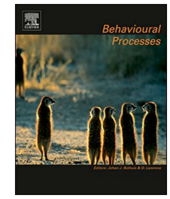
Behavioural Processes 166 (2019) 103877

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc




# Does socio-ecology drive differences in alertness between wolves and dogs when resting?

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ARTICLE INFO

*Keywords:*
Alertness
Domestication
Dog
Heart rate
Resting
Wolf

ABSTRACT

Variation in resting behaviour across animals may be driven by adaptations towards their environment. Wolves and dogs seem promising models to examine this idea as they share a common ancestor, but occupy different socio-ecological niches. While wolves generally avoid humans, hunt, defend their territory, and raise offspring cooperatively, most dogs live in human-shaped environments. Hence, we hypothesized wolves to be more alert towards their environment than dogs, i.e. the degree of activation along the sleep-wake continuum (alertness) should be greater in wolves than in dogs. We estimated alertness via cardiac output. We tested similarly raised and kept pack-living wolves and dogs in two different behavioural conditions: (1) inactive wakefulness: animal is lying, head in an upward position with eyes opened, (2) resting: animal is lying, head in downward position with eyes mainly closed. In contrast to our expectations, we found that in both conditions wolves had a lower heart rate and higher heart rate variability than dogs, i.e. wolves might be less alert/more relaxed than dogs. Although our results are preliminary, we suggest that the higher alertness of dogs compared to wolves is potentially driven by differences in their socio-ecology (i.e. domestication) causing greater attention of dogs to human behaviour.

## 1. Introduction

The adaptations of wild species to the anthropogenic environment seem to result in domesticated animals that are less alert and sensitive towards their environment than their wild ancestors (Herre, 1981; Künzl and Sachser, 1999; Price, 1984). Wild animals need to find food, shelter, and mates, and, therefore, have to explore and cope with new and potentially dangerous environments and situations. For domesticated animals, however, risks have shifted as their environment is controlled by humans. As a result, they might be less alert to their environment and being neophobic or explorative may be less important for their fitness and survival (Kaiser et al., 2015; Price, 1984).

One example supporting this idea is experimental data showing that dogs (*Canis lupus familiaris*) were generally less neophobic, but also considerably less interested in novelty (i.e. spend less time exploring objects) in their environment than wolves (*Canis lupus*; Moretti et al., 2015). As wolves seem to be more sensitive towards (changes in) their environment than dogs, they might generally be more alert towards their environment than dogs. Also, domestic guinea pigs seem less attentive towards their environment than wild cavies. When the behaviour of these animals was compared under standardized conditions, wild cavies showed more orienting behaviour and were more explorative than domestic guinea pigs (Künzl et al., 2003; Künzl and Sachser, 1999). Similar results were obtained when comparing wild and domesticated rats. Likewise, it took wild rats much longer to explore a new environment than domesticated rats (Stryjek et al., 2012). Wild junglefowl also explore novel environments longer than domesticated chickens do; in addition, they show more pronounced alert behaviour (i.e. walk alert versus stand alert) and vocalize more in response to a (stimulated) predator attack than its domesticated form (Schütz et al., 2001). Hence, wild animals compared to their domesticated forms seem to be more sensitive to changes in their environment.

The reduction in alertness of domesticated species may be related to a general down-regulation of the basal activity and reactivity of the two stress response systems, the hypothalamic-pituitary-adrenocortical (HPA) system – responsible for the regulation of stress hormones (e.g. glucocorticoids; Creel et al., 2013) – and the sympathetic-adrenal-medullary (SAM) system. These systems are controlled by the autonomic nervous system (ANS) and are activated to mobilize energy in order to respond appropriately to environmental challenges (Künzl et al., 2003;

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https://doi.org/10.1016/j.beproc.2019.05.024
Received 18 July 2018; Received in revised form 24 January 2019; Accepted 29 May 2019
Available online 30 May 2019
0376-6357/ 

Künzl and Sachser, 1999). Actually, the domestic guinea pigs in our previous examples were not only less attentive to their environment compared to wild cavies, but it was also shown that the reactivity of both their HPA and SAM systems was reduced (Künzl and Sachser, 1999). We suggest the same difference between wolves and dogs.

Wolves are the closest living relatives of dogs (Botigué et al., 2017; Frantz et al., 2016; Pang et al., 2009; Skoglund et al., 2015; Thalmann et al., 2013). During domestication dogs have diverged from wolves in many ways, including ecology and behaviour (Axelsson et al., 2013; Kotrschal, 2018; Marshall-Pescini et al., 2017; Range and Virányi, 2014). Dogs live as a human family member and also exist free-ranging (Bonanni and Cafazzo, 2014; Miklósi and Topál, 2013), but usually still in human-dominated environments (Coppinger and Coppinger, 2001). Wolves tend to avoid close contact with humans and are more co-operative when hunting, taking care of offspring, and defending of territory (Mech and Boitani, 2003) than feral dog packs would be (Bonanni and Cafazzo, 2014). And wolves generally hunt, whereas free-ranging dogs mainly scavenge on human refuse (Marshall-Pescini et al., 2017).

In wolves immediate survival may directly depend on alertness; wolves need to be particularly sensitive towards the detection of prey, competitors, or foe. Dogs mostly live in human environments, where for (pet) dogs food, shelter, and safety are normally provided. But, even free-ranging dogs mainly rely on human refuse as a source of food which is predictable in when and where it becomes available (seasonally constant/fixed location; Marshall-Pescini et al., 2017). Hence, humans buffer the interactions between dogs and their environment (Frank, 1980) – although to varying degrees – and might thereby decrease the necessity of dogs to maintain high alertness, also during resting.

Actually, most animals rest; the most relaxed form of resting is sleep. Sleep can be defined as a state of rapidly reversible behavioural quiescence and reduced sensitivity to sensory stimuli (Siegel, 2008) with the following behavioural criteria: (1) a species-specific body position, (2) prolonged behavioural inactivity, (3) increased stimulus threshold for arousal, and (4) rapid behavioural reversibility when aroused (Flanigan et al., 1973). In mammals and birds two different stages of sleep are distinguished: rapid eye movement (REM) sleep and non-REM (NREM) sleep, while other animals seem to show a single type of sleep (Schmidt, 2014). Actually, behaviour alone may not be sufficient in determining whether an animal is sleeping or not. In fact, there are several intermediate states along the continuum between being awake and being asleep (Campbell and Tobler, 1984). An animal at rest, for example, could be described as behaviourally quiescent, but still responsive to sensory stimuli (Siegel, 2008). Hence, rest could be regarded as an intermediary state between being awake and sleeping, but is behaviourally similar to sleeping as resting can also include closed eyes and can be continuous without falling asleep.

Several terms and definitions have been proposed to characterize the states of activation on the sleep-wake continuum, including arousal, alertness, attention, and vigilance (see Oken et al., 2006 for review). Generally, waking up from sleep or arousal increases the levels of alertness and thereby decreases the threshold to respond to external or internal stimuli (Cooper, 1994; Pfaff et al., 2008; Tomlin and Villa, 1994). Arousal includes non-specific activation of the cerebral cortex of the brain (Lindsley, 1988; Oken et al., 2006) and triggers the ANS (Cooper, 1994; Pfaff et al., 2008). Razmjou (1996) actually defined arousal as: "a hypothetical construct that represents the level of central nervous system activity along a behavioural continuum ranging from sleep to alertness." Attention is a specific aspect of alertness, it is more focussed and employs specific brain systems; it can be used interchangeably with vigilance or sustained attention (Lindsley, 1988; Oken et al., 2006).

Besides the electroencephalogram (EEG), eye movements and the activity of the ANS – as indicated by heart rate (HR) and/or heart rate variability (HRV; Koella, 1982; Oken et al., 2006; Siegel, 2009; Viola et al., 2011) – are frequently used as physiological correlates of the level of activation along the sleep-wake axis. Lendrem (1984), for example, determined increased vigilance during sleep via the peeking – i.e. eyes opening – rate of doves exposed to a predator just prior to a sleeping bout. Several species of duck and the Black-tailed godwit also have shown greater than normal vigilance when sleeping in potentially dangerous places or in relatively small groups (Dominguez, 2003; Gauthier-Clerc et al., 1998, 2002; Gauthier-Clerc and Tamisier, 2000). Hayes et al. (1994) found that increased vigilance in awake Bighorn sheep was positively correlated with HR. In humans reductions in vigilance during a driving test came with decreased HR (Schmidt et al., 2009) and increased HRV, indicating relaxation (Mackie and O'Hanlon, 1977; O'Hanlon and Kelly, 1977; Riemersma et al., 1977). In dogs HR decreases and HRV increases from wakefulness to sleeping (Varga et al., 2018). Hence, the degree of attentiveness and being ready for action generally correlates well with the tonus of the SAM system; i.e. a reduction in the activity of the SAM system corresponds to a decrease in alertness (Künzl and Sachser, 1999).

