Diurnal activity patterns of equally socialized and kept wolves, Canis lupus, and dogs, Canis lupus familiaris

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Owing to domestication, dog behaviour differs from wolf behaviour, which should also affect time budgets. At the Wolf Science Center, wolves and mongrel dogs are raised and kept in a similar way; thus, it is an ideal place to compare the time budgets of wolves and dogs in search of potential domestication-related shifts. Seven wolf packs and four dog packs were observed over a full year. We focused on major behavioural categories, such as resting and foraging, and calculated the proportion of time they spent on each of these activities. Based on mainstream domestication hypotheses we predicted dogs to be generally more active than wolves because domestication would have relaxed the need for behavioural efficiency. As expected, wolves and dogs differed in their time budgets. Wolves slept, walked and vocalized more than dogs, whereas dogs foraged, sat and manipulated objects more. Human presence around the enclosure increased the activity of both, but dogs were more active than wolves in this situation. Season and time of day had the same effect on dogs and wolves. We conclude that dogs are not too different from wolves in intrinsic motivation affecting their time budgets, except for the increased responses of dogs to humans. This suggests that humans are more important as social Zeitgeber for dogs than for equally socialized wolves.

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In general, domesticated animals share a ‘domestication syndrome’ (Darwin, 1859; Wilkins et al., 2014), featuring a number of linked anatomical and behavioural features. This syndrome is thought to be caused by selection for tameness (Belayaev, 1979; Trut et al., 2004), rendering domesticated animals gentler and more tractable than their wild ancestors and affecting their anatomy and physiology (Trut et al., 2009; Agnvall et al., 2015; Fam et al., 2018; Hecht et al., 2021). Hence, domestication affects the way animals relate to their environment and should also modulate the intrinsic motivational factors of domesticated animals and their responses to external Zeitgeber (i.e. an environmental agent or event that provides the stimulus to trigger the biological clock of an organism, Aschoff, 1954). This in turn, could affect their time budgets (Künzl & Sachser, 1999; Robert et al., 1987; Troxell-Smith et al., 2016).

All dogs originated from wolves through the process of domestication, which began in the Palaeolithic some 35,000 years ago (Botigué et al., 2017; Thalmann et al., 2013). Although the nature of this process is still discussed (Hare & Tomasello, 2005; Hare et al., 2012; Range & Virányi, 2014, 2015; Wilkins et al., 2014; Marshall-Pescini et al., 2017), its outcomes are becoming clearer from an increasing number of experimental studies (Frank & Frank, 1982, 1985; Frank, 1987; Kubinyi et al., 2007; Range & Virányi, 2015; Kaminski et al., 2019). For example, dogs do not fear humans as wolves do (Klinghammer & Goodman, 1987), they are more attentive and attracted to humans (Miklósi et al., 2003; Gácsi et al., 2009) and more willing to respect both conspecific and human hierarchies (Range et al., 2015, 2019b). As a result, they are good at cooperating with humans.

Given the large influence of ecology and a number of potential Zeitgeber, including social factors, on the time budgets of wolves and dogs, a direct comparison in search of potential intrinsic changes due to domestication seems virtually impossible if the animals do not share the same environment and the same experiences from early on. At the Wolf Science Center (WSC), Ernstbrunn, Austria, wolves and dogs are similarly raised and kept. This allows fair comparisons of wolves’ and dogs’ cognitive skills and social and cooperative orientation towards conspecifics or humans (Cafazzo et al., 2018; Range et al., 2015, 2019a, 2019b). This also

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offers a unique opportunity for comparing time budgets of wolves and dogs in the absence and presence of humans.

Wolf packs consist of a breeding pair and their offspring (Packard, 2003). Within-pack cooperation allows for hunting large prey, defending territory and raising young (Mech & Peterson, 2003; Mech & Boitani, 2003). Wolves in the wild show a bimodal activity pattern with crepuscular activity peaks (Vilà et al., 1995; Ciucci et al., 1997; Merrill & Mech, 2003; Theuerkauf et al., 2007; Theuerkauf, 2009; Kirilyuk et al., 2021), potentially associated with optimal hunting conditions. Such environmental factors called 'Zeitgeber' affect the activity of most animals, including wolves, entraining potential intrinsic rhythms (Aschoff, 1954; Heldmaier et al., 1989; Aronson et al., 1993; Grandin et al., 2006). For example, the diurnal and circannual variation of light in temperate zones is the major environmental cue for entraining individual activity and sleep—wake rhythms. In general, wolves tend to be more active during winter, as they are adapted to low temperatures and because of increased prey accessibility (Price, 1999). Wolf reproduction is timed accordingly: female wolves have a single annual oestrus period during the winter month (Scott & Fuller, 1965; Christie & Bell, 1971), which ensures that the pups are born in early spring at peak prey availability (Mech & Boitani, 2003). Variations in daily and circannual activity patterns may be induced by their need to avoid humans (Ciucci et al., 1997; Vilà et al., 1995) or by temperature peaks during the day (Ciucci et al., 1997; Theuerkauf, 2009). Furthermore, as wolves tend to respond to prey densities, wolf behaviour and prey behaviour mutually affect each other (Theuerkauf, 2009). Therefore, seasonality (notably temperature), prey density and avoiding humans seem to be the main factors influencing the activity of wolves in the wild. Although the WSC wolves are captive, they should still adjust their behaviour to the season. Furthermore, as they interact daily with their trainers, who were also their hand-raisers, human presence should also affect their time budgets, but potentially to a lesser degree than in the dogs.

