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

Hillary Jean-Joseph [a, b, *], Gabriella Dooey [b, c], Kurt Kotrschal [a, b]

[a] *Department of Behavioral and Cognitive Biology, University of Vienna, Vienna, Austria*
[b] *Wolf Science Center, Domestication Lab, Konrad-Lorenz Institute of Ethology, University of Veterinary Medicine, Vienna, Austria*
[c] *School of Environment and Life Sciences, University of Salford, Salford, U.K.*

ARTICLE INFO

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.

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 (Belyaev, 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

* Corresponding author.
E-mail address: hillary.jean-joseph@univie.ac.at (H. Jean-Joseph).

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; Ciuccie 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 wolf circadian and circannual activity patterns may be induced by their need to avoid humans (Ciuccie 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 & Bhadra, 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; Wandeler 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 (Leonhard & 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 daylight time 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

Table 1
List of the subjects

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

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

reproduction. After the animals were integrated into conspecific packs at 5 months old, they had daily contact with their hand-raisers and trainers and, less regularly, with unfamiliar people (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 deer, pig, rabbit or chicken to make wolf and dog feeding as similar as possible. Wolves and dogs also received veterinary and obedience training from puppyhood and participated in several behavioural tests on a daily to weekly basis. Water was available ad libitum for all wolves and dogs.

During the observation period, one wolf (Shima, 21 April 2019) and one dog (Meru, 12 August 2019) died of natural causes. Thus, the composition of some packs changed. One dog, Zuri, was moved from Pack 9 to Pack 10 on 13 June 2019 (see Table 1). Therefore, after 21 April 2019, only 15 wolves were observed and after 12 June 2019, only 10 dogs (see Table 1). One dog, Haida, joined the WSC on 10 October 2017, when she was already an adult, and thus she was excluded from analysis.

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, each part of the day was equally represented in the final sample for each individual/pack. Between seasons, the number of observations per individual/pack varied, as we had fewer observations in summer (June, July, August), mainly due to the transition in observers. Packs were only observed when all members were present. We also avoided conducting observations during particular events, such as guided tours, feeding or training demonstrations for visitors. We used the instantaneous scan sampling method (Bateson & Martin, 2021) to assess the behaviour of each member of the observed pack (see Table 2 for our ethogram). Each observation lasted 30 min divided into 30 intervals of 1 min. We conducted multiple observations per day but never observed the same pack twice in a row. We never

Table 2
Ethogram

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	SeB
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
Immobile		
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	ISt
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 blinders. 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 115 708 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 lmer 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 chisq.posthoc.test (version 0.1.2).