In general, parasympathetic activity increases with resting and the onset of sleep, resulting in a comparatively low HR and high HRV; also, through deeper and rhythmic respiration a sinus arrhythmia (RSA; i.e. a sinusoid change of HR with breathing in and out) is produced at the onset of sleep (Oken et al., 2006). During periods of NREM sleep, cardiac activity is relatively stable and remains under dominant vagal control, while sympathetic activity is reduced (Cabiddu et al., 2012; Chouchou and Desseilles, 2014; Coote, 1982; Vanoli et al., 1995; Viola et al., 2011). In contrast, REM sleep is associated with fluctuations in parasympathetic and sympathetic control, causing rapid changes in HR and HRV (Cabiddu et al., 2012; Coote, 1982; Lanfranchi et al., 2007; Monti et al., 2002); the levels of this variability seem to be species-specific (Coote, 1982). In fact, substantial differences in sleep patterns have been found between closely related species (Aulsebrook et al., 2016; Lesku et al., 2008; Siegel, 2005). This suggests an adaptive nature of these patterns, related to species-specific ecologies and lifestyles; however, there is not much evidence in support of this hypothesis (Siegel, 2005, 2009). So, comparing resting between wolves and dogs may provide new insights in this direction because of their shared common ancestry, but differences in social-ecology.

Hence, we examined potential differences in states of activation along the sleep-wake continuum (i.e. alertness) in similarly raised and kept, and therefore fully comparable, pack-living wolves and dogs in order to investigate whether differences in their socio-ecology would align with their levels of alertness at rest. We compared alertness in two different behavioural conditions: (1) inactive wakefulness, and (2) resting. We decided to use the broader term resting instead of sleeping in the behavioural definitions, because it is difficult to determine if an animal is asleep just by observing its behaviour (Campbell and Tobler, 1984). HR and HRV were used as physiological correlates of alertness, i.e. as indicators of sympathetic/parasympathetic activity. To help us determine the most likely periods of proper relaxation in the resting condition, we selected only periods where we could identify patterns with a regular respiratory sinus arrhythmia in the HR, as this is normally produced at the start of a sleep cycle (Oken et al., 2006). As domesticated animals are suggested to be less alert to their environment than their wild relatives (Herre, 1981; Künzl and Sachser, 1999; Price, 1984), we hypothesized that alertness in both the (1) awake (and alert) and (2) resting state would be higher (e.g. higher HR, lower HRV) in wolves than in dogs, also correlating with a lower arousal threshold than dogs.

## 2. Methods

### 2.1. Ethical approval

All animals participating in this study were housed at the Wolf Science Center (www.wolfscience.at) located in Game Park Ernstbrunn

**Table 1**
Sex, pack membership, individual body mass, date of birth, and relatedness of individual wolves and dogs.

| Subject | Subspecies | Sex | Pack # | Body mass (kg) | Date of birth |
|---|---|---|---|---|---|
| Amarok | Wolf | ♂ | 1 | 39.75 | 07-04-12* |
| Chitto | Wolf | ♂ | 2 | 42.03 | 04-04-12 |
| Nanuk | Wolf | ♂ | 3/4 | 40.05 | 28-04-09 |
| Tala | Wolf | ♀ | 2 | 38.03 | 07-04-12* |
| Yukon | Wolf | ♀ | 3(5) | 35.75 | 02-05-09 |
| Wamblee | Wolf | ♂ | 5 | 37.70 | 18-04-12 |
| Asali | Dog | ♂ | 6 | 31.95 | 13-09-10 |
| Hakima | Dog | ♂ | 7 | 15.45 | 13-09-10 |
| Kilio | Dog | ♂ | 8 | 26.95 | 18-12-09* |
| Maisha | Dog | ♂ | 9 | 24.60 | 18-12-09* |
| Meru | Dog | ♂ | 8 | 29.00 | 01-10-10 |
| Rafiki | Dog | ♂ | 9 | 19.60 | 30-11-09 |

* Wolf or dog siblings.

in Austria (License No. AT00012014) and were kept in strict accordance with the Austrian Federal Act on the Protection of Animals (Animal Protection Act – TSchG, BGBl. I Nr. 118/2004). All animals could choose voluntarily to participate in the experimental sessions. If they were not motivated to leave their home enclosure for an experimental session, it was cancelled and repeated on a different day. All methods applied were non-invasive and in accordance with the Austrian Animal Experiments Act (BGBl. I Nr. 114/2012, Tierversuchsgesetz 2012 – TVG 2012); no ethical approval was necessary for the execution of this study. The CITES (www.cites.org) permits for our wolves are: (2009) Triple D Farm, USA: AT09-E-0018; (2012) Minnesota Wildlife Connection, USA: 12AT330200INEGCJ93; and Haliburton Forest, Canada: AT12-E0020.

### 2.2. Subjects

This study involved 6 wolves (*Canis lupus*) and 6 dogs (*Canis lupus familiaris*; Table 1). All wolves and dogs were hand-raised at the Wolf Science Center from 10 days of age till 5 months old. Then they were integrated into already existing packs. For more information about the general raising and upbringing of our animals see Range and Virányi (2014). The subjects were between 2.0–6.5 years of age when being tested – wolves: mean (SD) = 3.6 (1.7); dogs: mean (SD) = 3.3 (0.5).

The wolves were fed with carcasses of deer, rabbit, or chicken 3–4 times a week, while the dogs were fed with Royal Canine® Medium Adult dry food daily which was regularly enriched with small pieces of deer, rabbit, or chicken. The wolves and dogs also received daily vet and obedience training and cooperated in a number of behavioural tests on a weekly basis; all animals were used to working in separation from their pack members. Participation was always voluntarily and rewarded by pieces of beef, sausage, or Royal Canine® German Shepard dry food. Water was available *ad libitum* to all wolves and dogs in their home enclosures, but was also available in the separate enclosures during testing. All animals were kept in packs in enclosures ranging between 2000-8000 $m^2$ in size, with natural landscape including trees, bushes, shelters, and natural objects such as stones, branches, and tree trunks.

### 2.3. Data collection

#### 2.3.1. Heart rate measurements

Heart rate (HR) was measured with the Polar® RS800CX HR monitor consisting of a chest belt with electrodes, a transmitter for wireless data transmission (WearLink® W.I.N.D) – attached to the chest belt – and a wrist watch data logger where the HR data was recorded and saved. The belt was placed around the chest of the animals just behind the shoulder blades, while making sure that the transmitter was placed over the heart for optimal transmission of the HR signal. The logger was placed on a collar around the neck of the animals. All wolves and dogs received positive reinforcement training prior to the experimental sessions to wear this HR monitor. Also, for improvement of signal transduction from the heart to the electrodes, the fur between skin and electrodes was wetted with 70% ethanol. This method was validated for dogs against the electrocardiogram (ECG; Essner et al., 2013, 2015; Jonckheer-Sheehy et al., 2012). Heart rate variability (HRV) in this study was expressed as: the root mean square of successive differences (RMSSD), as this is normally used for short-term HRV analysis (for RMSSD details see von Borell et al., 2007).

#### 2.3.2. Experimental conditions

We analysed cardiac output as a measure of alertness in 2 different behavioural conditions: (1) inactive wakefulness, and (2) resting (head down recumbency). The two categories were behaviourally defined as (see also Fig. 1):


**Fig. 1.** The two behavioural conditions: (1) an awake (and alert), but inactive wolf (A) and dog (B), and (2) a resting wolf (C) and dog (D).

1) Inactive wakefulness

Body touching the ground either with caudal, dorsal, or lateral side. Position of the paws varies, e.g. folded (under body) or stretched out. Head is in an upward position and can be moved around. Eyes are open, but increased blinking can occur.

2) Resting

Body touching the ground either with caudal, dorsal, or lateral side. Position of the paws varies, e.g. folded (under body) or stretched out. Head is in a downward position, either lying on paws, ground, or tucked under the body. Eyes are generally closed, but might be opened and closed again (peeking). Parts of the body occasionally twitching.

### 2.4. Procedure

Data for all dogs was collected from June-September 2013 and for the wolves from May-August 2014 and April-October 2015. The data was collected during the day (from 09:00-18:00); although most HR recordings were taken in the afternoon (typically between 12:00-14:00), some sessions were recorded in the morning (1 session of Nanuk, Hakima, Kilio, and Meru).

Data was collected from individual animals that were separated from their pack; a common procedure for wolves and dogs at the Wolf Science Center in which the animals show no signs of separation anxiety. At the start of each experimental session the focal animal was shifted from its enclosure into an airlock where the HR monitor was strapped on. This procedure was trained through positive reinforcement prior to the experimental sessions and had the full cooperation of all animals. Then the wolf/dog was shifted to a (known) enclosure or compartment (part of an enclosure) without other pack members for the period of testing.

Animals were observed by a human experimenter and video-taped between 45 min and 1 h, depending how quickly they relaxed. In one session Chitto was only observed for 30 min, because he relaxed immediately. In three other sessions the animals were observed longer than 1 h (Kilio and Nanuk: 1.5 h, Meru: 2 h) to make sure we observed resting behaviour long enough.

