (in lx) and temperature (in degrees C) at 1 min intervals. Based on the logged data we calculated mean light intensities at each nestbox in the evening (30 min before–30 min after sunset) and in the morning (30 min before–30 min after sunrise), and the mean night temperature (between 2300 and 0000 hours).

In the first season (early January to late March 2008) we recorded 69 individuals (45 males, 24 females) during four recording sessions (total of eight nights). Of these 69 individuals, 21 (30.4%) were yearlings. In the second season (mid-November 2008 to early April 2009), we recorded 60 individuals (37 males, 23 females) during six recording sessions (total of 12 nights). Seven of the 60 individuals (11.7%) were yearlings. Thirty-three individuals were recorded in both winters. Thus, in total we obtained 532 recordings of 96 different blue tit individuals (60 males, 36 females), with an average  $\pm$  SD of  $5.5 \pm 3.7$  recordings per individual (range 1–18). In 94% of cases individuals were recorded on both nights of one session.

## Sleep Parameters

We used PowerDirector NE Express from CyberLink ([www.cyberlink.com](http://www.cyberlink.com)) to analyse the video recordings. We quantified 10 parameters of blue tit sleeping behaviour (for definitions, see below): (1) sleep onset; (2) awakening time; (3) entry time; (4) leaving time; (5) evening latency; (6) morning latency; (7) sleep duration; (8) midpoint of sleep; (9) frequency of awakenings per hour; and (10) the proportion of time spent awake per night (excluding evening and morning latency). We chose to record these 10 sleep parameters because they reflect parameters that are commonly used in human sleep studies, in particular those that assess individual 'chronotypes' (Hume et al. 1998; Park et al. 2002; Roenneberg et al. 2003, 2004; Kronholm et al. 2006).

A bird was considered asleep when it showed the classical sleep position with the beak pointing backwards and tucked under the scapulars and feathers fluffed (Amlaner & Ball 1983). It was usually easy to distinguish sleep phases from awake phases, because awake birds were mostly actively preening or moving around in the nestbox (for an example, see [Supplementary Material](#)). Only a few cases were more ambiguous, when a bird sat quietly for some time with its head pointing forwards. This typically happened in the morning before the bird left the nestbox and we considered these periods as awake phases.

We defined sleep onset as the time when the first sleep bout of at least 30 s started. In birds, sleep bouts can be as short as 10 s (as measured via brain activity patterns; Szymczak et al. 1993; N. Rattenborg, personal communication) and we occasionally observed birds in the sleeping position for less than 30 s. However, we did not include these shorter bouts to define the onset of sleep, because usually birds still moved intensely during these first short sleep bouts. We defined awakening time as the time when the last sleep bout of minimum 10 s ended. We defined sleep duration as the difference between awakening time and sleep onset and calculated the midpoint of sleep by adding half of the sleep duration to the time of sleep onset.

Awakenings during the night were counted when they lasted more than 2 s. If birds only turned their head from one side to the other within 1–2 s they were not considered to be awake. Sleep bouts between awakening phases had to last a minimum of 10 s, otherwise two consecutive awake phases were pooled (including the short sleep bout).

We defined entry time as the time of entering the nestbox in the evening and leaving time as the time of leaving the nestbox in the morning. Generally birds entered the nestbox once in the evening and stayed inside until they left again the next morning. In four cases, we observed that a bird left again after entering in the evening to return 7–13 min later. In one case, a blue tit left the nestbox in the morning, but returned to it within 17 min. In these exceptional cases we used times of the second entry or first exit, respectively, as entry and leaving times. We defined evening latency as the difference (in min) between entry time and sleep onset and morning latency as the difference (in min) between awakening time and leaving time.

## Data Analysis

We converted entry times, leaving times, times of sleep onset and awakening times to times relative to sunset or sunrise (reference data from the town of Kaufering which is ca. 7 km from our study site). We log-transformed evening and morning latencies, which reduced the right skew of these two parameters.

In a first step, we decomposed the phenotypic variance in relative time of entry, sleep onset, awakening and leaving, and in sleep duration into four main components: long-term environmental (seasonal) effects; short-term environmental variation

shared among nestboxes; consistency within-individual birds; and residual variation (not shared among nestboxes). We did so by fitting univariate linear mixed-effect models that included sex and age (yearling versus adult) as fixed effects and with recording session, recording date and bird identity as random effects. We extracted the variance explained by the three random effects and the residual variance and calculated the proportion of the variance explained by these factors.

In a second step, we tested the effects of sex, age and light intensity at the nestbox on different sleep parameters, and we determined the variance components due to individual (individual consistency) and nestbox (spatial heterogeneity) after controlling for seasonal effects. In this analysis, temperature measurements were not included because differences between nestboxes are negligible. Some sleep parameters showed seasonal changes not only in their mean values, but also in their variances around the mean. This produces patterns of heteroscedasticity, which violates the assumption of identically distributed residuals and will affect the significance tests of fixed effects. Transformation did not resolve this issue. Therefore, we standardized entry time, leaving time, sleep onset, awakening time, sleep duration, midpoint of sleep and morning and evening latency for the analyses by subtracting the date-specific mean from the raw values and dividing by the date-specific standard deviation. This standardization removed seasonal and date-specific changes in means and variances and both factors (recording session and date) were therefore excluded from models with standardized values. We fitted univariate linear mixed models with sex, age and mean light intensity at the nestbox as fixed effects and individual and nestbox identity as crossed random effects (in 40 nestboxes more than one and up to four individuals were recorded on different nights and 58 individuals were recorded in two to five different nestboxes). Variance components were converted to proportion of variance explained and their significance was tested by likelihood ratio tests.

The time when individuals entered the nestbox in the evening (entry time, standardized) and the time when they began to sleep (sleep onset, standardized) were highly correlated ( $r_{528} = 0.98$ ). Similarly, we found a strong correlation between the time when birds woke up (awakening time, standardized) and when they left the nestbox in the morning (leaving time, standardized:  $r_{519} = 0.82$ ). Therefore, we further focus on sleep onset and awakening time.

We did not apply standardizations in the analysis of nocturnal awakenings, because seasonal effects for these traits were very weak. Therefore, we fitted separate linear mixed-effect models for frequency of awakenings and proportion of time spent awake as dependent variable, including sex and age as fixed effects and bird identity, nestbox, recording date and recording session as random effects. As for the other parameters, we then estimated variance components of the random factors.

We tested temperature effects on evening latency, morning latency, frequency of awakenings and proportion of time spent awake (the other parameters were strongly influenced by light). We calculated the average difference in mean night temperature and the average difference in sleep parameters between each of two consecutive recording nights and fitted linear models with difference in mean temperature as the independent variable and each sleep parameter as response variable.

Finally, we analysed the relationship between sleep onset and awakening time and between evening and morning latency, by fitting models with awakening time (or morning latency) as the response variable and sleep onset (or evening latency), sex, age and mean light intensity as fixed effects, and bird and nestbox identity as random effects. However, before fitting the models, we decomposed the explanatory variable sleep onset (or evening latency) into

its between-individual and its within-individual components (Van de Pol & Wright 2009) and fitted these two as separate predictors. This allowed us to evaluate within- and between-individual correlations separately.