RESULTS

Time Budgets

Overall, wolves' and dogs' diurnal time budgets were significantly different over the year (chi-square test: $\chi^2_{21} = 8720.8$, $P < 2.2e\text{-}16$; 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: $\chi^2_{21} = 4048.4$, $P < 2.2e\text{-}16$; 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
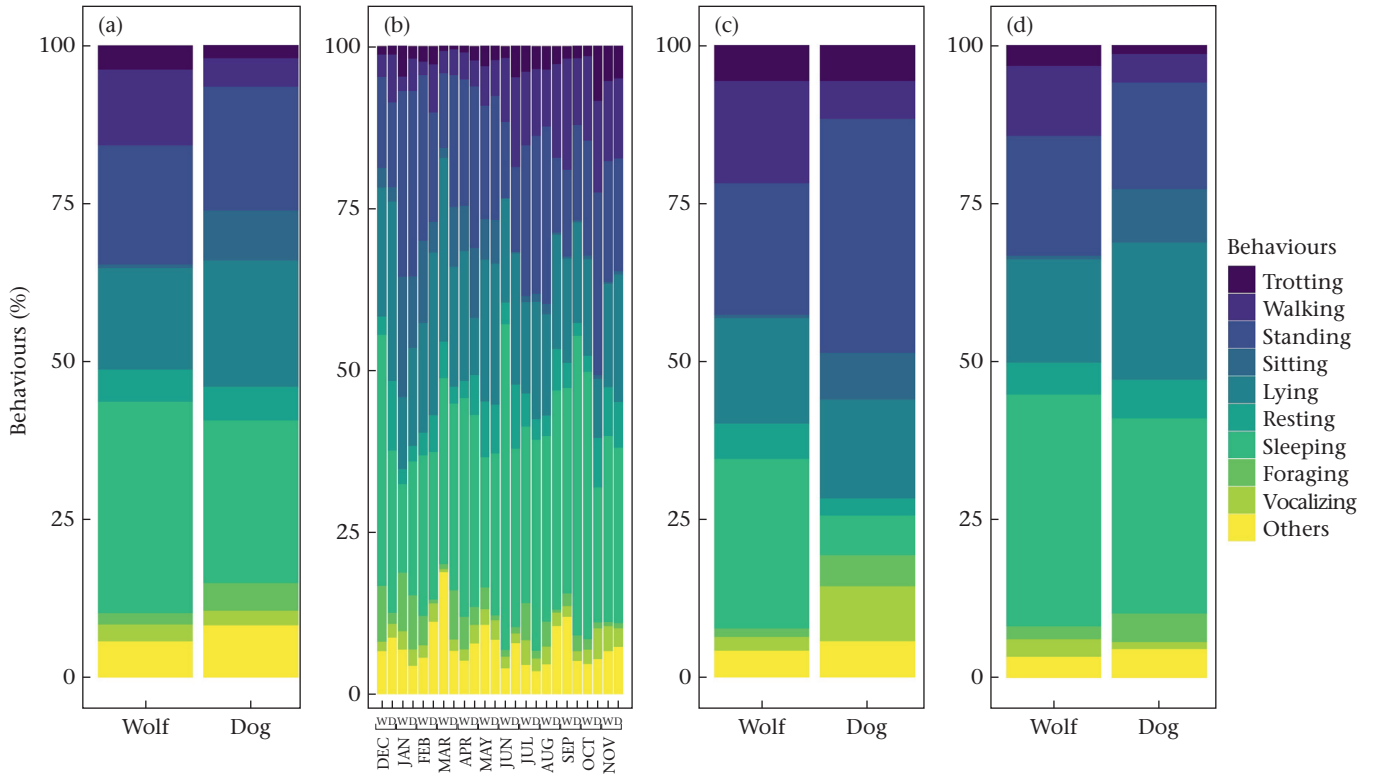
Figure 1. Bar plot of the differences in wolves' and dogs' behaviours. (a) Overall comparison; (b) over the months; (c) in the presence of humans; (d) in the absence of humans. Category 'Others' includes eating, drinking, defecating, urinating, hunting, object manipulation, social interaction and displays of stress behaviour.

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

Table 3
Pairwise post hoc comparison

Behaviours	nW	Overall	P	Human present[a]			Human absent[a]			W–W	D–D
		nD		nW	nD	P	nW	nD	P	P	P
Cantering	65	83	<0.001	39	72	1	26	11	<0.001	<0.001	<0.001
Defecating	16	6	1	2	0	1	14	6	1	1	1
Digging	11	131	<0.001	0	40	<0.001	11	91	1	1	0.001
Drinking	143	96	1	46	20	1	97	76	1	1	1
Eating	433	97	<0.001	115	42	<0.001	318	55	1	1	<0.001
Foraging	1289	1894	<0.001	216	342	<0.001	1073	1552	<0.001	<0.001	1
Hunting	6	6	1	2	0	1	4	6	1	1	1
Lying	11307	8490	<0.001	2782	1095	<0.001	8522	7395	<0.001	1	<0.001
Sitting	409	3389	<0.001	80	518	<0.001	329	2871	<0.001	1	0.127
Standing	13336	8364	0.082	3463	2601	<0.001	9873	5763	<0.001	<0.001	<0.001
Maintenance	873	698	<0.001	249	47	<0.001	624	651	<0.001	0.109	<0.001
Not visible	1772	1554	<0.001	2	0	1	1	0	1	1	–
Object manipulation	35	455	<0.001	8	73	<0.001	27	382	<0.001	1	1
Resting	3583	2254	1	930	187	<0.001	2653	2067	<0.001	0.449	<0.001
Sexual	52	0	<0.001	20	0	<0.001	32	0	<0.001	0.704	–
Sleeping	23635	10978	<0.001	4463	442	<0.001	19172	10536	<0.001	<0.001	<0.001
Social	740	379	0.4	241	127	0.037	499	252	<0.001	<0.001	<0.001
Stress	1	0	1	1	0	–	0	0	–	1	–
Trotting	2687	876	<0.001	948	398	<0.001	1739	478	<0.001	<0.001	<0.001
Urinating	32	25	1	5	3	1	27	22	1	1	1
Vocalizing	1857	989	0.06	367	612	<0.001	1490	377	<0.001	<0.001	<0.001
Walking	8520	1941	<0.001	2703	419	<0.001	5815	1522	<0.001	<0.001	<0.001
Total	70802	42705		16682	7038		52346	34113			

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.
[a] The data do not include the observations where the presence or absence of humans was not available (3328 of 113 507 occasions).