### 2.5. Data selection

HR patterns during sleep are characterized by a regular respiratory sinus arrhythmia (RSA; Oken et al., 2006) in both dogs (Hamlin et al., 1966) and wolves (Kreeger et al., 1990), i.e. consistent and regular HR increases with inspiration and decreases with respiration (Figs. 2C, D). In both wolves and dogs, the RSA seems to dampen during (non-moving) wakefulness as other sensory input might also influence HR (Haddad et al., 1984; Kreeger et al., 1990; Figs. 2A, B). In red foxes similar HR changes have been observed (Kreeger et al., 1989). So, the HR recordings were checked for this pattern and only parts of the HR containing a clear and continuous RSA pattern (Figs. 2C, D) were selected for the behavioural condition resting, but only if they were longer than 1 min (Varga et al., 2018), i.e. all continuous RSA patterns shorter than 1 min were excluded from the analyses. Time domain analyses of HR(V) require the recording lengths of HR to be a similar period of time (von Borell et al., 2007). Hence, as the maximum duration of an RSA found in one animal was 1 min and 20 s, this time period was then used for further analyses in all animals. All these recordings were subsequently checked with the videos to see whether the behaviours in the behaviour category resting (i.e. animal is lying, head in downward position with eyes closed) matched with the RSA patterns found. Behaviour was continuously coded. If an animal moved within the 1 min and 20 s of the RSA this recording was excluded for analysis. This resulted in at least one HR recording of every animal and for most of them two (from separate days; see also Table S1) with a length of 1 min and 20 s. Thereafter, of all these selected recordings, the complete videos were checked for the presence of continuous behaviour(s) in the condition inactive wakefulness. Any HR parts coinciding with this behaviour category were selected (Figs. 2A, B), also covering a time period of 1 min and 20 s. When multiple usable HR parts were found within one video recording, only a single one was randomly selected for analysis. Subsequently, in all the selected HR data files, HR was error-corrected using the AVEC-method; the confidence level used for outliers was set to 75% (see Schöberl et al., 2015 for details). Normally, HR files containing more than 5% errors are excluded (von Borell et al., 2007). In our case the only file that had more than 5% errors (Tala: 5.9%) was included in the analysis for comparability, the more as it underwent the same error correction procedure as all other files.

### 2.6. Statistical analyses

The response variables mean HR and RMSSD were both analysed in separate linear mixed effect (LME) models in which: (1) subspecies (wolf or dog), (2) condition (inactive wakefulness or resting), (3) body mass, (4) timing of session (morning or afternoon), and (5) temperature were included as fixed factors. Due to the circadian rhythm of sleep-wake patterns, the wolves and dogs might be more active during some parts of the day; hence, timing of the session (morning or afternoon) was included in the model. Although we measured the HR parameters of the wolves and dogs in different years, we considered temperature a more appropriate parameter to represent the environmental conditions during testing than season; hence, temperature was included in the models as a fixed factor. Animal identity (1), (2) sex, and (3) session number (1 or 2), were added as random effects in all models. Animal identity was included as a random factor to account for repeated measures. Sex was added to control for any effects of sex on the data, as there was not enough data to statistically test for it. However, as the variance explained by the factor sex was zero in both global models, it was excluded as a random factor. Session number (1 or 2) was added to account for the fact that the measurements were selected out of one period of recording on the same day. The mean HR data was altered with a reciprocal transformation (and multiplied by a 1000) and the RMSSD data with a square root transformation to induce a better homogenization of the variance.

Then, we investigated if the time it took (latency) the wolves and dogs to first show the behaviour inactive wakefulness was different between the two subspecies. Possibly the wolves or dogs relax faster, causing a lower HR. Hence, we measured the period of time from the beginning of a measurement (i.e. all humans except the observer left and the observer was not moving) till the required behaviour was first observed. A LME model was then calculated with the "time till behaviour inactive wakefulness $1^{st}$ occurred" as response variable and subspecies (wolf or dog), timing of session (morning or afternoon), and temperature as fixed factors. Animal identity and sex were included as a random factor; however, sex was excluded in the global model (see above).

The wolf in Fig. 2 shows a higher respiratory rate (RR) in the resting condition than the dog. Hence, to examine if this difference indeed manifested on the group level and influenced HR, we analysed the respiratory rate (RR) per minute of the wolves and the dogs. RR was calculated by counting the number of peaks (e.g. number of peaks of wolf in Fig. 2 = 21) in the HR data files and averaging them over a minute. Consequently, we ran an LME model with as random factor animal identity (sex was excluded; see above). Fixed factors included: (1) subspecies (wolf/dog) and (2) body mass.

The global models of our four response variables (mean HR, RMSSD, time till behaviour 1 st occurred, and RR) were then standardized to help interpret their (model-averaged) estimates as the input variables were measured on different scales (Grueber et al., 2011). These models were then reduced to find the best model fit and ranked using the corrected Akaike Information Criteria (AICc) – the AICc is used when

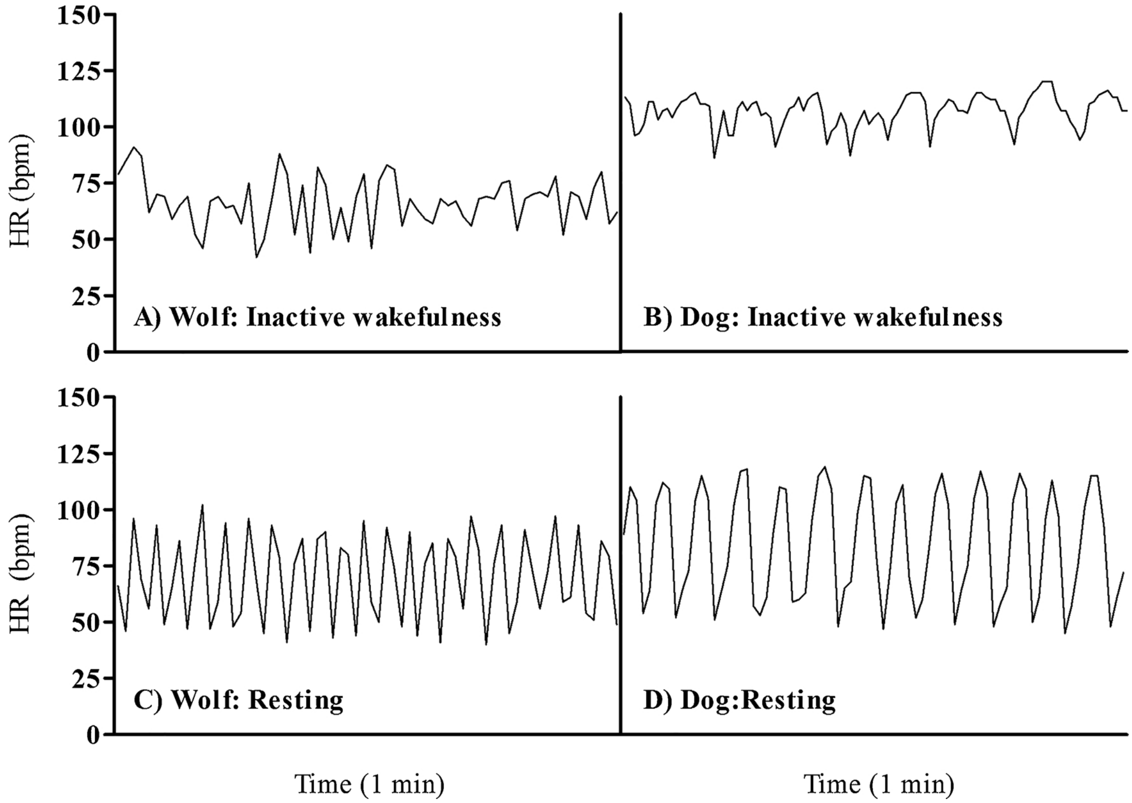


**Fig. 2.** One minute HR patterns of an awake (and alert), but inactive wolf (A) and dog (B), and a resting wolf (C) and dog (D) with respiratory sinus arrhythmia patterns.

**Table 2**
Top-ranked models.

| Response variable with selected model(s) | logLik | AICc | df | ΔAICc | Akaike weight |
|---|---|---|---|---|---|
| A) Mean HR | | | | | |
| Subspecies + Condition + Body mass + Time + Temperature | −69.53 | 163.1 | 9 | 0.00 | 0.300 |
| Subspecies + Condition + Time + Temperature | −71.88 | 164.4 | 8 | 1.35 | 0.153 |
| Subspecies + Condition + Time | −73.73 | 165.0 | 7 | 1.91 | 0.116 |
| B) RMSSD | | | | | |
| Subspecies + Condition + Body mass | −106.28 | 230.1 | 7 | 0.00 | 0.377 |
| Subspecies + Condition | −108.58 | 231.7 | 6 | 1.65 | 0.165 |
| C) Time till behaviour 1st occurred | | | | | |
| Time | −149.91 | 310.5 | 4 | 0.00 | 0.216 |
| Temperature | −149.93 | 310.5 | 4 | 0.04 | 0.211 |
| Time + Temperature | −148.14 | 310.6 | 5 | 0.09 | 0.206 |
| *Intercept* | −151.60 | 310.7 | 3 | 0.22 | 0.193 |
| D) RR | | | | | |
| *Intercept* | −54.67 | 116.8 | 3 | 0.00 | 0.665 |

**Table 3**
Model-averaged coefficients (full-model averaging) and their standard errors (SE), confidence intervals (CI), and relative importance (RI).

| Response variable with fixed factors | Estimate | SE | CI lower limit (2.5%) | CI higher limit (97.5%) | RI |
|---|---|---|---|---|---|
| A) Mean HR | | | | | |
| *Intercept* | *12.93* | *0.44* | *12.03* | *13.83* | |
| **Subspecies** | **4.63** | **2.09** | **0.46** | **8.79** | **1.00** |
| **Condition** | **1.85** | **0.34** | **1.16** | **2.54** | **1.00** |
| **Time** | **1.43** | **0.57** | **0.27** | **2.59** | **1.00** |
| Temperature | −0.86 | 0.59 | −2.04 | 0.31 | 0.80 |
| Body mass | −2.09 | 2.34 | −6.73 | 2.55 | 0.53 |
| B) RMSSD | | | | | |
| *Intercept* | *16.06* | *0.55* | *14.94* | *17.19* | |
| **Subspecies** | **6.62** | **2.92** | **0.79** | **12.45** | **1.00** |
| **Condition** | **6.94** | **1.11** | **4.67** | **9.20** | **1.00** |
| Body mass | −3.62 | 3.10 | −9.78 | 2.54 | 0.70 |
| C) Time till behaviour 1st occurred | | | | | |
| *Intercept* | *427.70* | *251.40* | *−70.03* | *925.46* | |
| Time | 232.40 | 281.00 | −334.68 | 799.51 | 0.51 |
| Temperature | −188.00 | 230.70 | −653.67 | 277.58 | 0.50 |