Owing to occasional technical failure (i.e. discharged batteries, poor quality of the recording) and to the fact that information about age was not available for all individuals, we have varying numbers of missing values in the analyses. In the final models we included 498–509 observations of 94 individuals in 127–128 different nestboxes for parameters 1–8. For parameters describing nocturnal awakenings (9, 10) we included 442 observations of 89 individuals in 119 nestboxes. We defined the beginning of the breeding season as the date when the first nest material was found in a nestbox in the study area. Following this definition, six recordings (in March and April) belonged to the breeding season, while all others (November–February) were considered the nonbreeding (winter) season.

All analyses were conducted in R 2.9.0 (<http://cran.r-project.org>) using the lmer function from the lme4 package for mixed models (Bates et al. 2008) and the cor.test function from the stats package for Pearson correlations.

#### Ethical Note

A recent study showed that subcutaneous implantation of passive integrated transponder (PIT) tags did not negatively influence fledging success, survival and recruitment of great tits (Nicolaus et al. 2008). These PIT tags are essentially the same as the RFID transponders we used. In our study population, RFID transponders have been applied since the beginning of 2007. We did not observe long- or short-term effects of implantation on the condition of adults and chicks. Recaptured individuals carrying a transponder did not differ significantly in their body mass from new captures without a transponder (after correcting for age and tarsus length:  $N = 225$ ,  $P = 0.49$ ) and in all cases the transponder was well placed and the lesion well healed. Adults did not modify their feeding behaviour after implantation during the breeding season. There was no difference in mean brood mass between nests with newly implanted adults and recaptures ( $N = 204$ ,  $P = 0.76$ ; measured 4 days after capture). Permits were obtained from the Bavarian government and the Bavarian regional office for forestry LWF.

## RESULTS

### Seasonal Patterns in Timing and Duration of Sleep

The average time of sleep onset showed a strong seasonal pattern: individuals began to sleep earliest in December and latest in April (Table 1). Sleep onset relative to sunset also changed seasonally (Table 1, Fig. 1a). During the shortest days in November–January, most birds began to sleep after sunset when average light intensities were low (approaching 0 lx), whereas birds started to sleep before sunset in February–March at higher light intensities (50–400 lx). In April, the average onset of sleep coincided with sunset. In all cases, birds started to sleep before the end of civil twilight (when the centre of the sun is 6° below the horizon). Recording session explained 33% of the variance in relative sleep onset times, while recording date within sessions explained 14%. Individual identity explained an additional 23% of the variation.

The average awakening times showed a similar seasonal pattern (Table 1, Fig. 1b). Of the total variance in relative awakening time, 17% was explained by recording session, 15% by recording night (within session) and 39% by individual identity. Independent of the season, most blue tits woke up before sunrise but after the start of civil twilight (when the sun is 6° below the horizon), usually at low light intensities (0–20 lx).

Sleep duration increased from November to December and decreased from January to April (Table 2, Fig. 2). Relative sleep duration also followed the patterns of relative sleep onset and awakening time, with recording session explaining 26% of the variance, recording night within session 17% and individual identity 29%.

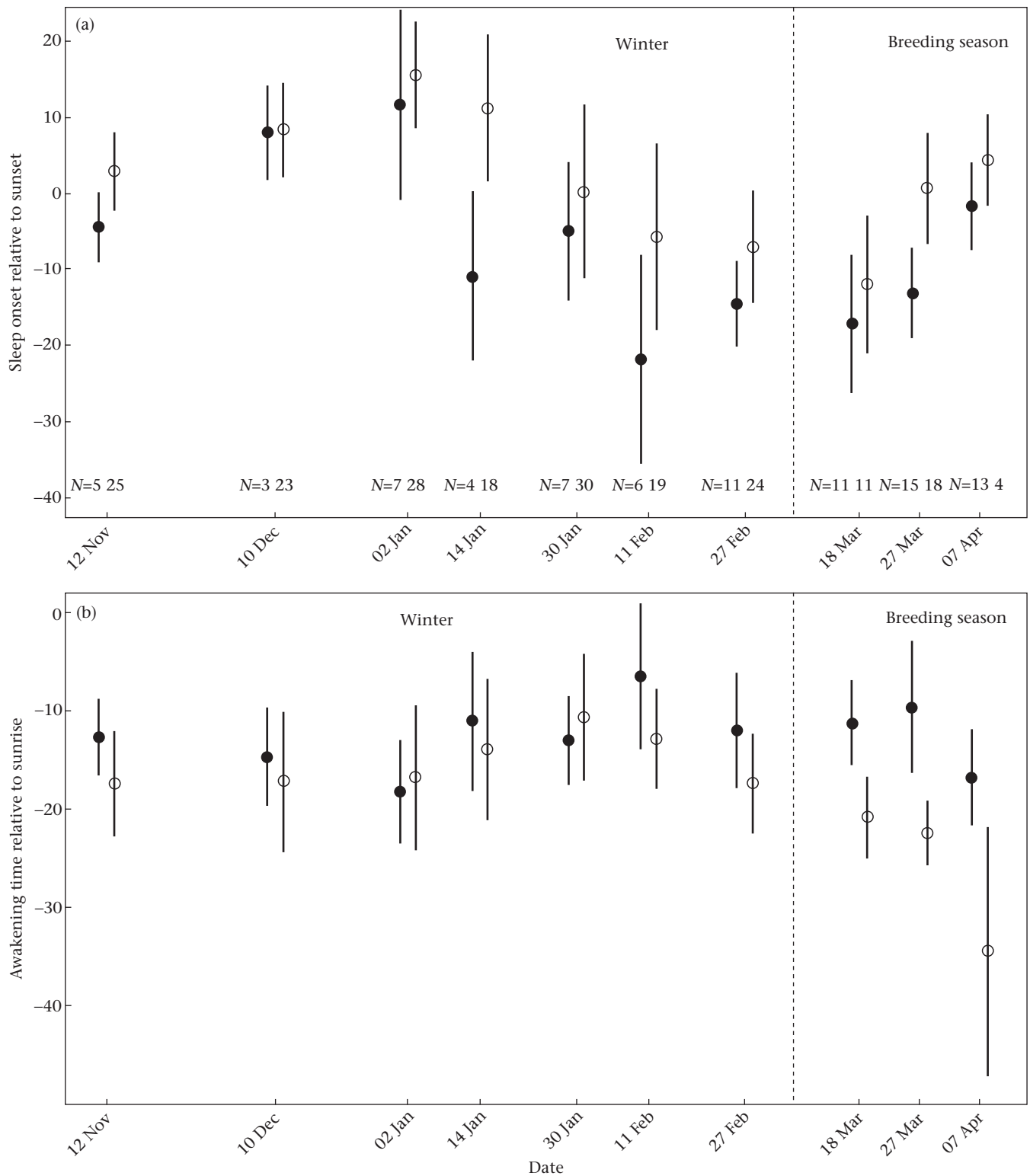
### Variation in Times Awake in the Nestbox