Table 4
Results of the activity model

	Estimate	SE	χ^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			
Time[b]	−0.090	0.038	5.149	1	**0.023**
Temperature[b]	−0.188	0.054	10.932	1	**0.001**
Age[b]	−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.

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: $\chi^2_{21} = 1008.9$, $P < 2.2\text{e-}16$). 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: $\chi^2_2 = 866.903$, $P < 0.001$; 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
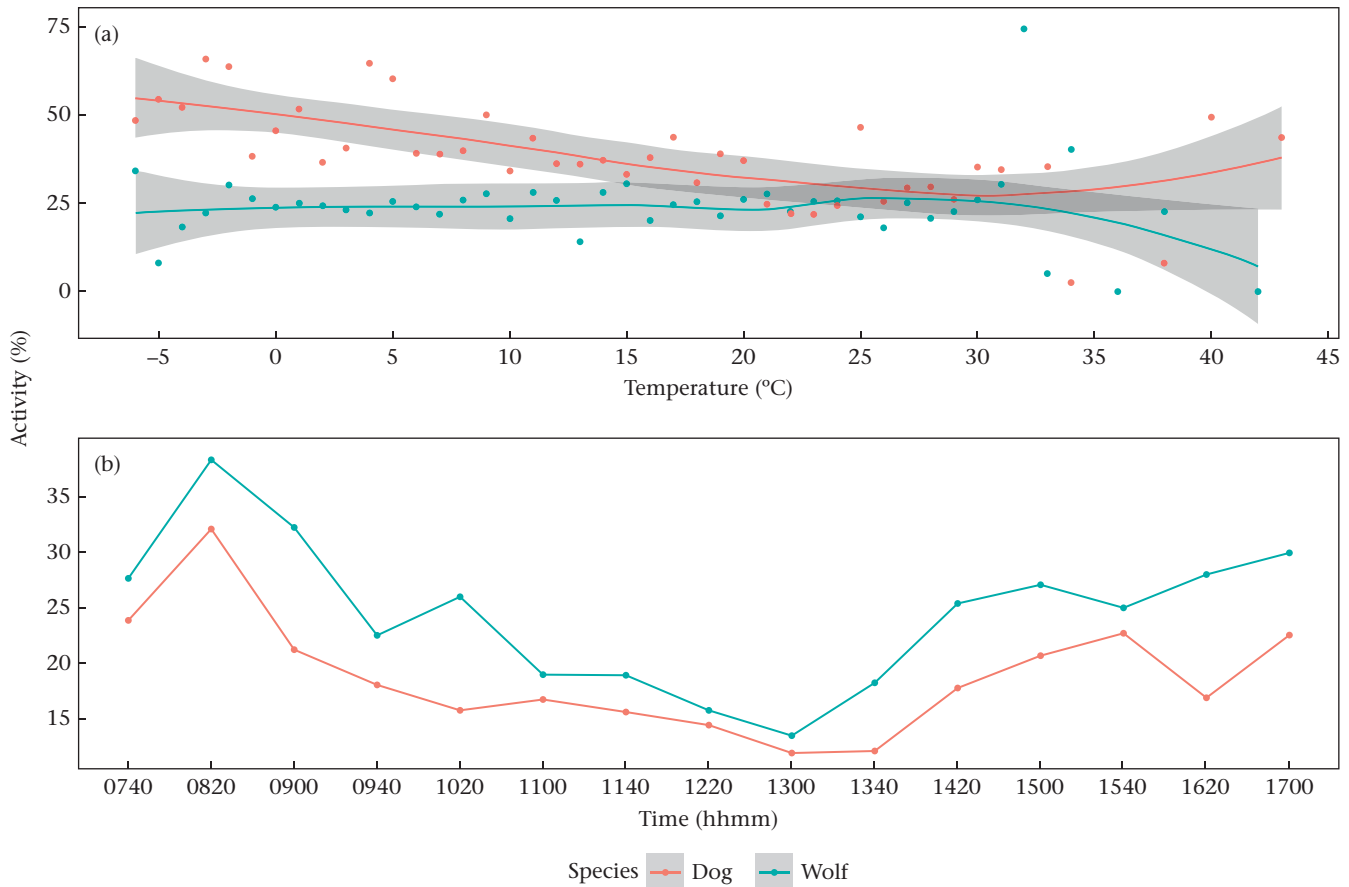