Dogs are much more diverse than wolves in their appearance, genetics (Parker et al., 2017) and lifestyle. Free-ranging dogs (i.e. dogs not under direct human control; Cafazzo et al., 2010) represent up to 80% of the world’s 1 billion dogs (Lord et al., 2013; Hughes & Macdonald, 2013). The socioecology of these dogs differs from that of wolves. They live near humans and usually scavenge on refuse (Majumder et al., 2016; Vanak & Gompper, 2009). Unlike wolves, free-ranging dogs are ‘facultatively social’ (Majumder et al., 2014), living in relatively stable groups composed of several males and females (Bonanni & Cafazzo, 2014). Most females have two oestrus periods per year instead of one like wolves and are generally promiscuous, which could explain why males generally do not participate in raising the pups (Pal, 2005; Cafazzo et al., 2014). Humans are directly and indirectly responsible for 63% of the early deaths of pups and so can be a threat to free-ranging dogs (Paul et al., 2016). Conversely, humans can also provide food to dogs that beg (Bhadra & Bharda, 2014; Majumder et al., 2014) and support pup-raising females. Therefore, humans may play important roles also for free-ranging dogs.

A minority of the world’s dogs live in close companionship with human partners. Companion dogs depend on their humans in nearly every aspect of their life (Leonard et al., 2002; Scott & Fuller, 1965; Vanak et al., 2009; Wandelier et al., 1993; Kotrschal, 2018; Smith & Van Valkenburgh, 2021). Companion dogs tend to be active when the owner is present (Piccione et al., 2014), but rest more than shelter dogs (Hoffman et al., 2019), and their activity patterns vary more than those of wolves or free-ranging dogs (Griss et al., 2021), because the owners are the social Zeitgeber of their dogs (Leonard & Randler, 2009) and, to a certain degree, also vice versa. In fact, pet dogs adjust their sleep—wake cycle to that of their owners (Randler et al., 2018), which includes conforming to their owners’ ‘social jetlag’ (i.e. different sleep timing on workdays and free days). Despite not being companion dogs, the WSC dogs share close relationships with their hand-raisers, who also act as animal keepers and trainers. Hence, it is possible that these familiar humans play the role of owner-like social Zeitgeber for the WSC dogs.

Recently, we studied the resting patterns of the WSC wolves and dogs in search of domestication effects. We found considerable variation in the heart rates and heart rate variability of resting wolves and dogs, depending on the social context. For example, dogs and wolves were more relaxed when resting in their pack than when alone (Kortekaas & Kotrschal, 2019). Moreover, dogs, but not wolves, responded to the presence of familiar humans in a similarly relaxed way as their pack members (Jean-Joseph et al., 2019). When the animals were awake, wolves barely modulated their arousal due to humans’ presence, whereas dogs were generally more alert around humans than when they were alone or with their pack mates. As a follow-up of Jean-Joseph et al. (2020), and by taking into account the major factors that could affect wolves and dogs in the wild (e.g. seasonality, biological cycle) and factors specific to the WSC (i.e. the presence of familiar and unfamiliar humans), we assessed the daytime light budgets and activities of the WSC’s animals over a full year. We hypothesized that the behaviour of dogs as domesticated animals may be less motivated by energy efficiency than that of their wild form, the wolves, since humans provide them with food; hence, dogs would be less energy efficient in their behaviour than wolves, showing overall greater activity. Furthermore, according to the hypersociability hypothesis (von Holdt et al., 2017), selection during domestication has genetically predisposed dogs for hypersocial responses towards humans. Based on this hypothesis, we expected dogs to be more social towards humans and hence alter their behaviours more than wolves in the presence of humans. Finally, we expected that, due to their outdoor life and a generally similar physiology of dogs and wolves, both would be similarly affected by environmental factors, such as temperature and season.

METHODS

Ethical Note

This research was discussed and approved by the institutional ethics committee at the University of Veterinary Medicine, Vienna, in accordance with GSP guidelines and national legislation (ETK-12/11/2018). All the animals participating in the study were housed at the WSC, located in the Game Park Ernstbrunn in Austria (Licence No. AT00012014), and remained there after the study. Throughout the study, no animal was manipulated or exposed to stressful situations. The subjects were observed from outside their enclosure, a situation they are well used to and hence is not stressful to them.

Subjects

We observed seven wolf packs (16 individuals, 11 males and five females; Table 1) and four groups of dogs (11 individuals, five males and six females; Table 1). In 2018, when we started this study, subjects were between 2 and 10 years of age (wolves: mean ± SD = 7 ± 3.1; dogs: mean ± SD = 6 ± 1.6). All animals were hand-raised from 10 days after birth in small groups of four to six in a 1000 m² outdoor enclosure with access to an indoor room where the hand-raisers spent the nights with them. At 5 months they were moved to other enclosures ranging from 2000 m² to 8000 m². They remained hormonally intact (i.e. not neutered or spayed), but male wolves and dogs were vasectomized to prevent unwanted
reproduction. After the animals were integrated into conspecific packs at 5 months old, they had daily contact with their handlers, trainers and, less regularly, with unfamiliar people and visitors in the new facility (e.g. new scientific staff, visitor taking part in special visitor programmes). The wolves were fed carcasses of deer, pig, rabbit or chicken three to four times a week, while the dogs were fed The Good Stuff dry food daily regularly enriched with small pieces of raisers and trainers and, less regularly, with unfamiliar people.