Statistically important predictors are in **bold**.

sample sizes are small (Burnham et al., 2011). Subsequently, the ΔAICc was calculated by subtracting the lowest AICc from the AICc of each candidate model and Akaike weights were computed, as well. These measures were used to identify the model with the strongest support. However, also models with a ΔAICc less than 2 were retained (Burnham and Anderson, 2002; Burnham et al., 2011; Symonds and Moussalli, 2011). Hence, only models with a ΔAICc less than 2 are reported (Table 2). For three of our responses variables multiple models with a ΔAICc < 2 were found, i.e. for the response variables mean HR, RMSSD, and time till behaviour 1st occurred. For each of these models the factors were averaged to determine which of the fixed effects had the strongest effect on the different response variables (full-model averaging; Grueber et al., 2011; Nakagawa and Freckleton, 2011). We considered fixed effects to affect the response variables “significantly” if their 95% confidence intervals did not include zero (Grueber et al., 2011) and were deemed important (Table 3). Statistical analyses were carried out in R (version 3.0.3; R Core team), using the packages: arm, car, lme4, lmerTest, and MuMIn.

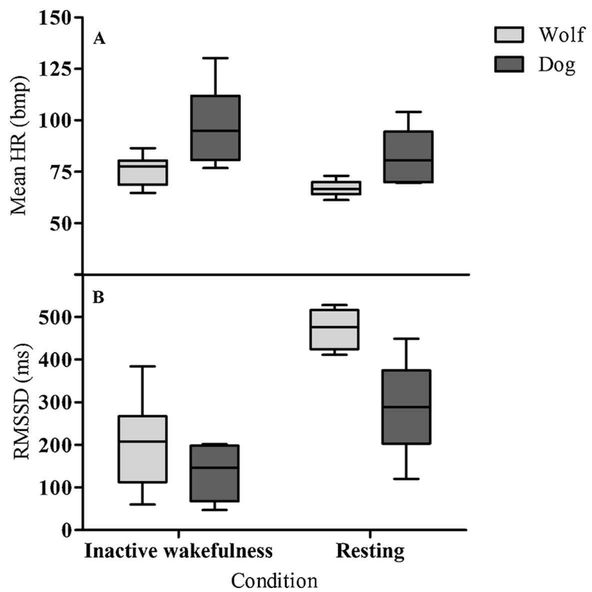


**Fig. 3.** Mean HR (A) and RMSSD (B) of wolves (N = 6) and dogs (N = 6) in the two different conditions. Boxes encompass the interval between the 25th and 75th percentiles, the horizontal line represents the median, and whiskers give the 5 and 95 percentiles.

## 3. Results

### 3.1. Cardiac parameters

Subspecies (i.e. wolf or dog), condition, and timing of the session were the three factors identified as important by the model-averaged results in explaining the mean heart rate (HR; Table 3A). The wolves had a lower HR than the dogs, both in the inactive and the resting condition (Fig. 3A; see Fig. 4A, B for individual HR). Also, the animals measured in the morning generally seemed to have a lower HR than those measured in the afternoon. Body mass did not affect the HR.

The heart rate variability (HRV) models – expressed as the root mean square of successive differences (RMSSD, see above) – showed an effect of subspecies and condition (Table 3B): the wolves showed a higher RMSSD than the dogs in both the alert, but inactive and the resting condition (Fig. 3B; see Fig. 4C, D for individual RMSSD). Potentially influencing factors such as body mass, temperature, and time of session did not seem to affect the RMSSD (Table 3B).

### 3.2. Other parameters

To investigate if the wolves or dogs relaxed faster – i.e. lied down faster – and, hence, influenced HR, we looked at the latency till the behaviour inactive wakefulness 1st occurred. However, the model-averaged results showed little evidence that any of the fixed factors influenced the time till the behaviour inactive wakefulness first occurred (Table 3C). The factor subspecies was not even included in the top-ranked models (Table 2C). Actually, the selected models do not seem to improve their AICc compared to the null model much (i.e. intercept model; Table 2C). Hence, these models do not seem explain the variation of this response variable better than the corresponding null model (Burnham and Anderson, 2002). Thus, we could not find a difference with regard to how fast the wolves or dogs were to lie down (Fig. S1).

To exclude the possibility that the HR differences in the resting condition between the wolves and dogs were caused by differences in their respiratory rate (RR), we investigated if the RR was influenced by either the subspecies and/or their body weight. However, the model with the best fit regarding the RR only included the intercept or random

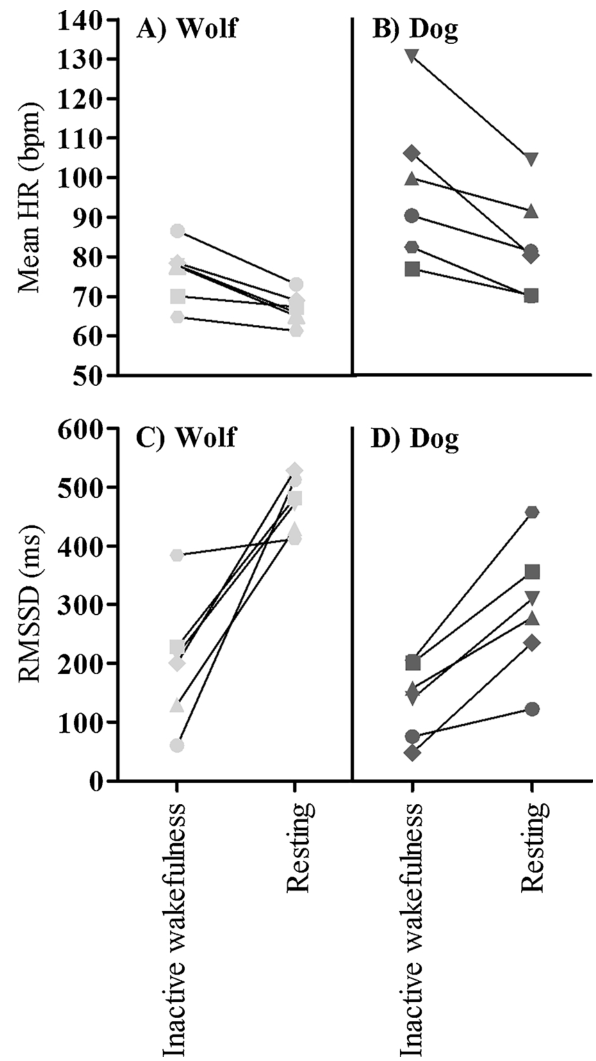


**Fig. 4.** Mean HR of individual wolves (A) and dogs (B) and RMSSD of individual wolves (C) and dogs (D) in the two different conditions.

effects (Table 2D). Hence, no effect of the subspecies (Fig. S2) or body mass was found on the RR.

## 4. Discussion

In contrast to our predictions, we found that the wolves not only had a lower heart rate (HR) than the dogs in the inactive wakefulness and resting conditions, but also a higher heart rate variability (HRV). Hence, the wolves might not only have been less alert (i.e. showed less sympathetic activation) than the dogs when they were resting, but also when they were awake, but inactive. This is surprising, as we expected wolves to be more alert than dogs, because they seem to live in a potentially more challenging environment.

It is generally assumed that the wild forms of species are more alert and sensitive towards their environment (Herre, 1981; Künzl and Sachser, 1999; Künzl et al., 2003) than their domesticated counterparts – this was already part of Darwin's (1859) "domestication syndrome". Indeed, this idea was found to be true for wild cavies versus domestic guinea pigs where also the basal activity of the sympathetic-adrenal-medullary (SAM) system was reduced in the latter (Künzl and Sachser, 1999). However, the basal activity of the hypothalamic-pituitary-adrenocortical (HPA) system showed no such difference. Similarly, the basal corticosterone levels in chickens and their wild relative the red junglefowl did not differ (Fallahsharoudi et al., 2015). Yet, in rats

(Albert et al., 2008) and white-backed munia (Suzuki et al., 2012) basal corticosterone levels were lower in the domesticated strains. Likewise, basal cortisol levels were lower in silver foxes selected for tameness (Trut et al., 2009). Hence, it seems that domestication affects the stress response systems in various domesticated animal species differently (Wilkins et al., 2014), potentially also depending on the socio-ecological environment these animals were exposed to during domestication (Kaiser et al., 2015).