Figure 2. Levels of activity (percentage of behaviours per observation that were active) in wolves and dogs (a) with temperature and (b) over the day. All behaviours of the ethogram were considered as active except for sleeping, resting and immobile (lying, sitting and standing). The lines represent the model regression lines and the grey shaded area is the 95% confidence interval for the models.
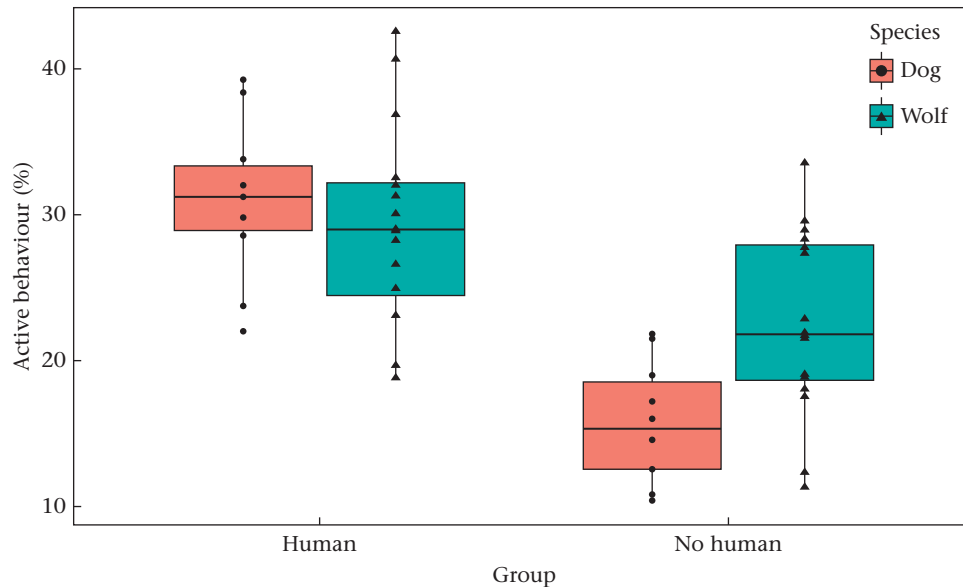
Figure 3. Wolves' and dogs' activity in relation to the presence or absence of humans around their enclosure. The graph is based on a selected range of temperature (10–25 °C) and time (1100–1300) to decrease the effect of temperature and time on the subjects' behaviours. However, statistical analyses were based on the full data set. 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. The dots represent the individual values of activity for dogs and wolves.

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 level 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.

Table 5
Results of the proximity model

	Estimate	SE	χ^2	df	P[a]
Intercept	0.380	0.391			
Species (0: wolf; 1: dog)	1.741	0.521			
Human (0: present; 1: absent)	-0.446	0.047			
Activity (0: not active; 1: active)	0.659	0.023	810.441	1	**<0.001**
Temperature[b]	0.251	0.087	7.586	1	**0.006**
Age[b]	-0.110	0.173	0.343	1	0.558
Sex (0: M; 1: F)	0.233	0.101	2.285	1	0.131
Wolf: Human present	0.556	0.064	74.140	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): temperature: 11.14 (8.76) °C; age 85.3 (30.5) months.