Evening and morning latency did not show obvious seasonal changes (Table 2), and were usually short, with evening latency being shorter and less variable (mean  $\pm$  SD =  $3.1 \pm 0.8$  min) than morning latency ( $5.6 \pm 1.6$  min). In the evening, after entering the box, birds moved or looked around in the nestbox, preened their plumage and fluffed up their feathers. After the birds woke up in the morning, we observed them stretching, preening, moving inside the box and sitting at the entrance hole looking outside. Between two consecutive recording nights, birds on average had

**Table 1**  
Mean, SD (in min) and range (earliest–latest) of time of sleep onset and awakening for each recording date

Date	Session	Sunset	Sunrise	Sleep onset				Awakening time			
				N	Mean	SD	Range	N	Mean	SD	Range
12 Nov 2008	1	16:42	7:21	29	16:44	5.35	16:32–16:53	29	7:03	5.66	6:52–7:13
13 Nov 2008	1	16:41	7:22	29	16:42	6.38	16:30–16:53	28	7:06	5.32	6:56–7:18
10 Dec 2008	2	16:23	7:57	21	16:30	6.00	16:20–16:41	22	7:42	6.28	7:24–7:50
11 Dec 2008	2	16:23	7:58	26	16:31	7.06	16:16–16:41	26	7:40	7.03	7:23–7:50
2 Jan 2008	3	16:34	8:06	34	16:50	7.09	16:39–17:02	34	7:49	7.34	7:36–8:05
3 Jan 2008	3	16:35	8:06	33	16:48	9.42	16:20–16:58	31	7:48	7.13	7:22–7:59
14 Jan 2009	4	16:49	8:02	22	16:54	13.86	16:23–17:09	22	7:46	6.84	7:36–8:02
15 Jan 2009	4	16:51	8:01	22	16:59	12.55	16:29–17:14	22	7:49	7.51	7:35–8:05
30 Jan 2008	5	17:12	7:47	37	17:08	10.44	16:41–17:26	37	7:34	5.35	7:25–7:42
31 Jan 2008	5	17:13	7:46	34	17:15	13.10	16:47–17:35	28	7:37	7.50	7:25–7:49
11 Feb 2009	6	17:33	7:28	25	17:23	13.63	16:54–17:44	25	7:17	6.84	7:06–7:37
12 Feb 2009	6	17:34	7:27	23	17:25	15.62	16:48–17:50	24	7:14	6.05	7:04–7:30
27 Feb 2008	7	17:57	7:01	32	17:48	8.21	17:30–18:09	32	6:39	5.80	6:24–6:49
28 Feb 2008	7	17:58	6:59	33	17:48	8.91	17:26–18:06	33	6:48	6.02	6:35–7:09
18 Mar 2009	8	18:26	6:21	19	18:22	9.34	18:01–18:41	19	6:02	7.32	5:50–6:15
19 Mar 2009	8	18:28	6:19	22	18:05	10.87	17:44–18:22	22	6:04	6.23	5:55–6:19
27 Mar 2008	9	18:40	6:03	33	18:30	10.92	18:00–18:54	33	5:47	7.91	5:36–6:06
28 Mar 2008	9	18:41	6:01	28	18:39	9.93	18:19–18:56	28	5:43	9.23	5:32–6:02
7 Apr 2009	10	18:56	5:41	15	18:55	6.45	18:44–19:06	15	5:19	12.22	4:53–5:34
8 Apr 2009	10	18:57	5:39	13	18:56	7.65	18:43–19:07	11	5:19	13.55	4:47–5:36

Local times of sunset and sunrise (the following morning) are also given. All times refer to Central European Time.



**Figure 1.** Seasonal changes in (a) sleep onset and (b) awakening time for female (filled circles) and male (open circles) blue tits. Times are given in minutes relative to sunset or sunrise (negative values indicate time before, positive values time after sunset/sunrise). Values of two consecutive nights within one recording session were averaged. Means and SD are shown. Sample sizes (number of individuals) are indicated above the X-axis.

longer evening and morning latencies when mean night temperatures were higher (linear models;  $N = 202$ ; evening latency:  $d = 13.04 \pm 4.02$  SE,  $Z = 3.25$ ,  $P = 0.01$ ; morning latency:  $d = 24.85 \pm 10.06$  SE,  $Z = 2.47$ ,  $P = 0.04$ ).

On average  $\pm$  SD, birds woke up between  $38 \pm 10$  and  $99 \pm 50$  times (range 23–230) on different recording nights with an average frequency of  $2.8 \pm 0.6$  to  $9.5 \pm 4.8$  awakenings per hour (Table 3). During these awakening phases birds usually preened, scratched,