Table 1
List of the subjects

| Individual | Species | Sex | Date of birth | Pack |
|------------|---------|-----|---------------|------|
| Amarok     | Wolf    | d   | 4 Apr 2012    | 1    |
| Aragorn    | Wolf    | d   | 4 May 2008    | 2    |
| Chitto     | Wolf    | d   | 7 Apr 2012    | 3    |
| Etu        | Wolf    | d   | 4 May 2016    | 4    |
| Geronimo   | Wolf    | d   | 2 May 2009    | 5    |
| Kaspas     | Wolf    | d   | 4 May 2008    | 5    |
| Kenai      | Wolf    | d   | 1 Apr 2010    | 1    |
| Maikan     | Wolf    | d   | 4 May 2016    | 4    |
| Nanuk      | Wolf    | d   | 28 Apr 2009   | 6    |
| Shima      | Wolf    | ♀  | 4 May 2008    | 2    |
| Taima      | Wolf    | ♀  | 4 May 2016    | 7    |
| Tala       | Wolf    | ♀  | 4 Apr 2012    | 3    |
| Tekoa      | Wolf    | d   | 4 May 2016    | 7    |
| Una        | Wolf    | ♀  | 7 Apr 2012    | 6    |
| Wamblee    | Wolf    | d   | 22 Apr 2012   | 5    |
| Yukon      | Wolf    | ♀  | 2 May 2009    | 5    |
| Asali      | Dog     | d   | 19 Sep 2010   | 8    |
| Bora       | Dog     | ♀  | 2 Aug 2011    | 8    |
| Gambo      | Dog     | d   | 21 Mar 2014   | 10   |
| Haida      | Dog     | ♀  | 04 Jun 2007   | 10   |
| Hiari      | Dog     | d   | 21 Mar 2014   | 11   |
| Imara      | Dog     | ♀  | 21 Mar 2014   | 11   |
| Layla      | Dog     | ♀  | 2 Aug 2011    | 9    |
| Meru       | Dog     | d   | 1 Oct 2010    | 11   |
| Panya      | Dog     | ♀  | 2 Apr 2014    | 9    |
| Zuri       | Dog     | ♀  | 24 May 2011   | 9/10 |

* a Subject excluded from the statistical analyses.
* b Subject died during the observation period.
* c Pack change on 13 June 2019.

Data Collection

We conducted 29 h of preliminary observations to construct the ethogram for the main study (see Table 2, Appendix Table A1).

Data collection started on 1 December 2018 and ran until the end of November 2019. Three scientific interns (G.D., R.S., K.W.) collected the data (Appendix Table A1). Observations were conducted from dawn to dusk to take daylight hour variation in behaviours into account. As daylight varies with season, the number of observations per month for each individual/pack differed somewhat. However, averaged across the study, the number of observations per month was relatively equal.

### Table 2

| Behaviour | Definition | Code |
|-----------|------------|------|
| Resting   | Not asleep or engaging in other behaviours, lying down, head down, eyes open | R    |
| Sleeping  | Lying down with head on the ground and eyes closed | S    |
| Foraging  | Searching with nose on the ground and sniffing or visual investigation (nose and eyes pointed to the ground to investigate an item) | F    |
| Eating    | Swallowing food provided, or animals they have caught, or grass in the enclosure | E    |
| Drinking  | Swallowing liquid, provided or e.g. puddles | Dr   |
| Hunting   | Chasing or stalking an animal that is not a conspecific | H    |
| Vocalizing| Howling, barking, whining | V    |
| Digging   | Using paws to remove substrate | Di   |
| Object manipulation | Playing, touching, moving, licking, biting an object, a form of enrichment or part of the enclosure | OM   |
| Urinate   | Releasing urine | U    |
| Defecate  | Releasing faeces | D    |
| Stress behaviour | Yawning, body shaking, lip licking, scratching | STB  |
| Social behaviour | All social behaviours, affiliative (e.g. play bow, greeting, etc.) or agonistic (e.g. jaw spar, fight, etc.) | SoB  |
| Sexual behaviour | Mounting, mating | Sex  |
| Maintenance behaviour | Autogrooming or scent rolling | MB   |

Locomotion

| Walking | Slow movement in one direction, at least one leg in contact with the ground; diagonal walk | W    |
| Trotting | Medium pace; diagonal two-beat gait in which the left rear and right front legs move together and the left fore and right hind legs move together | T    |
| Cantering | Fast movement in one direction, a three-beat gait with left hind leg starting, the right hind and left leg striking the ground together and the right foreleg landing and supporting the whole weight of the animal. There is a moment of suspension before the sequence is repeated and the sequence may be reversed | C    |

Immobil

| Sitting | Rear on the ground, with rear legs tucked in and the front legs extended | IS   |
| Standing | All four feet are on the ground with torso off the ground | ST   |
| Lying | Torso on the ground; position of paws may vary, head up, eyes open | IL   |
| Not visible | Animal cannot be seen | NV   |
observed the same pack twice during the same time slot across the same month. Upon arrival at the enclosure, the observer waited at least 2 min next to the fence and was visible to the animals to habituate them. A timer with an audible signal on every minute interval was used to ensure the observer’s accuracy. At each sound signal, the observer noted the behaviour of each individual, always in the same order (i.e. min 1: ind1, ind2, ind3; min 2: ind1, ind2, ind3).