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 at 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
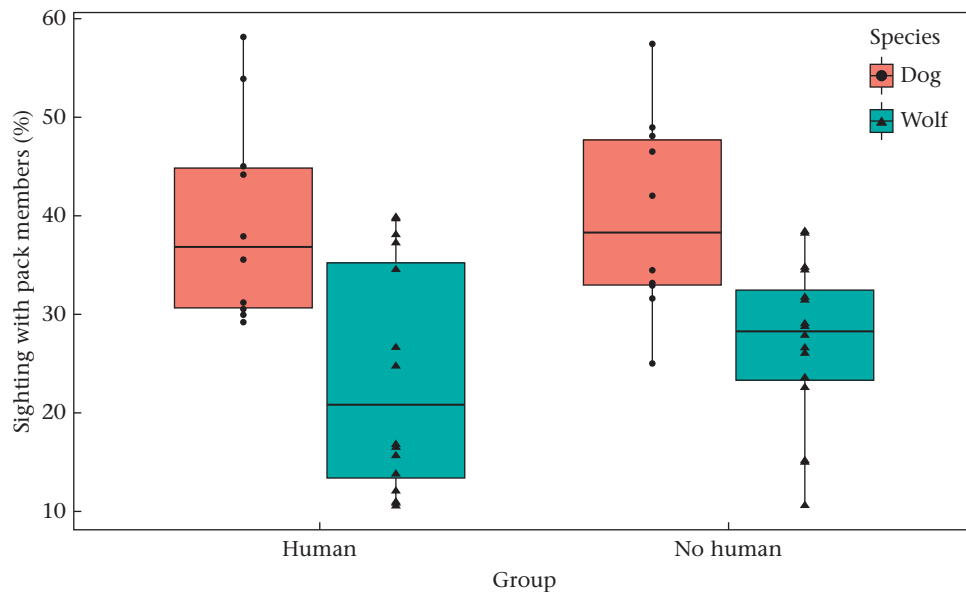
Figure 4. Wolves' and dogs' proximity to their pack in relation to the presence or absence of humans around their enclosure. The whiskers represent the minimum (bottom) and maximum (top) data points, the edges of the box represent the interquartile (Q3−Q1) and the bold line is the median. The dots represent the individual values of activity for dogs and 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 11 662 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.

Acknowledgments

References

Agnvall, B., Katajamaa, R., Altimiras, J., & Jensen, P. (2015). Is domestication driven by reduced fear of humans? Boldness, metabolism and serotonin levels in divergently selected red junglefowl (*Gallus gallus*). *Biology Letters, 11*(9), 20150509. https://doi.org/10.1098/rsbl.2015.0509

Aronson, B. D., Bell-Pedersen, D., Block, G. D., Bos, N. P. A., Dunlap, J. C., Eskin, A., Garceau, N. Y., Geusz, M. E., Johnson, K. A., Khalsa, S. B. S., Koster-Van Hoffen, G. C., Koumenis, C., Lee, T. M., LeSauter, J., Lindgren, K. M., Liu, Q., Loros, J. J., Michel, S. H., Mirmiran, M., … Zucker, I. (1993). Circadian rhythms. *Brain Research Reviews, 18*(3), 315—333. https://doi.org/10.1016/0165-0173(93)90015-R

Aschoff, J. (1954). Zeitgeber der tierischen Tagesperiodik. *Naturwissenschaften, 41*(3), 49—56. https://doi.org/10.1007/BF00634164

Baayen, R. H. (2008). *Analyzing linguistic data: A practical introduction to statistics using R.* Cambridge University Press.

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language, 68*(3), 255—278. https://doi.org/10.1016/j.jml.2012.11.001

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. ArXiv, 1406.5823 [Stat] http://arxiv.org/abs/1406.5823.

Bateson, M., & Martin, P. (2021). *Measuring behaviour: An introductory guide.* Cambridge University Press.

Belyaev, D. K. (1979). Destabilizing selection as a factor in domestication. *Journal of Heredity,70*(5), 301—308. https://doi.org/10.1093/oxfordjournals.jhered.a109263

Bentosela, M., Wynne, C. D. L., D'Orazio, M., Elgier, A., & Udell, M. A. R. (2016). Sociability and gazing toward humans in dogs and wolves: Simple behaviors with broad implications. *Journal of the Experimental Analysis of Behavior, 105*(1), 68—75. https://doi.org/10.1002/jeab.191

Bhadra, A., & Bhadra, A. (2014). Preference for meat is not innate in dogs. *Journal of Ethology, 32*(1), 15—22. https://doi.org/10.1007/s10164-013-0388-7

Bonanni, R., & Cafazzo, S. (2014). Chapter 3—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 J. Kaminski, & S. Marshall-Pescini (Eds.), *The social dog* (pp. 65—104). Academic Press. https://doi.org/10.1016/B978-0-12-407818-5.00003-6.

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., Daly, K., Unterländer, M., Burger, J., Kidd, J. M., & Veeramah, K. R. (2017). Ancient European dog genomes reveal continuity since the Early Neolithic. *Nature Communications, 8*, 16082. https://doi.org/10.1038/ncomms16082

Boyle, S. A., Berry, N., Cayton, J., Ferguson, S., Gilgan, A., Khan, A., Lam, H., Leavelle, S., Mulder, I., Myers, R., Owens, A., Park, J., Siddiq, I., Slevin, M., Weidow, T., Yu, A. J., & Reichling, S. (2020). Widespread behavioral responses by mammals and fish to zoo visitors highlight differences between individual animals. *Animals, 10*(11), 2108. https://doi.org/10.3390/ani10112108