Early dogs probably cooperated with humans in hunting, guarding, and herding (Clutton-Brock, 1995). Nowadays, dogs are employed in a much wider range of tasks, e.g. search and rescue work, various kinds of assistance, including pedagogy and therapy, or simply social companion (Kotrschal, 2016, 2018; Miklósi, 2007). Most of these tasks include prolonged monitoring, particularly of people, and generally, vigilance towards the environment (Adams and Johnson, 1993, 1995; Helton, 2009). In fact, dogs are well able to follow ostensive referential communicative cues (Reid, 2009; Topál et al., 2014), e.g. gazing or pointing (Gácsi et al., 2009; Soproni et al., 2002; Virányi et al., 2008), are sensitive to the attentional states of humans (Call et al., 2003; Schwab and Huber, 2006), and seem to be able to discriminate between basic human emotions (Buttelmann and Tomasello, 2013; Müller et al., 2015). Hence, dogs may have experienced a selective pressure towards keeping high levels of alertness, i.e. to be ready for action when needed, even when resting. Actually, while humans generally do not wake up after rapid eye movement (REM) sleep, dogs do wake up following active sleep (Adam and Johnson, 1993), giving them the opportunity to be more alert towards their surroundings after a period of reduced responsiveness. In contrast to dogs, that need to stay individually focused on human demands, alertness in wolves might be shared between pack members via asynchronous sleep-wake cycles. This decreases individual investment (i.e. metabolic energy) into vigilance, while at the same time increases safety.

The “human factor” in the dogs’ environment may also be more inconsistent and unpredictable – due to individual differences in attitudes, personalities, etc. – than the socio-ecological environment of wolves. For example, dogs living with “extrovert” owners show relatively high baseline cortisol levels and are seemingly more stressed than dogs living with a “neurotic” and more caring owner which reveal lower levels of baseline cortisol. Hence, personalities and life styles of owners potentially affect HPA modulation in their dogs (Kotrschal et al., 2009; Schöberl et al., 2017). In fact, irregular human activity suppresses or disturbs sustained sleep in dogs (Adams and Johnson, 1993). In rats unpredictable husbandry procedures caused less active waking, less deep sleep, and increased disruptive REM sleep, e.g. decreases in the time to the first REM period and increases in the total time of REM sleep and number of behavioural transitions during REM sleep (Cheeta et al., 1997). Actually, humans seem to have evolved towards short but high intensity sleep (with a high percentage of REM sleep) of about 7 h per day (Samson and Nunn, 2015). Humans are powerful social “Zeitgeber” for their dogs which tend to sleep when their owners do (Wells, 2009); also, the sleep patterns of dogs seem to coincide with those of their humans (Lucas et al., 1977). We, therefore, suggest that living together with humans might have resulted in dogs that sleep shorter and lighter – i.e. in a state of chronically elevated alertness and maintaining lower arousal thresholds – and with a greater number of REM bouts than wolves, which remains to be shown. So, the adaptation of dogs’ resting patterns might have evolved in parallel to that of humans – analogous to the adjustments of humans and dogs towards a starch rich diet (Axelsson et al., 2013).

The higher alertness of dogs might also increase survival in free-ranging dogs, which form up to 80% of dogs worldwide (Hughes and Macdonald, 2013; Lord et al., 2013). In contrast to pet dogs, their interactions are not so much mediated by humans; but, humans seem to be a major cause of free-ranging dog mortality (Paul et al., 2016). Hence, even free-ranging dogs depend on humans and the possible threats in the human-dominated environment to free-ranging dogs may be more severe than those in the natural environment of wolves (Frank, 1980). This may contribute to the selection for high alertness in dogs, the more as free-ranging dogs rely less on their pack members than wolves do (Marshall-Pescini et al., 2017). Wolf alertness might in fact be more context-specific than dog alertness. For example, wolves showed more interest in novel objects than dogs, but were also more neophobic (Moretti et al., 2015). If wolves encounter unfamiliar items in their environment these can potentially be dangerous (Peterson and Ciucci, 2003). Dogs, on the other hand, live in the domain of human culture since early prehistory (Skoglund et al., 2015), coming with an ever increasing diversity of artefacts and, hence, seem to be easier habituated to such objects than wolves.

In the resting condition our wolves and dogs were probably in a state of low-attention drowsiness. This stage is also described as the “transition to sleep stage” (Wauquier et al., 1979) or “light sleep” (Mitler and Dement, 1977). Actually, drowsiness seems to include eye movements, i.e. opening and closing of the eyes (Kis et al., 2014; Wauquier et al., 1979), besides a relaxed body position on the ground. Although not observed in all our wolves and dogs, most animals during the resting condition did open their eyes occasionally. However, it was not always easy to observe the eye movements of the animals as the view was blocked by fence and vegetation in the test enclosures. Wauquier et al. (1979) actually only scored light non REM (NREM) sleep if eyes were not moving (Wauquier et al., 1979; Yasuma et al., 1997); hence, our animals were most likely in state of low-attention drowsiness.

In fact, most resting data was collected from animals within 2 min after they closed their eyes, i.e. when a state of low-attention drowsiness is most likely to occur. The duration of a drowsiness episode for dogs is estimated between 1.2–2.4 minutes (Table S2; Mitler and Dement, 1977; Wauquier et al., 1979, 1981) after which the NREM sleep stage normally commences (Lucas et al., 1977). However, these ranges were collected from dogs kept indoors, partially at night, and from animals kept in kennels. As the data in this study was collected outdoors, from animals living exclusively outdoors, stimulus enhancement in the form of visual or auditory signals from their own or other pack members might have caused the drowsiness state to last longer in the wolves and dogs; also, because data was collected during the day. Therefore, a comparison of normal pet dogs with our socialized wolves may have revealed even more extreme differences. Furthermore, the outdoor environment might also have resulted in an increase in the latency to first show NREM sleep. In other studies, the minimum period of time for NREM sleep to commence was about 30–60 minutes (Table S2; Kis et al., 2014; Wauquier et al., 1981). As our recordings were on average 1 h long, the animals might not have had time to fall into NREM sleep.

Our cardiac results seem to support this idea. In the resting condition, we found a mean HR (SD) of 66.6 (4.0) beats per minute (bpm) in the wolves and 82.7 (13.2) bpm in the dogs (Fig. 3A). When Kreeger et al. (1990) recorded HR of four wolves during sleep – defined as: “lying down with eyes closed” – the wolves showed a resting HR of 56 bpm. So, based on the HR alone, our wolves may have been only lightly asleep during the rest periods we recorded. Generally, studies examining the resting cardiac activity of dogs tend to be hard to compare because of inconsistencies in the description of their resting behaviour. Noszczyk-Nowak et al. (2009) and Blake et al. (2018), for example, had dog owners rate the behaviours of their dogs, while Wyatt and Mitchell (1974) just reported the HR of dogs “lying quietly”. The resting HR of our dogs seems to fall within the range of the average HRs found in beagle dogs during the night (Matsunaga et al., 2001; Miyazaki et al., 2002; Nakagawa et al., 2009) and was somewhat higher than the HRs measured of 25 pet dogs during the night (Blake et al., 2018). However, one cannot be sure these dogs were actually asleep or resting. Minimum averages reported (Matsunaga et al., 2001; Olsson et al., 2004) seem to be moderately lower than our results, assuming that in these periods the dogs were actually asleep. Also, the reported RMSSD by Blake et al.

(2018) is higher than found in our dogs. Only a single study reported HR values of dogs in combination with EEG sleep stage recordings (Varga et al., 2018). They found an average HR of around 61 bpm on the first occurrence of the drowsiness state which was significantly higher than that of their NREM and REM sleep stages. This is slightly lower than found in our dogs, although Varga et al. (2018) measured HR of pet dogs sleeping inside a room with only their owner present.

Actually, most domesticated animals, including dogs, are considered to spend a considerable proportion of their time in a state of low-attention drowsiness (Campbell and Tobler, 1984). But, without an electroencephalogram (EEG) the exact sleep stage (e.g. REM, NREM) remains uncertain, mainly because behavioural proxies alone might under- or overestimate sleep parameters (Aulsebrook et al., 2016). However, as we identified patterns with a regular respiratory sinus arrhythmia in the HR for the resting state, typically seen during sleep, we are confident that the animals were in a high state of relaxation when measuring their cardiac parameters.

As the respiratory rate (RR) could influence heart rate, we also investigated the RR of the wolves and dogs, but did not find differences. The mean RR (SD), 17.1 (4.7) breaths/min, of our wolves does seem to be within the range described by Kreeger et al. (1988, 1990) in “sleeping” wolves (12–19 breaths/min). For dogs the general sleeping RR is suggested to be below 30 breaths/min. However, an extensive study by Rishniw et al. (2012) examined the RR of 114 pet dogs and found a mean RR (SD) of only 14 (3) breaths/min with a maximum RR of 23 breaths/min, while the resting RR was higher (19 breaths per minute). Hence, like the wolves, our dogs, 16.3 (3.9) breaths/min, seem to be around the averages found for dogs.

It has been suggested that an (inverse) association between physiological parameters (e.g. HR and RR) and body mass exists in dogs, i.e. smaller dogs should exhibit a higher HR than larger dogs. Yet, we did not find an effect of body weight on the HR, RMSSD, and RR of the wolves and dogs which conforms with the results of several other studies (Ferasin et al., 2010; Lamb et al., 2010; Nganvongpanit et al., 2011; Rishniw et al., 2012), even though the body mass in some of these studies ranged from 1.3 to 80 kg (Ferasin et al., 2010). Hezzell et al. (2013) in their meta-study did conclude that in dogs age, breed, disease status, and also body mass influenced HR (negative correlation). However, these parameters only explained a minor part of the variation in HR found. Hence, it seems that body mass generally has a limited effect on HR and autonomous nervous system (ANS) activity (Cruz Aleixo et al., 2017). Other parameters seem to be more important in explaining HR patterns, as also our data suggests.