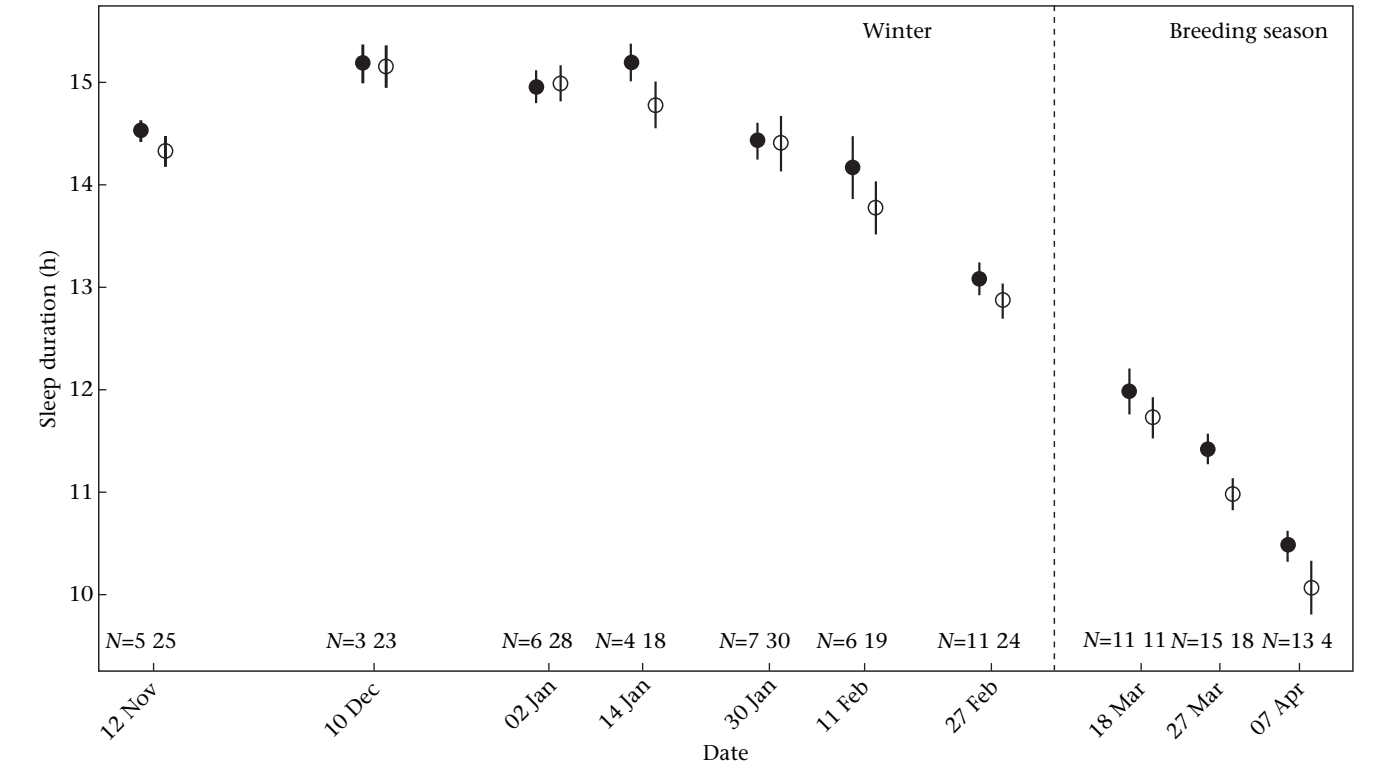


**Table 2**  
Mean, SD and range (shortest–longest) of sleep duration (in h), evening latency (time difference between entry of nestbox and sleep onset, in min) and morning latency (time difference between awakening and leaving the nestbox, in min) for each recording date

Date	Sleep duration (h)				Evening latency (min)				Morning latency (min)			
	N	Mean	SD	Range	N	Mean	SD	Range	N	Mean	SD	Range
12 Nov 2008	29	14.3	0.2	14.1–14.6	29	2.9	1.1	1.5–6.8	29	5.2	3.5	0.4–12.7
13 Nov 2008	28	14.4	0.2	14.1–14.7	29	3.5	1.4	1.2–7.7	29	5.7	4.8	0.2–18.2
10 Dec 2008	21	15.2	0.2	14.8–15.5	21	2.2	1.2	0.9–4.7	22	6.6	6.3	0.2–23.7
11 Dec 2008	26	15.2	0.2	14.7–15.5	26	2.2	1.0	0.7–5.5	26	5.5	6.6	0.3–28.1
2 Jan 2008	34	15.0	0.2	14.6–15.4	34	2.8	1.8	1.3–11.7	34	7.2	6.1	0.8–27.7
3 Jan 2008	31	15.0	0.2	14.7–15.4	33	2.6	1.4	1.0–5.7	31	5.9	5.6	0.6–26.6
14 Jan 2009	22	14.9	0.3	14.5–15.4	22	2.8	0.8	1.0–4.4	22	6.4	6.3	0.3–28.1
15 Jan 2009	22	14.8	0.3	14.3–15.4	22	2.3	0.7	1.0–3.8	22	6.3	6.8	0.1–31.3
30 Jan 2008	37	14.4	0.2	14.0–15.0	37	2.5	1.0	0.9–5.5	37	4.8	3.4	0.4–12.5
31 Jan 2008	28	14.4	0.3	13.9–15.0	34	2.5	0.8	0.9–4.2	28	6.9	4.8	1.1–16.5
11 Feb 2009	25	13.9	0.3	13.5–14.4	25	2.6	1.7	0.8–8.6	25	7.8	8.3	0.5–36.1
12 Feb 2009	23	13.8	0.3	13.3–14.7	23	2.4	0.8	1.1–4.1	24	6.7	9.2	0.3–43.7
27 Feb 2008	32	12.9	0.2	12.5–13.2	32	3.0	1.7	1.0–9.2	32	3.1	2.6	0.1–9.3
28 Feb 2008	33	13.0	0.2	12.7–13.7	33	4.0	2.0	1.0–9.6	33	6.3	5.8	0.5–23.3
18 Mar 2009	19	11.7	0.3	11.4–12.2	19	3.9	2.1	1.1–9.1	19	2.9	2.4	0.3–7.5
19 Mar 2009	22	12.0	0.3	11.6–12.6	22	2.7	1.6	0.6–6.7	22	1.7	1.2	0.2–4.5
27 Mar 2008	33	11.3	0.3	10.8–11.8	33	3.5	1.9	0.9–7.5	33	3.1	2.9	0.5–14.4
28 Mar 2008	28	11.1	0.3	10.6–11.7	28	4.0	2.0	1.0–9.7	28	3.9	4.3	0.5–21.7
7 Apr 2009	15	10.4	0.2	9.8–10.7	15	4.6	2.2	1.3–8.6	15	5.4	5.1	0.3–17.2
8 Apr 2009	11	10.4	0.3	9.7–10.9	13	4.3	2.2	1.4–9.7	11	5.6	6.0	0.8–16.4

stretched legs and wings or moved inside the box. The number of awakenings per night did not change seasonally, but increased markedly in April. Given the changes in sleep duration, the frequency of awakenings decreased from a mean  $\pm$  SD of  $3.8 \pm 0.6$  awakening phases per hour in November to  $3.0 \pm 0.6$  in December and then increased to  $9.5 \pm 4.8$  in April (Table 3). Recording session explained 32% of the variance in frequency of awakenings whereas recording night within session explained only 2%. The duration of the longest continuous sleep bout was highest in the first half of

January and shortest in April (Table 3). Recording session explained 30% of the variance in the maximum duration of sleep bouts, whereas recording night explained 3%. On average, birds spent 92–99% of their sleep duration actually asleep, which corresponds to a total time spent awake at night of  $12 \pm 6$  min SD (range 5–27 min) in February and  $49 \pm 25$  min (range 17–93 min) in April (Table 3). Recording session explained 33% of the variance in the proportion of time spent awake, whereas recording night explained 7%. Birds woke up more frequently at night and spent a greater



**Figure 2.** Seasonal changes in sleep duration (h) for female (filled circles) and male (open circles) blue tits. Values of two consecutive nights within one recording session were averaged. Means and SD are shown. Sample sizes (number of individuals) are indicated above the X-axis.

**Table 3**

Mean, SD and range of frequency of nocturnal awakenings (awakenings per hour), proportion of the night birds spent awake and duration of the longest continuous sleep bout (in min) for each recording date