Additionally, the observer noted the presence or absence of visitors/staff and if dogs were visible to the study animals (unfamiliar visitor dogs, the trainers’ dogs and other WSC packs’ dogs that are familiar without being their pack’s members) However, we chose not to analyse the data on dogs visible to the study animals as these data represented less than 1% of the data set (1142 data points) and were likely to be insufficient to draw conclusions on the effect of these dogs on our subjects and also because the dogs were always paired with a human. Visitors/staff and dogs were noted as ‘present’ if they were within 15 m of the enclosure’s wire fences and not hidden by wooden fences or blenders. Several independent variables were coded: identity of the observer, date and time of the observation, which enclosure the observed pack was in (as enclosures have different size and vegetation coverage, which could lead to packs’ preference for some enclosures over the others), temperature, weather (i.e. sunny, cloudy, rainy, snowy), proximity between the individual and the pack (alone, within one body length or within three body lengths) and, finally, whether there was a female in heat in the pack. The variable ‘activity’ was later derived from the observed behaviour. Activity was coded as ‘no’ (i.e. subject is not active) when the subject was observed sleeping, resting, lying, sitting or standing immobile or ‘yes’ (i.e. the subject is active) when the subject was performing any other behaviour.

We conducted a total of 1567 30 min observations. One observation was discarded because the subject observed went out of sight after 3 min and did not return. Therefore, our final sample size was 1566 observations (783 h) and 115708 1 min data points. For all models (below), we excluded all scans where the subject was not visible. Consequently, final sample size for the activity model was 110 176 data points (24 434 active) and 110 176 data points (34 589 subject not alone) for the proximity model.

Statistical Analyses
We tested interobserver reliability (IOR) and found that the category ‘proximity at three body lengths’ scored low IOR (<70%); thus, it was not analysed. After exclusion of the unreliable category, IOR was 93.4%.

We compared the yearly daylight time budgets of wolves and dogs, performing first a Pearson chi-square test and, second, a pairwise post hoc chi-square. As a follow up, we divided the data set in two (human present and human absent) and then performed a Pearson chi-square test and pairwise post hoc chi-square on both data sets. For each test, we used the Bonferroni correction to adjust the P value for multiple testing to decrease the likelihood of potential type I error.

To test what factor could influence dogs’ and wolves’ activity, we used a generalized linear mixed model (GLMM, Baayen, 2008) with binomial error structure and logit link function. Temperature (in Celsius, chosen to represent the seasonal variation), start time of the observation (in hours, to represent the daily variation) as well as wolf or dog, the presence of humans (yes or no) and their interaction were included as fixed effects. Sex and age of the subject (in months) were added as fixed effect factors to control for their influence on wolves’ and dogs’ activity. Subject ID, pack, enclosure and observation ID were included as random effects. Furthermore, a combination of pack and enclosure was included as the last random effect to account for pack preference for particular enclosures. Additionally, we included all the identifiable random slopes (temperature within subject ID, age within pack, enclosure and observation ID and age, temperature, start time of the observation within enclosure/pack) to avoid inflated type I error rate (Schielzeth & Forstmeier, 2009; Barr et al., 2013). Correlations among random intercepts and slopes were unidentifiable (absolute correlation parameter mostly equal to 1) and therefore were excluded from the model (Matuschek et al., 2017). As a result, the model fit decreased moderately (model with correlation: logLik = -48369.15 (df = 30); model without correlation: logLik = -48376.22 (df = 16)).

To test the proximity of our subject to their pack members, we also used a GLMM with a binomial error structure and logit link structure with the same statistical approach as above; wolf or dog, the presence of humans (yes or no) and their interaction were included as fixed effects. Temperature, sex, age of the subject (in months) and the activity of the subject (active or not active) were added as fixed effect factors to control for their influence on wolves’ and dogs’ proximity to their pack mates. Subject ID, pack, enclosure, observation ID and the combination of pack and enclosure were included as random effects. Additionally, we included the only identifiable random slope, age within the combination of pack and enclosure. The final model fit was logLik = -4179.81 (df = 15).

For both models, age, temperature and start time of the observation were z-transformed (to a mean of zero and a standard deviation of one). Species, presence of humans, sex and activity were dummy coded (i.e. the categorical predictors were replaced by one or several dummy variables, consisting of 0 and 1, and then centred to a mean of zero before including them in the model).

To test the significance of our four fixed effects of interest, we used a likelihood ratio test (R function anova with argument test set to “Chisq”; Dobson & Barnett, 2018) to compare our full models (Forstmeier & Schielzeth, 2011) to our null models. The significance of the individual effect was assessed with likelihood ratio tests comparing the full models with their respective reduced models.

For both models, stability was assessed by comparing the estimates of the full model to the estimates of reduced models, suppressing levels of random effect one at a time (Nieuwenhuis et al., 2012). We found no issues of stability in our models. We verified the absence of collinearity using the variance inflation factor (Field, 2013) for a standard linear model excluding all the random effects, which revealed no issues of collinearity in the two models. All statistical analyses were performed with R (version 4.0.5, R Core Team, 2021) using the function Imer of the R package lme4 (version 1.1–26; Bates et al., 2014) with the optimizer ‘bobyqa’. Tests of the individual fixed effects were derived using likelihood ratio tests (Barr et al., 2013; R function drop1 with argument ‘test’ set to ‘Chisq’). Pairwise post hoc chi-square analyses were made with the package chisqposthoc.test (version 0.1.2).