Finally, we are aware that our findings remain tentative as they are based on a limited sample size. Still, we think that the identical raising and keeping conditions of the wolves and dogs that participated in this study provide a unique base for a fair comparison of their resting state. Currently, additional studies are carried out to further investigate the causes for the differences in alertness found between the wolves and dogs and in which the environmental factors are better controlled in the different conditions, e.g. including the presence and absence of a familiar human.

In conclusion, we suggest that the increased alertness of the dogs during rest, in comparison to the wolves, may be the result of adaptations towards their different socio-ecological environments which has probably shaped their physiology.

## Funding

This project was financially supported by the Austrian Science Fund (FWF), projects W1262-B29 and W1234-G17. We would also like to acknowledge several of our sponsors, including Game Park Ernstbrunn for hosting the Wolf Science Center and Royal Canin for financial support.

## Declarations of interest

None.

## Acknowledgements

The Wolf Science Center was established by Zsófia Virányi, Kurt Kotrschal, and Friederike Range and we thank all the helpers who made this possible, hence, indirectly supporting this research. Special thanks go to Alice Charalabidis and Zina Morbach for their help with the data collection. We also want to thank Marleen Hentrup, Rita Takács, Bea Belényi, Charles Gent, Christina Mayer, and Marianne Heberlein for their help with the heart rate belt training and for the strapping on and taking off of the heart rate monitor prior to and at the end of data collection sessions. We also would like to thank Marianne Heberlein for her help with the statistical analyses and Ludwig Huber, Friederike Range, Zsófia Virányi, and two anonymous reviewers for their helpful comments and suggestions which helped us to improve our manuscript.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.beproc.2019.05.024.

## References

Adams, G.J., Johnson, K.G., 1993. Sleep-wake cycles and other night-time behaviours of the domestic dog *Canis familiaris*. Appl. Anim. Behav. Sci. 36 (1-2), 233–248.
Adams, G.J., Johnson, K.G., 1995. Guard dogs: sleep, work and the behavioural responses to people and other stimuli. Appl. Anim. Behav. Sci. 46 (1-2), 103–115.
Albert, F.W., Shchepina, O., Winter, C., Römpler, H., Teupser, D., Palme, R., Ceglarek, U., Kratzsch, J., Sohr, R., Trut, L.N., Thiery, J., Morgenstern, R., Plyusnina, I.Z., Schöneberg, T., Pääbo, S., 2008. Phenotypic differences in behavior, physiology and neurochemistry between rats selected for tameness and for defensive aggression towards humans. Horm. Behav. 53 (3), 413–421.
Aulsebrook, A.E., Jones, T.M., Rattenborg, N.C., Roth, T.C.I.I., Lesku, J.A., 2016. Sleep ecophysiology: integrating neuroscience and ecology. Trends Ecol. Evol. 31 (8), 590–599.
Axelsson, E., Ratnakumar, A., Arendt, M.L., Maqbool, K., Webster, M.T., Perloski, M., Liberg, O., Arnemo, J.M., Hedhammar, A., Lindblad-Toh, K., 2013. The genomic signature of dog domestication reveals adaptation to a starch-rich diet. Nature 495 (7441), 360–364.
Blake, R.R., Shaw, D.J., Culshaw, G.J., Martinez-Pereira, Y., 2018. Poincaré plots as a measure of heart rate variability in healthy dogs. J. Vet. Cardiol. 20 (1), 20–32.
Bonanni, R., Cafazzo, S., 2014. The social organisation of a population of free-ranging dogs in a suburban area of Rome: a reassessment of the effects of domestication on dogs’ behaviour. In: Kaminski, J., Marshall-Pescini, S. (Eds.), The Social Dog: Behaviour and Cognition. Academic Press, London, pp. 65–104.
von Borell, E., Langbein, J., Després, G., Hansen, S., Leterrier, C., Marchant-Forde, J., Marchant-Forde, R., Minero, M., Mohr, E., Prunier, A., Valance, D., Veissier, I., 2007. Heart rate variability as a measure of autonomic regulation of cardiac activity for assessing stress and welfare in farm animals - A review. Physiol. Behav. 92 (3), 293–316.
Botigué, L.R., Song, S., Scheu, A., Gopalan, S., Pendleton, A.L., Oetjens, M., Taravella, A.M., Seregély, T., Zeeb-Lanz, A., Arbogast, R.M., Bobo, D., 2017. Ancient European dog genomes reveal continuity since the Early Neolithic. Nat. Commun. 8, 16082.
Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach, 2nd ed. Springer-Verlag, New York.
Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav. Ecol. Sociobiol. 65 (1), 23–35.
Buttelmann, D., Tomasello, M., 2013. Can domestic dogs (*Canis familiaris*) use referential emotional expressions to locate hidden food? Anim. Cogn. 16 (1), 137–145.
Cabiddu, R., Cerutti, S., Viardot, G., Werner, S., Bianchi, A.M., 2012. Modulation of the sympatho-vagal balance during sleep: frequency domain study of heart rate variability and respiration. Front. Physiol. 3, 45.
Call, J., Bräuer, J., Kaminski, J., Tomasello, M., 2003. Domestic dogs (*Canis familiaris*) are sensitive to the attentional state of humans. J. Comp. Psychol. 117 (3), 257–263.
Campbell, S.S., Tobler, I., 1984. Animal sleep: a review of sleep duration across phylogeny. Neurosci. Biobehav. Rev. 8 (3), 269–300.
Cheeta, S., Ruigt, G., van Proosdij, J., Willner, P., 1997. Changes in sleep architecture following chronic mild stress. Biol. Psychiatry 41 (4), 419–427.
Chouchou, F., Desseilles, M., 2014. Heart rate variability: a tool to explore the sleeping brain? Front. Neurosci. 8, 402.
Clutton-Brock, J., 1995. Origins of the dog: domestication and early history. In: Serpell, J. (Ed.), The Domestic Dog: Its Evolution, Behaviour and Interactions With People. Cambridge University Press, Cambridge, pp. 7–20.
Cooper, R., 1994. Normal sleep. In: Cooper, R. (Ed.), Sleep. Chapman & Hall, London, pp.