Date	N	Frequency of awakenings			Proportion of time spent awake			Maximum sleep bout (min)		
		Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
12 Nov 2008	24	3.8	0.6	2.5–5.6	0.03	0.01	0.01–0.05	93.5	27.5	45.8–147.8
13 Nov 2008	23	3.9	0.6	2.8–5.1	0.04	0.02	0.02–0.08	96.2	27.4	55.9–157.6
10 Dec 2008	20	3.3	0.6	2.6–4.5	0.02	0.01	0.01–0.04	112.1	39.6	60.0–211.4
11 Dec 2008	25	3.0	0.6	2.3–4.2	0.02	0.01	0.01–0.03	116.3	34.3	62.0–197.9
2 Jan 2008	28	3.3	0.8	1.9–5.1	0.02	0.01	<0.01–0.03	121.2	38.9	64.6–237.5
3 Jan 2008	26	3.5	0.8	2.0–5.1	0.02	0.01	0.01–0.03	123.1	38.0	68.9–246.6
14 Jan 2009	14	3.5	0.9	2.7–6.1	0.03	0.01	0.01–0.04	114.1	33.7	53.9–190.9
15 Jan 2009	14	3.1	0.7	2.1–4.6	0.02	0.01	0.01–0.04	129.8	61.7	51.7–245.5
30 Jan 2008	33	3.7	0.8	2.2–6.0	0.03	0.02	0.01–0.07	109.8	37.9	50.4–219.8
31 Jan 2008	26	3.8	0.8	2.3–5.7	0.03	0.01	0.01–0.07	101.4	25.5	54.4–155.5
11 Feb 2009	23	3.0	0.9	1.8–5.3	0.02	0.01	0.01–0.04	118.2	40.4	59.3–202.2
12 Feb 2009	21	2.8	0.6	1.9–4.2	0.01	0.01	0.01–0.03	120.2	45.5	45.4–195.2
27 Feb 2008	30	4.0	1.6	2.4–10.2	0.02	0.02	0.01–0.09	89.0	28.2	40.6–157.0
28 Feb 2008	32	5.2	1.6	3.2–9.6	0.04	0.02	0.02–0.11	71.6	20.6	34.7–131.8
18 Mar 2009	13	3.8	1.5	1.9–7.8	0.03	0.01	0.01–0.04	85.5	22.3	57.0–123.7
19 Mar 2009	16	3.2	0.9	2.0–5.1	0.02	0.01	0.01–0.03	115.3	34.0	69.5–191.9
27 Mar 2008	31	4.8	2.5	2.2–14.0	0.03	0.02	0.01–0.09	80.9	34.4	34.3–197.2
28 Mar 2008	26	4.5	1.3	2.8–7.6	0.04	0.02	0.01–0.07	71.6	21.9	34.4–122.9
7 Apr 2009	14	7.8	5.1	3.1–22.3	0.06	0.04	0.03–0.14	50.3	24.4	17.6–106.1
8 Apr 2009	11	9.5	4.8	4.3–20.5	0.08	0.04	0.03–0.15	39.6	17.6	20.8–74.1

proportion of the night awake when the night was warmer (linear models;  $N = 202$ ; frequency awake:  $d = 0.18 \pm 0.05$  SE,  $Z = 3.59$ ,  $P = 0.007$ ; proportion awake:  $d = 0.0033 \pm 0.00069$  SE,  $Z = 4.80$ ,  $P = 0.001$ ).

#### Effects of Local Light Conditions

Each nestbox in the study area was exposed to slightly different light conditions owing to variation in the direction of the entrance hole and variation in the surrounding vegetation. Light intensity measured at the nestbox in the evening had no effect on entry time, sleep onset, sleep duration and midpoint of sleep, but it significantly influenced evening latency (Table 4). However, in contrast to our expectations, birds started sleeping later in darker locations, that is, they spent more time in the box before sleep onset and they slept less in total. Light intensity at the nestboxes in the morning had no effect on morning latency, leaving time, sleep duration and midpoint of sleep, but significantly predicted awakening time (Table 4). As expected, birds that slept in brighter locations woke up earlier.

#### Effects of Sex and Age

Sleep behaviour of blue tits was both age and sex dependent (Table 4). In the evening, males on average entered the nestbox and

started to sleep 9 min later than females. In the morning, males woke up on average 6 min earlier than females and they left the nestbox on average 9 min earlier. This sex difference was most pronounced at the end of the winter. During the start of the breeding season (March–April), males on average woke up 15 min earlier than females (versus 3 min during the winter, November–February). Overall, there was a strong sex effect on sleep duration (Fig. 2), whereby males slept on average 15 min less than females. This effect was again most pronounced at the beginning of the breeding season; during March–April males slept 24 min less than females (versus 11 min during the winter, November–February).

We also found a difference in morning latencies between females and males (Table 4). After waking up, females stayed on average 134 s longer in the nestbox than males. Midpoint of sleep and evening latency were not significantly affected by sex (Table 4). There was no significant difference in the frequency of awakenings per night between males and females (linear mixed model:  $d = 0.52 \pm 0.39$  SE,  $Z = 1.34$ ,  $P = 0.18$ ). However, we found that females spent a greater proportion of the time between sleep onset and awakening time actually awake (mean  $\pm$  SD =  $0.035 \pm 0.02$ ) than males ( $0.026 \pm 0.01$ ; linear mixed model:  $d = 0.01 \pm 0.003$  SE,  $Z = 3.26$ ,  $P = 0.001$ ).

An individual's age did not influence entry time, sleep onset, evening latency, awakening time, sleep duration or midpoint of

**Table 4**

Effects of sex, age and light intensity on eight sleep parameters

Sleep parameter	N	Sex (females–males)						Age (adults–yearlings)			Light intensity around sunset (lx)			Light intensity around sunrise (lx)		
		Obs	Ind	Box	d	SE	P	d	SE	P	b	SE	P	b	SE	P
Entry time	509	94	128		–0.85	0.15	<b>&lt;0.0001</b>	–0.01	0.13	0.92	–0.06	0.04	0.18			
Sleep onset	509	94	128		–0.83	0.15	<b>&lt;0.0001</b>	–0.02	0.13	0.88	–0.07	0.04	0.09			
Awakening	500	94	127		0.74	0.17	<b>&lt;0.0001</b>	–0.22	0.13	0.09				–0.14	0.04	<b>0.0006</b>
Leaving time	502	94	127		0.85	0.17	<b>&lt;0.0001</b>	–0.38	0.13	<b>0.005</b>				–0.07	0.04	0.08
Evening latency	509	94	128		0.10	0.15	0.49	–0.04	0.13	0.77	–0.13	0.05	<b>0.01</b>			
Morning latency	500	94	127		0.32	0.16	<b>0.05</b>	–0.42	0.14	<b>0.002</b>				0.04	0.04	0.32
Sleep duration	498	94	127		0.90	0.15	<b>&lt;0.0001</b>	–0.15	0.13	0.25	0.08	0.05	0.09	–0.08	0.04	0.07
Midpoint	498	94	127		–0.19	0.16	0.23	–0.11	0.13	0.46	–0.05	0.05	0.41	–0.10	0.05	0.06

Effect sizes were estimated in linear mixed-effect models that included individual and nestbox identity as random effects. Effects of sex and age were estimated as differences in means  $d$  and effects of light intensity as standardized slopes  $b$ . Sample sizes  $N$  are given for the total number of observations (Obs), the number of individuals (Ind) and the number of different nestboxes (Box). Significant  $P$  values are shown in bold.

sleep (Table 4). However, we found a significant effect on leaving time and morning latency (Table 4). Yearlings spent on average 2 min longer in the nestbox after waking up, and left the nestbox on average 4 min later than adult birds. This age effect was only pronounced during the winter (leaving time:  $d = -0.60 \pm 0.16$  SE,  $Z = -3.79$ ,  $P < 0.001$ ; morning latency:  $d = -0.49 \pm 0.15$  SE,  $Z = -3.18$ ,  $P < 0.002$ ) and disappeared during the breeding season (leaving time:  $d = 0.07 \pm 0.17$  SE,  $Z = 0.40$ ,  $P > 0.6$ ; morning latency:  $d = -0.37 \pm 0.28$  SE,  $Z = -1.35$ ,  $P = 0.18$ ).