RESULTS
Time Budgets
Overall, wolves’ and dogs’ diurnal time budgets were significantly different over the year (chi-square test: χ²21 = 8720.8, P < 2.2e-16; Fig. 1a and b). Dogs foraged and sat significantly more than wolves (see Table 3 for P values and details of the other behaviours). Wolves slept, lay on the ground, trotted, walked and vocalized more. Additionally, wolves and dogs differed in the frequency of behaviours they displayed in the presence of humans (chi-square test: χ²21 = 4048.4, P < 2.2e-16; Fig. 1c); dogs foraged, sat and vocalized more than wolves. On the other hand, when near humans, wolves trotted, walked, stood and lay on the ground more, as well as rested and slept more than the dogs. Wolves and dogs
also differed in the behaviours displayed in the absence of humans (chi-square test: $\chi^2_{20} = 6887.8, P < 2.2e-16$; Fig. 1d). Dogs were observed foraging and sitting more often than wolves which trotted, walked, stood, lay on the ground, rested and slept more than dogs. Finally, wolves vocalized more than dogs in the absence of humans (see Table 3).

Dog behaviours also differed between the absence and the presence of humans (chi-square test: $\chi^2_{18} = 5116.6, P < 2.2e-16$). In

![Figure 1. Bar plot of the differences in wolves' and dogs' behaviours. (a) Overall comparison; (b) over the months; (c) in the presence of humans; (d) in the absence of humans.](image)

**Table 3**

| Behaviours               | nW | Overall $P$ | nD | Human present $P$ | Human absent $P$ | W–W $P$ | D–D $P$ |
|--------------------------|----|-------------|----|------------------|------------------|----------|----------|
| Cantering                | 65 | 0.001       | 63 | <0.001           | 39               | 72       | 1        |
| Defecating               | 16 | 1           | 6  | <0.001           | 2                | 0        | 1        |
| Digging                  | 11 | 0.001       | 13 | <0.001           | 0                | 40       | <0.001   |
| Drinking                 | 143| 1           | 96 | <0.001           | 46               | 20       | 1        |
| Eating                   | 433| 0.001       | 97 | <0.001           | 115              | 42       | <0.001   |
| Foraging                 | 1289| 0.001      | 1894| <0.001           | 216              | 342      | <0.001   |
| Hunting                  | 6  | <0.001      | 6  | 2                | 0                | 1        | <0.001   |
| Lying                    | 11307| 0.001     | 8490| <0.001           | 2782             | 1095     | <0.001   |
| Sitting                  | 409| <0.001      | 3389| 0.001           | 80               | 518      | <0.001   |
| Standing                 | 13336| 0.001     | 8364| 0.082           | 3463             | 2601     | <0.001   |
| Maintenance              | 873| <0.001      | 698 | <0.001           | 240              | 47       | <0.001   |
| Not visible              | 1772| <0.001     | 1554| <0.001           | 2                | 0        | 1        |
| Object manipulation      | 35 | 0.001       | 455 | <0.001           | 8                | 73       | <0.001   |
| Resting                  | 3583| <0.001     | 2254| 0.127           | 930              | 187      | <0.001   |
| Sexual                   | 52 | 0           | 0  | <0.001           | 20               | 0        | <0.001   |
| Sleeping                 | 23635| <0.001    | 10978| <0.001          | 4463             | 442      | <0.001   |
| Social                   | 740| 0.4         | 379 | <0.001           | 241              | 127      | 0.037    |
| Stress                   | 1  | 1           | 0  | <0.001           | 1                | 0        | <0.001   |
| Trotting                 | 2687| <0.001      | 876 | <0.001           | 948              | 398      | <0.001   |
| Urinating                | 32 | 1           | 25 | <0.001           | 5                | 3        | 1        |
| Vocalizing               | 1857| 0.06        | 989 | <0.001           | 367              | 612      | <0.001   |
| Walking                  | 8520| <0.001      | 1941| <0.001           | 2703             | 419      | <0.001   |
| Total                    | 70802| 0.127      | 42705| <0.001          | 16682            | 7038     | 0.037    |

A dash indicates $P$ values could not be calculated due to low sample size. nW: number of occurrences for the wolves; nD: number of occurrences for the dogs; W–W: comparison within the wolves, absence versus presence of humans; D–D: comparison within the dogs, absence versus presence of humans.

* The data do not include the observations where the presence or absence of humans was not available (3328 of 113 507 occasions).
the presence of humans, dogs cantered, trotted, walked and vocalized more than in the absence of humans. In the absence of humans, dogs were observed standing, lying on the ground, resting and sleeping more than when humans were present (see Table 3). Wolves' behaviour also differed between the presence and the absence of humans (chi-square test: \( \chi^2_{21} = 1008.9, P < 2.2e-16 \)). In the presence of humans, wolves cantered more whereas in the absence of humans they foraged, trotted, walked, stood, slept and vocalized more and displayed more social behaviours (Table 3).