3–46.
Coote, J.H., 1982. Respiratory and circulatory control during sleep. J. Exp. Biol. 100 (1), 223–244.
Coppinger, R., Coppinger, L., 2001. Dogs: a New Understanding of Canine Origin, Behavior and Evolution. Chicago University Press, Chicago.
Creel, S., Dantzer, B., Goymann, W., Rubenstein, D.R., 2013. The ecology of stress: effects of the social environment. Funct. Ecol. 27 (1), 66–80.
Cruz Aleixo, A.S., Alfonso, A., Oba, E., Ferreira de Souza, F., Salgueiro Cruz, R.K., Fillippi, M.G., Chiacchio, S.B., Tsunemi, M., Gomes Lourenço, M.L., 2017. Scaling relationships among heart rate, electrocardiography parameters, and body weight. Top. Companion Anim. Med. 32 (2), 66–71.
Darwin, C., 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. John Murray, London.
Dominguez, J., 2003. Sleeping and vigilance in the Black-tailed godwit. J. Ethol. 21 (1), 57–60.
Essner, A., Sjöström, R., Ahlgren, E., Lindmark, B., 2013. Validity and reliability of Polar RS800CX heart rate monitor, measuring heart rate in dogs during standing position and a trot on a treadmill. Physiol. Behav. 114-115, 1–5.
Essner, A., Sjöström, R., Ahlgren, E., Gustås, P., Edge-Hughes, L., Zetterberg, L., Hellström, K., 2015. Comparison of Polar® RS800CX heart rate monitor and electrocardiogram for measuring inter-beat intervals in healthy dogs. Physiol. Behav. 138, 247–253.
Fallahsharoudi, A., de Kock, N., Johnsson, M., Ubhayasekera, S.J., Bergquist, J., Wright, D., Jensen, P., 2015. Domestication effects on stress induced steroid secretion and adrenal gene expression in chickens. Sci. Rep. 5, 15345.
Ferasin, L., Ferasin, H., Little, C.J., 2010. Lack of correlation between canine heart rate and body size in veterinary clinical practice. J. Small Anim. Pract. 51 (8), 412–418.
Flanigan Jr, W.F., Wilcox, R.H., Rechtschaffen, A., 1973. The EEG and behavioral continuum of the crocodilian *Caiman sclerops*. Electroencephalogr. Clin. Neurophysiol. 34 (5), 521–538.
Frank, H., 1980. Evolution of canine information processing under conditions of natural and artificial selection. Z. Tierpsychol. 53 (4), 389–399.
Frantz, L.A., Mullin, V.E., Pionnier-Capitan, M., Lebrasseur, O., Ollivier, M., Perri, A., Linderholm, A., Mattiangeli, V., Teasdale, M.D., Dimopoulos, E.A., Tresset, A., Duffraisse, M., McCormick, F., Bartosiewicz, L., Gál, E., Nyerges, ÉA., Sablin, M.V., Bréhard, S., Mashkour, M., Bălăşescu, A., Gillet, B., Hughes, S., Chassaing, O., Hitte, C., Vigne, J.D., Dobney, K., Hänni, C., Bradley, D.G., Larson, G., 2016. Genomic and archaeological evidence suggest a dual origin of domestic dogs. Science 352 (6290), 1228–1231.
Gácsi, M., Györi, B., Virányi, Z., Kubinyi, E., Range, F., Belényi, B., Miklósi, A., 2009. Explaining dog wolf differences in utilizing human pointing gestures: selection for synergistic shifts in the development of some social skills. PLoS One 4 (8), e6584.
Gauthier-Clerc, M., Tamisier, A., Cezilly, F., 1998. Sleep–vigilance trade-off in Green-winged Teals (*Anas crecca crecca*). Can. J. Zool. 76 (12), 2214–2218.
Gauthier-Clerc, M., Tamisier, A., 2000. Sleep-vigilance trade-off in Gadwall during the winter period. Condor 102 (2), 307–313.
Gauthier-Clerc, M., Tamisier, A., Cézilly, F., 2002. Vigilance while sleeping in the breeding Pochard *Aythya ferina* according to sex and age. Bird Study 49 (3), 300–303.
Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. J. Evol. Biol. 24, 699–711.
Haddad, G.G., Jeng, H.J., Lee, S.H., Lai, T.L., 1984. Rhythmic variations in R-R interval during sleep and wakefulness in puppies and dogs. Am. J. Physiol. 247 (1), H67–H73.
Hamlin, R.L., Smith, C.R., Smetzer, D.L., 1966. Sinus arrhythmia in the dog. Am. J. Physiol. 210 (2), 321–328.
Hayes, C.L., Krausman, P.R., Wallace, M.C., 1994. Habitat, visibility, heart rate, and vigilance of bighorn sheep. Desert Bighorn Council Transactions 38, 6–11.
Helton, W.S., 2009. Canine ergonomics: introduction to the science of working dogs. In: Helton, W.S. (Ed.), Canine Ergonomics: The Science of Working Dogs. CRC Press, Boca Raton, pp. 1–16.
Herre, W., 1981. Domestikation. Ein experimenteller Beitrag zur stammesgeschichte. Naturwiss Rundschau 34, 456–463.
Hezzell, M.J., Dennis, S.G., Humm, K., Agee, L., Boswood, A., 2013. Relationships between heart rate and age, body weight and breed in 10,849 dogs. J. Small Anim. Pract. 54 (6), 318–324.
Hughes, J., Macdonald, D.W., 2013. A review of the interactions between free-roaming domestic dogs and wildlife. Biol. Conserv. 157, 341–351.
Jonckheer-Sheehy, V.S.M., Vinke, C.M., Ortolani, A., 2012. Validation of a Polar human heart rate monitor for measuring heart rate and heart rate variability in adult dogs under stationary conditions. J. Vet. Behav. 7 (4), 205–212.
Kaiser, S., Hennessy, M.B., Sachser, N., 2015. Domestication affects the structure, development and stability of biobehavioural profiles. Front. Zool. 12 (1), S19.
Kis, A., Szakadát, S., Kovács, E., Gácsi, M., Simor, P., Gombos, F., Topál, J., Miklósi, A., Bódizs, R., 2014. Development of a non-invasive polysomnography technique for dogs (*Canis familiaris*). Physiol. Behav. 130, 149–156.
Koella, W.P., 1982. A modern neurobiological concept of vigilance. *Experentia* 38 (12), 1426–1437.
Kotrschal, K., Schöberl, I., Bauer, B., Thibeaut, A.M., Wedl, M., 2009. Dyadic relationships and operational performance of male and female owners and their male dogs. Behav. Proc. 81 (3), 383–391.
Kotrschal, K., 2016. Hund & Mensch: Das Geheimnis Unserer Seelenverwandtschaft. Brandstätter Verlag, Vienna.
Kotrschal, K., 2018. How wolves turned into dogs and how dogs are valuable in meeting human social needs. PAIJ 1 (1), 6.
Kreeger, T.J., Seal, U.S., Callahan, M., Beckel, M., 1988. Use of xylazine sedation with yohimbine antagonism in captive gray wolves. J. Wildl. Dis. 24 (4), 688–690.
Kreeger, T.J., Monson, D., Kuechle, V.B., Seal, U.S., Tester, J.R., 1989. Monitoring heart rate and body temperature in red foxes (*Vulpes vulpes*). Can. J. Zool. 67 (10), 2455–2458.
Kreeger, T.J., Kuechle, V.B., Mech, L.D., Tester, J.R., Seal, U.S., 1990. Physiological monitoring of gray wolves (*Canis lupus*) by radio telemetry. J. Mammal. 71 (2), 258–261.
Künzl, C., Sachser, N., 1999. The behavioral endocrinology of domestication: a comparison between the domestic guinea pig (*Cavia aperea f. porcellus*) and its wild ancestor, the cavy (*Cavia aperea*). Horm. Behav. 35 (1), 28–37.
Künzl, C., Kaiser, S., Meier, E., Sachser, N., 2003. Is a wild mammal kept and reared in captivity still a wild animal? Horm. Behav. 43 (1), 187–196.
Lamb, A.P., Meurs, K.M., Hamlin, R.L., 2010. Correlation of heart rate to body weight in apparently normal dogs. J. Vet. Cardiol. 12 (2), 107–110.
Lanfranchi, P.A., Fradette, L., Gagnon, J.F., Colombo, R., Montplaisir, J., 2007. Cardiac autonomic regulation during sleep in idiopathic REM sleep behavior disorder. Sleep 30 (8), 1019–1025.
Lendrem, D.W., 1984. Sleeping and vigilance in birds II. An experimental study of the Barbary dove (*Streptopelia risoria*). Anim. Behav. 32 (1), 243–248.
Lesku, J.A., Roth, T.C., Rattenborg, N.C., Amlaner, C.J., Lima, S.L., 2008. Phylogenetics and the correlates of mammalian sleep: a reappraisal. Sleep Med. Rev. 12 (3), 229–244.
Lindsley, D.B., 1988. Activation, arousal, alertness, and attention. In: Hobson, J.A. (Ed.), States of Brain and Mind. Birkhäuser, Boston, pp. 1–3.
Lord, K., Feinstein, M., Smith, B., Coppinger, R., 2013. Variation in reproductive traits of members of the genus Canis with special attention to the domestic dog (*Canis familiaris*). Behav. Proc. 92, 131–142.
Lucas, E.A., Powell, E.W., Murphree, O.D., 1977. Baseline sleep–wake patterns in the pointer dog. Physiol. Behav. 19 (2), 285–291.
Mackie, R.R., O'Hanlon, J.F., 1977. A study of the combined effects of extended driving and heat stress on driver arousal and performance. In: Mackie, R.R. (Ed.), Vigilance: Theory, Operational Performance, and Physiological Correlates. Plenum Press, New York, pp. 537–558.
Marshall-Pescini, S., Cafazzo, S., Virányi, Z., Range, F., 2017. Integrating social ecology in explanations of wolf–dog behavioral differences. Curr. Opin. Behav. Sci. 16, 80–86.
Matsunaga, T., Harada, T., Mitsui, T., Inokuma, M., Hashimoto, M., Miyauchi, M., Murano, H., Shibutani, Y., 2001. Spectral analysis of circadian rhythms in heart rate variability of dogs. Am. J. Vet. Res. 62 (1), 37–42.
Mech, L.D., Boitani, L., 2003. Wolf social ecology. In: Mech, L.D., Boitani, L. (Eds.), Wolves: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago, pp. 1–34.
Miklósi, Á., 2007. Dogs in anthropogenic environments: society and family. Dog Behaviour, Evolution, and Cognition. Oxford University Press, Oxford, pp. 47–65.
Miklósi, Á., Topál, J., 2013. What does it take to become "best friends"? Evolutionary changes in canine social competence. Trends Cogn. Sci. 17 (6), 287–294.
Mitler, M.M., Dement, W.C., 1977. Sleep studies on canine narcolepsy: pattern and cycle comparisons between affected and normal dogs. Electroencephalogr. Clin. Neurophysiol. 43 (5), 691–699.
Miyazaki, H., Yoshida, M., Samura, K., Matsumoto, H., Ikemoto, F., Tagawa, M., 2002. Ranges in diurnal variation and the pattern of body temperature, blood pressure and heart rate in laboratory beagle dogs. Exp. Anim. 51 (1), 95–98.
Monti, A., Medigue, C., Nedelcoux, H., Escourrou, P., 2002. Autonomic control of the cardiovascular system during sleep in normal subjects. Eur. J. Appl. Physiol. 87 (2), 174–181.
Moretti, L., Hentrup, M., Kotrschal, K., Range, F., 2015. The influence of relationships on neophobia and exploration in wolves and dogs. Anim. Behav. 107, 159–173.
Müller, C.A., Schmitt, K., Barber, A.L., Huber, L., 2015. Dogs can discriminate emotional expressions of human faces. Curr. Biol. 25 (5), 601–605.
Nakagawa, K., Miyagawa, Y., Takemura, N., Hirose, H., 2009. Age-related changes in blood pressure, heart rate and heart rate variability in healthy beagle dogs. Adv. Anim. Cardiol. 42, 8–15.
Nakagawa, S., Freckleton, R.P., 2011. Model averaging, missing data and multiple imputation: a case study for behavioural ecology. Behav. Ecol. Sociobiol. 65, 103–116.
Nganvongpanit, K., Kongsawasdi, S., Chuatrakoon, B., Yano, T., 2011. Heart rate change during aquatic exercise in small, medium and large healthy dogs. Thai J. Vet. Med. 41, 455–462.
Noszczyk-Nowak, A., Paslawska, U., Nicpoń, J., 2009. ECG parameters in 24-h Holter monitoring in healthy dogs. Bull. Vet. Inst. Pulawy 53, 449–502.
O'Hanlon, J., Kelly, G., 1977. Comparison of performance and physiological changes between drivers who perform well and poorly during prolonged vehicular operation. In: Mackie, R.R. (Ed.), Vigilance: Theory, Operational Performance, and Physiological Correlates. Plenum Press, New York, pp. 87–109.
Oken, B.S., Salinsky, M.C., Elsas, S.M., 2006. Vigilance, alertness, or sustained attention: physiological basis and measurement. Clin. Neurophysiol. 117 (9), 1885–1901.
Olsson, K., Lagerstedt, A.S., Bergström, A., Häggström, J., 2004. Change of diurnal heart rate patterns during pregnancy and lactation in dogs (*Canis familiaris*). Acta Vet. Scand. 44 (3), 105–110.
Pang, J.F., Kluetsch, C., Zou, X.J., Zhang, A.B., Luo, L.Y., Angleby, H., Ardalan, A., Ekström, C., Sköllermo, A., Lundeberg, J., Matsumura, S., Leitner, T., Zhang, Y., Savolainen, P., 2009. mtDNA Data indicate a single origin for dogs south of Yangtze River, less than 16,300 years ago, from numerous wolves. Mol. Biol. Evol. 26 (12), 2849–2864.
Paul, M., Sen, S., Sau, S., Nandi, A.K., Bhadra, A., 2016. High early life mortality in free-ranging dogs is largely influenced by humans. Sci. Rep. 6, 19641.
Peterson, R.O., Ciucci, P., 2003. The wolf as a carnivore. In: Mech, L.D., Boitani, L. (Eds.), Wolves: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago, pp. 104–130.
Pfaff, D., Ribeiro, A., Matthews, J., Kow, L.M., 2008. Concepts and mechanisms of