Longitudinal analysis of seven individuals (six males and one female) that were recorded as yearlings in the first winter and as adults in the second winter confirmed the cross-sectional age effect on leaving time. Leaving times were significantly earlier when individuals were adult (paired  $t$  test:  $t_6 = -2.47$ ,  $P = 0.05$ ). Although not significant, the longitudinal comparison of morning latencies showed a similar trend. Individuals spent less time in the nestbox after waking up when they were adults (paired  $t$  test:  $t_6 = -1.22$ ,  $P = 0.27$ ).

Nocturnal awakenings were also age dependent. Yearlings spent a slightly greater proportion of the night awake (mean  $\pm$  SD =  $0.032 \pm 0.02$ ) than adults ( $0.029 \pm 0.02$ ; linear mixed model:  $d = -0.008 \pm 0.003$  SE,  $Z = -3.09$ ,  $P = 0.002$ ) and adults had longer continuous sleep bouts than yearlings ( $d = 0.22 \pm 0.09$ ,  $Z = 2.47$ ,  $P = 0.01$ ).

#### Individuality in Sleep Behaviour

After controlling for season, sex, age and light conditions we still found considerable variation in all sleep parameters and a substantial part of this variation was between individuals. Individuals were consistent in their sleeping behaviour, such that most investigated sleep parameters showed highly significant repeatabilities of about 0.4 (Table 5). Repeatabilities for the two sexes were generally similar, with the exception of awakening time and leaving time where females showed a higher and lower repeatability than males, respectively (details not shown). Note that repeatability estimates are less accurate for females, because we recorded considerably fewer females than males.

Sleep onset and awakening time were negatively correlated, both between individuals (linear mixed model:  $b = -0.26 \pm 0.11$  SE,  $Z = -2.35$ ,  $P = 0.02$ ) and within individuals ( $b = -0.13 \pm 0.04$  SE,  $Z = -2.96$ ,  $P = 0.003$ ). Thus, individuals that started sleeping earlier in the evening woke up later the next morning and vice versa (Fig. 3a). A negative correlation suggests that there are long-sleeping and short-sleeping individuals, whereas a positive correlation would have indicated that there are evening and morning types (birds sleep the same amount but shift the timing of sleep).

The time birds spent in the nestbox before sleep onset (evening latency) and the time they spent in the box after waking up (morning latency) were strongly positively correlated between individuals (linear mixed model:  $b = 0.49 \pm 0.10$  SE,  $Z = 4.67$ ,  $P < 0.0001$ ; Fig. 3b), but not within individuals ( $b = 0.05 \pm 0.04$  SE,  $Z = 1.07$ ,  $P = 0.28$ ). This means that some individuals showed longer latencies than others, while a day with a short latency in the evening did not predict a short latency in the morning (after accounting for between-individual differences).

#### DISCUSSION

Our study comprehensively describes the sleep behaviour of a population of free-living blue tits roosting in nestboxes. Most sleep variables changed seasonally, largely following changes in daylength. We found additional effects of the light intensity near the roosting site (nestbox) on awakening time and evening latency. Males generally slept less than females by starting to sleep later and waking up earlier. This pattern was most pronounced in the early breeding season. First-year birds left the nestbox on average later than adults and they spent a greater proportion of the night awake, but overall they did not differ from adults in their sleep duration. Repeated measurements of the same individuals revealed a significant repeatability of the majority of sleep parameters, suggesting that sleep behaviour is an individual-specific trait.

Our results are restricted to individuals that used artificial nestboxes for roosting. Although there were ample free boxes available for roosting, a substantial proportion of the population did not roost in a nestbox. We do not know where these birds roosted, and we cannot exclude that their sleeping behaviour differed from birds that roosted in boxes. In this population, the risk of predation inside the nestbox is essentially zero, there is negligible intra- and interspecific competition for nestboxes (an excess of boxes with small entrance hole excluding most other species is available in the study site), and birds are relatively well protected from weather conditions. Hence, it can be expected that sleep disturbance is minimal in nestboxes, and this could affect the quality and quantity of sleep. Information on sleep behaviour of blue tits outside nestboxes is not available, and is difficult to obtain.

#### Seasonal Changes and Light Effects

Sleep onset and awakening time of blue tits were strongly related to sunset and sunrise. It is likely that light intensity itself functions as the main Zeitgeber. This is supported by our observation that light intensity in the morning predicted awakening

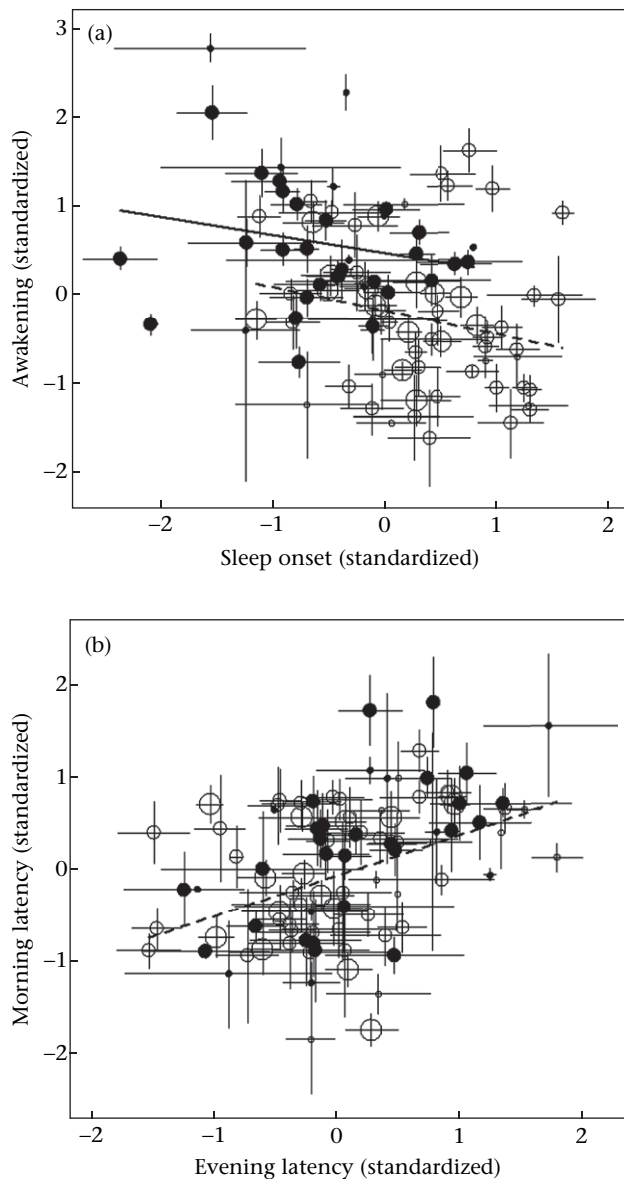
**Table 5**  
Repeatabilities of sleep parameters for individual blue tits or for particular nestboxes