### Activity

Overall, there was a significant effect of temperature, time of day and the interaction between wolf or dog and the presence or absence of humans on the activity of the subjects (full–null comparison likelihood ratio test: \( \chi^2 = 866.903, P < 0.001 \); Table 4). Activity decreased with increasing temperature (Table 4, Fig. 2a). It also decreased towards noon and then increased again (Table 4, Fig. 2b). Human presence had a different effect on wolves and dogs: dogs responded strongly to the presence of humans and were more active, whereas wolves were seemingly less responsive than dogs to the presence of humans (interaction between wolf/dog and human presence: Table 4, Fig. 3). We found no effect of sex and age of the individual.

### Proximity

Overall, there was a significant effect of temperature, activity (active or not), the interaction between wolf/dog and the presence or absence of humans on the proximity of the subjects to their pack members (full–null comparison likelihood ratio test: \( \chi^2_{3} = 101.642, P < 0.001 \); see Table 5). The likelihood of an individual being in proximity of a pack member increased with increasing temperature (Table 5). Not surprisingly, an increase in activity also decreased proximity (Table 5). In the presence of humans, dogs were in proximity of their pack members more than wolves (Table 5, Fig. 4). Sex and age of the individual had no effect (Table 5).

### DISCUSSION

We found more subtle effects of domestication than expected. First, domestication has evidently not affected the impact of the presence of humans, dogs cantered, trotted, walked and vocalized more than in the absence of humans. In the absence of humans, dogs were observed standing, lying on the ground, resting and sleeping more than when humans were present (see Table 3). Wolves' behaviour also differed between the presence and the absence of humans (chi-square test: \( \chi^2_{21} = 1008.9, P < 2.2e-16 \)). In the presence of humans, wolves cantered more whereas in the absence of humans they foraged, trotted, walked, stood, slept and vocalized more and displayed more social behaviours (Table 3).

| Estimate | SE  | \( \chi^2 \) | df  | \( P^a \) |
|----------|-----|-------------|-----|----------|
| Intercept | -1.959 | 0.153 |     |          |
| Species (0: wolf; 1: dog) | 0.254 | 0.193 |     |          |
| Human (0: present; 1: absent) | 1.102 | 0.046 |     |          |
| Timeb | -0.090 | 0.038 | 5.149 | 1 | 0.023 |
| Temperatureb | -0.188 | 0.054 | 10.932 | 1 | 0.001 |
| Ageb | -0.102 | 0.100 | 1.011 | 1 | 0.315 |
| Sex (0: M; 1: F) | -0.202 | 0.118 | 2.742 | 1 | 0.098 |
| Wolf: human present | -0.503 | 0.058 | 74.186 | 1 | <0.001 |

Bold type indicates a significant \( P \) value.

\( ^a \) Not indicated in cases where the \( P \) value had a limited interpretation.

\( ^b \) Predictors were z-transformed to a mean of zero and a standard deviation of one; original means (SD): time: 12.16 (2.78) h; temperature: 11.14 (8.76) °C; age: 85.3 (30.5) months.

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**Figure 2.** Levels of activity (percentage of behaviours per observation that were active) in wolves and dogs (a) with temperature and (b) over the day. All behaviours of the ethogram were considered as active except for sleeping, resting and immobile (lying, sitting and standing). The lines represent the model regression lines and the grey shaded area is the 95% confidence interval for the models.
extrinsic Zeitgeber temperature and daily light regime, since our results have shown that level of activity in wolves and dogs varied in the same way. Both wolves and dogs showed the expected bimodal pattern of activity over the day, which suggests that the deviation from such patterns observed in companion dogs (Griss et al., 2021) is likely due to adjusting to certain humans rather than the result of domestication.

Second, we found no clear evidence for an overall decrease in behavioural efficiency (i.e. an intrinsically greater activity) in dogs. Dogs spent 78.5% of their overall time inactive and wolves 75% (see Appendix Table A2 for details). In the absence of humans, dogs were not more active than wolves, but they clearly were when humans were present. This would contradict the selection for tameness hypothesis predicting overall calmer, less agitated dogs than wolves, but is in line with the hypersociability hypothesis (Bentosela et al., 2016; von Holdt et al., 2017): dogs seem to be more interested in interacting with humans than wolves and are more excited about it. Moreover, this is in alignment with the generally higher cortisol levels found in dogs compared to wolves (Vasconcellos et al., 2016; Wirobski et al., 2021a, 2021b). This may be related to a generally higher, ‘ready-to-go’ metabolism in dogs than wolves, which maintain high reactivity for swiftly responding to the often unpredictable challenges in a human-dominated environment.

We expected distinct differences in the time budgets of wolves and dogs but found only minor variation between them in the time they devoted to different behaviours. However, the differences increased when compared between the presence and absence of humans. When humans were present, dogs were more active than in their absence (31.2% versus 16.1%; see Appendix Table A2 for details). Wolves’ activity also increased around humans but less than in dogs (29.8% versus 22.5%). Differences in time spent with various behaviours in dogs and wolves increased in the presence of humans: dogs remarkably increased cantering, trotting, standing and vocalizing, whereas wolves moderately increased trotting, walking and standing (see Appendix Table A2 for details). These results support our prediction that domestication has shifted the dogs’ focus towards responsiveness to humans and align with the previous findings (Jean-Joseph et al., 2020), which showed that dogs and wolves at rest reacted differently to the presence of humans: dogs were more relaxed (lower heart rate and higher heart variability) than wolves but when awake, dogs’ and wolves’ cardiac outputs were similar. Our results also line up with the study by Lazzaroni et al. (2020) showing that dogs (WSC, companion and free ranging) were more interested than wolves in interacting with humans. Hence, it seems than human presence influences both equally raised and kept dogs and wolves, but this effect is stronger and also qualitatively different in dogs, which seem more excited than wolves at the presence of humans.