generalized central nervous system arousal. Ann. N.Y. Acad. Sci. 1129 (1), 11–25.
Price, E.O., 1984. Behavioral aspects of animal domestication. Q. Rev. Biol. 59 (1), 1–32.
Range, F., Virányi, Z., 2014. Wolves are better imitators of conspecifics than dogs. PLoS One 9 (1), e86559.
Razmjou, S., 1996. Mental workload in heat: toward a framework for analyses of stress states. Aviat. Space Envir. Md. 67, 530–538.
Reid, P.J., 2009. Adapting to the human world: dogs' responsiveness to our social cues. Behav. Proc. 80 (3), 325–333.
Riemersma, J.B.J., Sanders, A.F., Wildervank, C., Gaillard, A.W., 1977. Performance decrement during prolonged night driving. In: Mackie, R.R. (Ed.), Vigilance: Theory, Operational Performance, and Physiological Correlates. Plenum Press, New York, pp. 41–58.
Rishniw, M., Ljungvall, I., Porciello, F., Häggström, J., Ohad, D.G., 2012. Sleeping respiratory rates in apparently healthy adult dogs. Res. Vet. Sci. 93 (2), 965–969.
Samson, D.R., Nunn, C.L., 2015. Sleep intensity and the evolution of human cognition. Evol. Anthropol. 24 (6), 225–237.
Schmidt, E.A., Schrauf, M., Simon, M., Fritzsche, M., Buchner, A., Kincses, W.E., 2009. Drivers' misjudgement of vigilance state during prolonged monotonous daytime driving. Accid. Anal. Prev. 41 (5), 1087–1093.
Schmidt, M.H., 2014. The energy allocation function of sleep: a unifying theory of sleep, torpor, and continuous wakefulness. Neurosci. Biobehav. Rev. 47, 122–153.
Schöberl, I., Kortekaas, K., Schöberl, F.F., Kotrschal, K., 2015. Algorithm-supported visual error correction (AVEC) of heart rate measurements in dogs, *Canis lupus familiaris*. Behav. Res. Methods 47 (4), 1356–1364.
Schöberl, I., Wedl, M., Beetz, A., Kotrschal, K., 2017. Psychobiological factors affecting cortisol variability in human-dog dyads. PLoS One 12 (2) e0170707.
Schütz, K.E., Forkman, B., Jensen, P., 2001. Domestication effects on foraging strategy, social behaviour and different fear responses: a comparison between the red junglefowl (*Gallus gallus*) and a modern layer strain. Appl. Anim. Behav. Sci. 74, 1–14.
Schwab, C., Huber, L., 2006. Obey or not obey? Dogs (*Canis familiaris*) behave differently in response to attentional states of their owners. J. Comp. Psychol. 120 (3), 169–175.
Siegel, J.M., 2005. Clues to the functions of mammalian sleep. Nature 437 (7063), 1264–1271.
Siegel, J.M., 2008. Do all animals sleep? Trends Neurosci. 31 (4), 208–213.
Siegel, J.M., 2009. Sleep viewed as a state of adaptive inactivity. Nat. Rev. Neurosci. 10 (10), 747–753.
Skoglund, P., Ersmark, E., Palkopoulou, E., Dalén, L., 2015. Ancient wolf genome reveals an early divergence of domestic dog ancestors and admixture into high-latitude breeds. Curr. Biol. 25 (11), 1515–1519.
Soproni, K., Miklósi, Á., Topál, J., Csányi, V., 2002. Dogs' (*Canis familiaris*) responsiveness to human pointing gestures. J. Comp. Psychol. 116, 27–34.
Stryjek, R., Modlińska, K., Pisula, W., 2012. Response to spatial and nonspatial change in wild (WWCPS) and Wistar rats. Pol. Psychol. Bull. 43 (2), 124–131.
Suzuki, K., Yamada, H., Kobayashi, T., Okanoya, K., 2012. Decreased fecal corticosterone levels due to domestication: a comparison between the white-backed Munia (*Lonchura striata*) and its domesticated strain, the Bengalese finch (*Lonchura striata var. domestica*) with a suggestion for complex song evolution. J. Exp. Zool. A. Ecol. Genet. Physiol. 317 (9), 561–570.
Symonds, M.R., Moussalli, A., 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav. Ecol. Sociobiol. 65 (1), 13–21.
Thalmann, O., Shapiro, B., Cui, P., Schuenemann, V.J., Sawyer, S.K., Greenfield, D.L., Germonpré, M.B., Sablin, M.V., López-Giráldez, F., Domingo-Roura, X., Napierala, H., Uerpmann, H.-P., Loponte, D.M., Acosta, A.A., Giemsch, L., Schmitz, R.W., Worthington, B., Buikstra, J.E., Druzhkova, A., Graphodatsky, A.S., Ovodov, N.D., Wahlberg, N., Freedman, A.H., Schweizer, R.M., Koepfli, K.-P., Leonard, J.A., Meyer, M., Krause, J., Pääbo, S., Green, R.E., Wayne, R.K., 2013. Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. Science 342 (6160), 1367–1375.
Topál, J., Kis, A., Oláh, K., 2014. Dogs' sensitivity to human ostensive cues: a unique adaptation? In: Kaminski, J., Marshall-Pescini, S. (Eds.), The Social Dog: Behaviour and Cognition. Academic Press, London, pp. 319–346.
Tomlin, R., Villa, H., 1994. Attention in cognitive science and second language acquisition. Stud. Second Lang. Acquis. 16 (2), 183–203.
Trut, L., Oskina, I., Kharlamova, A., 2009. Animal evolution during domestication: the domesticated fox as a model. Bioessays 31 (3), 349–360.
Vanoli, E., Adamson, P.B., Pinna, G.D., Ba-Lin, Lazzara, R., Orr, W.C., 1995. Heart rate variability during specific sleep stages. A comparison of healthy subjects with patients after myocardial infarction. Circulation 91, 1918–1922.
Varga, B., Gergely, A., Galambos, Á, Kis, A., 2018. Heart rate and heart rate variability during sleep in family dogs (*Canis familiaris*). Moderate effect of pre-sleep emotions. Animals 8, 107.
Viola, A.U., Tobaldini, E., Chellappa, S.L., Casali, K.R., Porta, A., Montano, N., 2011. Short-term complexity of cardiac autonomic control during sleep: REM as a potential risk factor for cardiovascular system in aging. PLoS One 6 (4) e19002.
Virányi, Z., Gácsi, M., Kubinyi, E., Topál, J., Belényi, B., Ujfalussy, D., Miklósi, Á., 2008. Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). Anim. Cogn. 11 (3), 373–387.
Wauquier, A., Verheyen, J.L., Van den Broeck, W.A.E., Janssen, P.A.J., 1979. Visual and computer-based analysis of 24 h sleep-waking patterns in the dog. Electroencephalogr. Clin. Neurophysiol. 46 (1), 33–48.
Wauquier, A., Van den Broeck, W.A.E., Awouters, F., Janssen, P.A.J., 1981. A comparison between astemizole and other antihistamines on sleep-wakefulness cycles in dogs. Neuropharmacology 20 (9), 853–859.
Wells, D.L., 2009. Behaviour of dogs. In: Jensen, P. (Ed.), The Ethology of Domestic Animals: An Introductory Text, 2nd edn. CABI, Wallingford, Oxfordshire, pp. 192–203.
Wilkins, A.S., Wrangham, R.W., Fitch, W.T., 2014. The "domestication syndrome" in mammals: a unified explanation based on neural crest cell behavior and genetics. Genetics 197 (3), 795–808.
Wyatt, H.L., Mitchell, J.H., 1974. Influences of physical training on the heart of dogs. Circ. Res. 35 (6), 883–889.
Yasuma, F., Hayashi, H., Shimokata, K., Yokota, M., Okada, T., Kitoh, J., 1997. Recording of electroencephalograms and electrocardiograms during daytime sleep in trained canines: preparation of the sleeping dogs. Psychiatry Clin. Neurosci. 51 (4), 237–239.