Sleep parameter	N			Individual			Nestbox		
	Obs	Ind	Box	R	$\chi^2$	P	R	$\chi^2_1$	P
Entry time*	509	94	128	<b>0.38</b>	55.92	<0.0001	0.08	5.48	0.02
Sleep onset*	509	94	128	<b>0.41</b>	65.21	<0.0001	0.06	3.77	0.05
Awakening time*	500	94	127	<b>0.46</b>	99.15	<0.0001	0.18	32.80	<0.0001
Leaving time*	502	94	127	<b>0.41</b>	84.63	<0.0001	0.23	41.29	<0.0001
Evening latency*	509	94	128	0.26	29.26	<0.0001	0.12	9.01	0.003
Morning latency*	500	94	127	<b>0.38</b>	76.43	<0.0001	0.20	25.82	<0.0001
Sleep duration*	498	94	127	<b>0.38</b>	69.74	<0.0001	0.19	32.71	<0.0001
Midpoint of sleep*	498	94	127	<b>0.42</b>	74.00	<0.0001	0.00	<0.0001	0.99
Frequency of awakenings (N/h)	442	89	119	<b>0.44</b>	65.01	<0.0001	0.09	9.08	0.003
Proportion time spent awake	442	89	119	0.25	65.30	<0.0001	0.18	45.09	<0.0001

Estimates are variance components from a linear mixed model for each sleep parameter with individual and nestbox identity fitted as random factors. Significance of the effects was calculated by likelihood ratio tests separately for the two components with one degree of freedom. Sample sizes N are given for the total number of observations (Obs), the number of individuals (Ind) and the number of different nestboxes (Box). Significant R values are shown in bold.

\* Controlled for seasonal effects by standardization.





**Figure 3.** Between-individual correlations (a) between sleep onset and awakening time and (b) between evening and morning latency. Values were standardized within recording dates and averaged within individuals. Males are shown with open and females with closed circles. Points indicate means and lines standard errors. The size of the dots reflects the number of observations: smallest = 1–2, intermediate = 3–9, largest = 10–18 observations per individual. Total  $N = 36$  for females, 60 for males. (a) Regression lines for females (solid) and males (dashed). The slopes for males and females were not significantly different ( $t_{92} = 0.24$ ,  $P = 0.81$ ). (b) The dashed line shows the regression line for males and females combined.

time. Blue tits slept longest in December and January when the days were shortest, and progressively slept less with increasing day-length. Over the course of the study, sleep duration decreased by about 5 h. This suggests that blue tits can tolerate a large range of sleep durations. We did not find evidence that blue tits compensated for the varying length of the night, for example by adjusting the amount of time they spent awake while in the nestbox. On the contrary, we observed a higher frequency of night-time awakenings in the early breeding season when nights became shorter compared to mid-winter. Thus, blue tits seemed to have less continuous sleep at the beginning of the breeding season.

As shown for migrating passerines, birds are indeed capable of dramatically reducing their daily amount of sleep, at least during

migration, without showing typical consequences of sleep deprivation (Rattenborg et al. 2004). To cope with changing sleep duration blue tits may adjust the depth of their sleep. Differences in sleep depth have already been observed in other species: blackbirds showed deeper sleep towards the end of the night, as measured by arousal thresholds (Szymczak et al. 1996) and king penguins, *Aptenodytes patagonicus*, increased sleep depth in the afternoon compared to the morning (Dewasmes & Loos 2002). However, white-crowned sparrows, *Zonotrichia leucophrys gambelii*, did not compensate for the reduction of sleep during migratory nights by increased sleep depth (Rattenborg et al. 2004).

Similar to mammals, birds show SWS and REM sleep that are unequally distributed across the night (Szymczak et al. 1993; Rattenborg et al. 2000). Each sleep state might serve a different function (Siegel 2005). When reducing the total amount of sleep, birds could change the proportion of these two states if one is more important for health or survival than the other. After short-term sleep deprivation pigeons, *Columba livia*, showed a slight increase in REM sleep and a more frequent switching between SWS and REM sleep during the recovery night (Tobler & Borbely 1988; Martinez-Gonzalez et al. 2008). This shows that birds are able to alter sleep composition, at least in response to sleep deprivation.

In theory, birds could also compensate for varying sleep duration at night by periods of sleep during daytime. This is perhaps unlikely, because birds in general are monophasic sleepers (except for some shorebirds and waterfowl), which spend a distinct proportion of the 24 h day asleep (Amlaner & Ball 1983). In blackbirds, diurnal sleep was extremely rarely seen (Szymczak et al. 1996). However, during periods of nocturnal migration, Swainson's thrushes were shown to increase their daytime sleep as a response to reduced night-time sleep (Fuchs et al. 2006). We cannot exclude that blue tits slept outside the nestbox or in other nestboxes during the day, but we never observed a blue tit sleeping in a nestbox during the day (based on full daytime recordings on four recording sessions).

Meddis (1975) proposed that sleep is little more than a spare-time activity which enforces inactivity during times of the day when it would be dangerous and/or energetically unproductive to be active. If indeed blue tits seek the secure shelter of a nestbox as soon as it gets too dark to orient or engage in other activities such as foraging, one would expect that birds always enter the nestboxes at approximately the same light intensity. However, this was not the case. In mid-winter (November–January) birds entered and started to sleep when there was almost no detectable light, whereas later in the year birds entered the nestboxes before sunset when light intensity was still relatively high. This suggests that birds might be forced to expand their activities beyond the short winter days, most likely to obtain enough food to survive the night.

Most blue tits woke up before sunrise, independently of the season, which is in agreement with observations on other birds including the closely related great tit (Hinde 1952; Dunnett & Hinde 1953; Fidler 1962). Like our blue tits, great tits started to sleep earlier relative to sunset in spring than in mid-winter. Weather conditions also seemed to influence the decision of a bird to start roosting or to wake up, but this may be because of the association with variation in light intensity (Dunnett & Hinde 1953; Davis 1958). We observed the largest differences in relative sleep onset or relative time of waking up between two consecutive nights when weather conditions changed. Rain or snowfall resulted in earlier roost times and later wakeup times in connection with low light intensities.

In contrast to Wellmann & Downs (2009), who found no significant effect of temperature on the amount of sleep in three songbird species held in captivity, we found that changes in sleep behaviour of blue tits between two consecutive nights were related to changes in mean night temperature. We observed more nocturnal awakenings on warmer nights, as well as longer evening and morning latencies.

However, the latter could also be influenced by weather or light conditions, because overcast and rainy nights were warmer than clear nights within the same recording session.

Unexpectedly, birds that roosted in nestboxes that received comparatively little light in the evening had longer sleep latencies. We had expected a positive correlation, under the hypothesis that the absence of light triggers the onset of sleep and the appearance of light triggers awakening. Birds that entered darker nestboxes should therefore spend less time awake in the box before sleep onset. This was obviously not the case. Why latency to sleep correlated negatively with light intensity remains puzzling.