Overall, our study agrees with previous work on the effects of visitors on canid welfare. The WSC wolves were out of sight during 2.5% of the observations (1772 occurrences versus 3.6% and 1554 occurrences for the dogs). This does not look like an important difference, but it is underscored by how this study was conducted: the observers actively tried to minimize occurrences of ‘subject not visible’ and when no subject was visible at all, the observation session was cancelled. This situation happened more often with wolves than with dogs, matching the result of a previous study on captive coyotes, Canis latrans (Schultz & Young, 2018): the captive wild canids tended to avoid open spaces and showed increased vigilance when visitors were present. However, these coyotes were not hand-raised and human-socialized the way the WSC wolves
are. Still, visitors and the noise they produce may have affected our results, as these factors increased the vigilance behaviour in captive wolves (Boyle et al., 2020). In fact, the wolves in our study spent just slightly more time standing vigilant when humans were around (21% against 19%).

We are aware that the familiarity of the humans present near the enclosure to the animals could have affected our results, particularly when the trainers (i.e. the familiar humans) were sighted more around the dogs’ enclosures than around those of the wolves, whereas the visitors (i.e. unfamiliar humans) were sighted more around the wolves’ enclosures than those of the dogs (see Appendix Table A3). However, the design of our study could not accurately discriminate between familiar and unfamiliar humans. Indeed, most of the time a mix of both familiar and unfamiliar humans were present at the enclosures. A conclusive analysis regarding the behavioural effects of the familiarity of the humans would have required the presence of either familiar or unfamiliar humans and not both at the same time. Humans were observed near the enclosures for 23 718 of the 110 176 data points (21.5% of the total data set whereas no human was present for 78.5% of the times, 86 458 occurrences). Within these 23 718 occurrences, 4650 times we observed only familiar humans present (4.2%) and 11662 times we observed only unfamiliar humans (10.6%). All other instances featured mixed groups of familiar and unfamiliar people (6.7%). Given the complexity of our models we considered the frequency of occurrence of either familiar or unfamiliar persons present insufficient for a conclusive analysis (see Appendix Table A4, Fig. A1).

We are aware of the lack of accuracy of the sampling method for some of the behaviours, but we chose to analyse and report them for the sake of completeness. For example, the observation of feeding behaviours may be underestimated because we chose not to observe them during feeding time due to differences in wolves’ and dogs’ feeding at the WSC. Dogs are fed dry food once or twice a day and tend to eat it all at once, whereas wolves were fed carcasses (whole chicken or rabbit or one portion of pig or deer) every 2 or 3 days. Therefore, wolves, but less so dogs, could have had access to some leftover food. Sexual behaviour, social interactions and stress-related behaviours are brief events that our observation method was not suited to record; ad libitum sampling would have been a more accurate method. However, we chose not to mix the two methods. Hence, our results for those behaviours are likely less accurate than the behaviours related to rest or locomotion, for example.

We were also unable to observe the animals’ nocturnal behaviour; due to the size of the enclosures and the vegetation, the animals could not be observed accurately at night even with night gear, and artificial light may have affected their behaviour. To overcome these shortcomings, full 24 h behaviour budgets could be investigated by using GPS collars with accelerometers.

To conclude, our study indicates that domestication has not affected much the role of major environmental factors, such as temperature and time of day, as Zeitgeber for dogs. We did not find marked overall changes in behaviour and activity between wolf and dog, as could have been predicted by selection for tameness as the major domestication mechanism. Rather, we found that wolf–dog differences were context dependent, with humans evidently being more important for the dogs than for equally socialized wolves.

**Author Contributions**

H.J.J.: Conceptualization, Methodology, Validation, Formal analysis, Writing: Original Draft, Visualization. G.D.: Methodology, Investigation, Data Curation, Writing: Review & Editing. K.K: Conceptualization, Writing: Review & Editing, Supervision, Funding acquisition. All authors have contributed to, seen and approved the manuscript.

**Data Availability**

The corresponding author will provide the data on request.

**Declaration of Interest**

The authors declare that the research was conducted in the absence of any commercial or financial relationship that could be construed as a potential conflict of interest.
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Appendix

Figure A1. The percentage of active behaviours in relation to the familiarity of the humans near the enclosure or in the absence of humans. (a) Graph based on the full data set. (b) Graph based on a selected range of temperature (10–25 °C) and time (1100–1300) to decrease the effect of temperature and time on the subjects’ behaviours. The whiskers represent the minimum (bottom) and maximum (top) data points, the edges of the box represent the interquartile (Q3–Q1) and the bold line is the median.