### *Sex and Age*

Our results clearly show that sleep behaviour is sex dependent. Males started to sleep later and woke up earlier than females and consequently males slept less per night. There are at least three explanations for a sex effect on sleep behaviour. (1) Male and female blue tits might have different sleep requirements, because of sex differences in physiology or in daytime activities. During the early breeding season, for example, females might have higher sleep requirements, because their bodies start to prepare physiologically for the energy-demanding egg production and incubation. If females spend more time foraging and can obtain sufficient food faster, they could spend more time sleeping. (2) Males and females may differ in the quality of their sleep. For example, males might wake up less often during the night, or they might spend different proportions of their sleep time in the two sleep states. Indeed, we found that females were awake during the night slightly longer than males. However, after subtracting the amount of time spent awake per night from total sleep duration, we found that males still slept significantly less than females. (3) Males and females may face different trade-offs with other activities. The sex difference in total sleep duration was most obvious at the beginning of the breeding season, when male–male competition is most intense. Males need to establish and defend territories and they sing in the early morning (dawn chorus), particularly when their mate is fertile. Activities such as dawn song can already be performed early in the morning, at times when it may not be bright enough to forage efficiently (Verner 1965). Females spent more time in the nestbox after waking up ( $P = 0.05$ ), which also supports the idea that males need more time to engage in other activities, such as singing and territory defence.

Yearlings woke up only slightly later than adults, but spent considerably more time in the nestbox and hence flew out later compared to adult birds. This pattern was also seen in a longitudinal analysis of the same individuals in different years. Although one would expect that first-year birds need more time to forage than adult birds (e.g. because of differences in experience and dominance), they may also face different trade-offs (e.g. higher risk of predation). We often observed individuals spending a considerable amount of time sitting at the entrance hole looking out and jumping back and forth between the entrance hole and the bottom of the box before eventually flying out. The effect of age on awakening and leaving time was only observed during winter and decreased towards the breeding season. These effects were also present when only males were considered, which is surprising, given that Poesel et al. (2006) showed that, during the breeding season, adult male blue tits started their dawn song earlier than yearling males. Males that began to sing earlier were more likely to gain extrapair paternity and had more mating partners, increasing their reproductive success (Poesel et al. 2006). This suggests that awakening time, or at least the time of leaving the nestbox, may be influenced by sexual selection.

Sleep duration was unaffected by age, at least when we compared yearlings and adults. Apparently, first-year blue tits do not have

different sleep requirements to adult birds. However, there might be an age effect on sleep behaviour earlier in life (before the first winter) or later in life (as observed in humans; e.g. Hume et al. 1998; Kronholm et al. 2006). In our study population, yearlings seemed to have a more interrupted sleep than older birds, since they spent a significantly larger proportion of the night awake and had shorter continuous sleep bouts.

### *Individual Consistency in Sleeping Behaviour*

Despite strong effects of environmental factors on sleep behaviour in blue tits, we also found consistent variation between individuals in all investigated sleep parameters. Time of sleep onset differed by as much as 56 min between individual males and by 45 min between individual females. Similarly, individual variation in awakening time amounted to about 37 min in males and 41 min in females on a given day. Previous work also described substantial interindividual differences in nightly resting times in blue and great tits. For example, Dunnett & Hinde (1953) studied four blue tits in aviaries and observed a range in emergence time from the nestbox of about half an hour on a given morning. Field observations by Hinde (1952) revealed differences of 35 min in roosting times (entering the nestbox) for both blue tits ( $N = 11$ ) and great tits ( $N = 11–23$ ) during a particular evening, and differences in emergence time (leaving the nestbox) of 14 min for blue tits ( $N = 3–6$  individuals) and 18 min for great tits ( $N = 3–15$  individuals) on a given morning.

In humans, it is well known that individuals vary dramatically in their daily sleep duration (Aeschbach et al. 2001, 2003; Van Dongen et al. 2005), with short sleepers sleeping less than 6 h and long sleepers more than 9 h. There is also variation in the preferred sleep timing, usually referred to as 'morningness' and 'eveningness' (Kerkhof 1985; Van Dongen et al. 2005), although this may partly be caused by social and cultural factors. We did not find evidence for the existence of morning or evening types in our population of blue tits. Instead, we found that relatively late sleep onset was linked with early awakening times and vice versa, both between and within individuals. This suggests that variation in the duration of sleep is more important, with populations consisting of long and short sleepers.

Most phenotypic sleep traits we investigated were highly repeatable within individuals and might therefore be regarded as 'personality' traits (Réale et al. 2007). The regulation of sleep and sleep timing might be genetically determined or related to individual quality or long-term condition. There is general agreement that sleep regulation has a homeostatic and a genetic basis (Dijk & Czeisler 1995; Andretic et al. 2008; Vassalli & Dijk 2009). Sleep patterns in humans are not only repeatable but also heritable, as indicated by twin and family-based studies. For example, de Castro (2002) found that genetic influences on sleep patterns accounted for 21–41% of the variance. Klei et al. (2005) reported heritabilities of 12–29% for different sleep measures and Gottlieb et al. (2007) provided heritability estimates of 17–22% for sleep duration and bed time. Obviously, whether sleep behaviour is also heritable in birds remains to be shown.

### *Causes and Consequences of Variation in Sleep Behaviour*

Further study is required to understand the causes and consequences of variation in sleep behaviour in natural populations of animals. For example, sleep demand could be condition dependent, or dependent on daytime activity. Beginning to sleep early and waking up late may be costly in terms of lost opportunities, during winter when foraging time is limited, or during the breeding season when competition for mates and territories takes place.

Some of the variation in sleep duration may be explained by variation in infestation with parasites. As shown in great tits,

females in nests that were experimentally infested with ectoparasitic hen fleas increased their investment in nest sanitation at a cost of sleep duration compared to females in noninfested nests (Christe et al. 1996). On the other hand, total sleep duration increased during infection in animals, including humans (Bryant et al. 2004).

In our study, most blue tits slept in nestboxes without any nest material, which may have reduced the number of ectoparasites. During handling in winter or during the nestling phase, we did not observe any parasites except feather mites, but a more detailed study on the effect of ectoparasites on sleep in blue tits would be useful. We would expect that ectoparasite presence or prevalence particularly influences the frequency or duration of the awake phases that interrupted sleep. These phases were usually rather short, only a few seconds, but they could last up to about 20 min. The number of times an individual woke up within a night varied considerably (see Results). Birds often scratched or preened during these awake phases, suggesting that the total amount of time spent awake at night may be associated with parasite infestation. We note that the time an individual spent awake at night was the least repeatable of all tested sleep parameters, suggesting it may be more influenced by external factors such as parasite load or daytime activity levels.

Our results show that sleep duration of the same individuals also varied from one night to the next. It would be interesting to test whether this was related to daytime activity levels or to the amount of sleep acquired in previous nights (Horne & Minard 1985; Tobler & Borbely 1988; Driver & Taylor 2000).

## Conclusion

This study shows that environmental factors (season, local light conditions and temperature) predict sleep parameters in free-living blue tits. Several aspects of sleep behaviour, in particular overall sleep duration, differed between males and females, or were dependent on the age of the individual. This might reflect sex- or age-dependent trade-offs between sleep and other activities. We found consistent variation between individuals in their sleep behaviour, suggesting that sleep behaviour is an individual-specific trait. It remains to be investigated to what extent these sleep patterns are heritable and whether and how sleep behaviour is related to other individual life history traits and to fitness. Different sleep traits could be advantageous under different environmental conditions, or they could reflect individual health or quality.

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## Supplementary Material

Supplementary material associated with this article is available, in the online version, at doi:10.1016/j.anbehav.2010.08.005.

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