Table A1
Observation effort per month

| Month       | Observer | No. of 30 min observation periods |
|-------------|----------|-----------------------------------|
| November 2018 | GD       | 58 (preliminary observations)    |
| December 2018 | GD       | 118                               |
| January 2019 | GD       | 124                               |
| February 2019 | GD       | 122                               |
| March 2019   | GD       | 135                               |
| May 2019     | GD       | 143                               |
| June 2019    | GD/RS    | 88                                |
| July 2019    | RS/KW    | 94                                |
| August 2019  | RS/KW    | 140                               |
| September 2019 | RS/KW   | 144                               |
| October 2019 | RS/KW    | 163                               |
| November 2019 | RS/KW   | 150                               |
Table A2
Percentage occurrence of each behaviour for the overall data set and when humans were present or absent

| Behaviours  | Overall | Human present | Human absent |
|-------------|---------|---------------|--------------|
|             | Wolves  | Dogs          | Wolves       | Dogs          | Wolves  | Dogs          |
| Cantering   | 0.09    | 0.19          | 0.23         | 1.02          | 0.05    | 0.03          |
| Defecating  | 0.02    | 0.01          | 0.01         | 0             | 0.03    | 0.02          |
| Digging     | 0.01    | 0.30          | 0            | 0.57          | 0.02    | 0.27          |
| Drinking    | 0.20    | 0.22          | 0.27         | 0.28          | 0.18    | 0.22          |
| Eating      | 0.61    | 0.23          | 0.69         | 0.60          | 0.61    | 0.16          |
| Foraging    | 1.82    | 4.43          | 1.29         | 4.86          | 2.05    | 4.55          |
| Hunting     | <0.01   | 0.01          | 0.01         | 0             | <0.01   | 0.02          |
| Lying       | 15.97   | 19.88         | 16.68        | 15.56         | 16.28   | 21.68         |
| Sitting     | 0.58    | 7.93          | 0.48         | 7.36          | 0.63    | 8.42          |
| Standing    | 18.83   | 19.58         | 20.76        | 36.96         | 18.86   | 16.89         |
| Maintenance | 1.23    | 1.63          | 1.49         | 0.67          | 1.19    | 1.91          |
| Not visible | 2.50    | 3.64          | 0.01         | 0             | <0.01   | 0             |
| Object manipulation | 0.05 | 1.06 | 0.05 | 1.04 | 0.05 | 1.12 |
| Resting    | 5.06    | 5.28          | 5.57         | 2.66          | 5.07    | 6.06          |
| Sexual     | 0.07    | 0             | 0.12         | 0             | 0.06    | 0             |
| Sleeping   | 33.38   | 25.70         | 26.75        | 6.28          | 36.62   | 30.88         |
| Social     | 1.04    | 0.89          | 1.44         | 1.80          | 0.95    | 0.74          |
| Stress     | <0.01   | 0             | <0.01        | 0             | 0       | 0             |
| Trotting   | 3.79    | 2.05          | 5.68         | 5.65          | 3.32    | 1.40          |
| Urinating  | 0.04    | 0.06          | 0.03         | 0.04          | 0.05    | 0.06          |
| Vocalizing | 2.62    | 2.31          | 2.20         | 8.69          | 2.84    | 1.10          |
| Walking    | 12.03   | 4.54          | 16.20        | 5.95          | 11.11   | 4.46          |
| Inactive   | 73.83   | 78.39         | 70.24        | 68.81         | 77.46   | 83.93         |
| Active     | 26.17   | 21.61         | 29.76        | 31.19         | 22.54   | 16.07         |

1 The data do not include the observations where the presence or absence of humans was not available (3328 occasions out of 113 507). Behaviours in italic are those considered as inactive.

Table A3
Percentage occurrence of the conditions no human present and familiar (trainer) or unfamiliar (visitor) human present

| No human | Trainer | Visitor | Mixed group |
|----------|---------|---------|-------------|
| Dog      | 82.90   | 6.57    | 3.35        | 7.18        |
| Wolf     | 75.83   | 2.82    | 14.90       | 6.45        |

Table A4
Individuals' count and activity score (%) in relation to the conditions no human present and familiar (trainer) or unfamiliar (visitor) human present

| Individual | No human | Trainer | Visitor |
|------------|----------|---------|---------|
| Wolves     |          |         |         |
| Amarok     | 980      | 28.34   | 47.43   |
| Aragorn    | 480      | 12.37   | 19.63   |
| Chitto     | 619      | 21.57   | 29.33   |
| Etu        | 1043     | 28.90   | 26.31   |
| Geronimo   | 696      | 21.87   | 37.14   |
| Kaspar     | 739      | 19.08   | 46.02   |
| Kenai      | 816      | 22.84   | 63.29   |
| Maikan     | 999      | 27.74   | 19.82   |
| Nanuk      | 405      | 11.29   | 35.88   |
| Shima      | 303      | 17.54   | 22.58   |
| Taima      | 938      | 29.55   | 48.86   |
| Tala       | 516      | 18.84   | 11.25   |
| Tekoa      | 1067     | 29.55   | 54.84   |
| Uha        | 651      | 18.05   | 42.10   |
| Wamblee    | 676      | 21.69   | 44.39   |
| Yukon      | 868      | 27.36   | 41.95   |
| Dogs       |          |         |         |
| Asali      | 679      | 16.03   | 41.63   |
| Bora       | 915      | 21.80   | 46.46   |
| Enzi       | 435      | 12.51   | 47.27   |
| Gombo      | 182      | 10.76   | 35.18   |
| Hlari      | 374      | 10.40   | 19.77   |
| Imara      | 581      | 14.60   | 29.89   |
| Layla      | 735      | 21.51   | 56.00   |
| Meru       | 327      | 12.58   | 30.88   |
| Panya      | 596      | 17.22   | 37.77   |
| Zuri       | 657      | 18.99   | 33.77   |

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