Cafazzo, S., Bonanni, R., Valsecchi, P., & Natoli, E. (2014). Social variables affecting mate preferences, copulation and reproductive outcome in a pack of free-ranging dogs. *PLoS One, 9*(6), Article e98594. https://doi.org/10.1371/journal.pone.0098594

Cafazzo, S., Marshall-Pescini, S., Lazzaroni, M., Virányi, Z., & Range, F. (2018). The effect of domestication on post-conflict management: Wolves reconcile while dogs avoid each other. *Royal Society Open Science, 5*(7), 171553. https://doi.org/10.1098/rsos.171553

Cafazzo, S., Valsecchi, P., Bonanni, R., & Natoli, E. (2010). Dominance in relation to age, sex, and competitive contexts in a group of free-ranging domestic dogs. *Behavioral Ecology, 21*(3), 443—455. https://doi.org/10.1093/beheco/arq001

Christie, D. W., & Bell, E. T. (1971). Some observations on the seasonal incidence and frequency of oestrus in breeding bitches in Britain. *Journal of Small Animal Practice, 12*(3), 159—167. https://doi.org/10.1111/j.1748-5827.1971.tb06213.x

Ciucci, P., Boitani, L., Francisci, F., & Andreoli, G. (1997). Home range, activity and movements of a wolf pack in central Italy. *Journal of Zoology, 243*(4), 803—819. https://doi.org/10.1111/j.1469-7998.1997.tb01977.x

Darwin, C. R. (1859). *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life.* J. Murray.

Dobson, A. J., & Barnett, A. G. (2018). *An introduction to generalized linear models* (4th ed.). Chapman & Hall/CRC. https://doi.org/10.1201/9781315182780

Fam, B. S. O., Paré, P., Felkl, A. B., Vargas-Pinilla, P., Paixão-Côrtes, V. R., Viscardi, L. H., & Bortolini, M. C. (2018). Oxytocin and arginine vasopressin systems in the domestication process. *Genetics and Molecular Biology, 41*, 235—242. https://doi.org/10.1590/1678-4685-GMB-2017-0069

Field, A. (2013). *Discovering statistics using IBM SPSS statistics.* Sage.

Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: Overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology, 65*(1), 47—55. https://doi.org/10.1007/s00265-010-1038-5

Frank, H. (1987). *Man and wolf: Advances, issues, and problems in captive wolf research.* W. Junk.

Frank, H., & Frank, M. G. (1982). Comparison of problem-solving performance in six-week-old wolves and dogs. *Animal Behaviour, 30*(1), 95—98.

Frank, H., & Frank, M. G. (1985). Comparative manipulation-test performance in ten-week-old wolves (*Canis lupus*) and Alaskan malamutes (*Canis familiaris*): A Piagetian interpretation. *Journal of Comparative Psychology, 99*(3), 266—274.

Gácsi, M., Gyoöri, B., Virányi, Z., Kubinyi, E., Range, F., Belényi, B., & Miklósi, Á. (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), Article e6584. https://doi.org/10.1371/journal.pone.0006584

Grandin, L. D., Alloy, L. B., & Abramson, L. Y. (2006). The social zeitgeber theory, circadian rhythms, and mood disorders: Review and evaluation. *Clinical Psychology Review, 26*(6), 679—694. https://doi.org/10.1016/j.cpr.2006.07.001

Griss, S., Riemer, S., Warembourg, C., Sousa, F. M., Wera, E., Berger-Gonzalez, M., Alvarez, D., Bulu, P. M., Hernández, A. L., Roquel, P., & Dürr, S. (2021). If they could choose: How would dogs spend their days? Activity patterns in four populations of domestic dogs. *Applied Animal Behaviour Science, 243*, 105449. https://doi.org/10.1016/j.applanim.2021.105449

Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences, 9*(9), 439—444. https://doi.org/10.1016/j.tics.2005.07.003

Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour, 83*(3), 573—585. https://doi.org/10.1016/j.anbehav.2011.12.007

Hecht, E. E., Kukekova, A. V., Gutman, D. A., Acland, G. M., Preuss, T. M., & Trut, L. N. (2021). Neuromorphological changes following selection for tameness and aggression in the Russian farm-fox experiment. *Journal of Neuroscience, 41*(28), 6144—6156. https://doi.org/10.1523/JNEUROSCI.3114-20.2021

Heldmaier, G., Steinlechner, S., Ruf, T., Wiesinger, H., & Klingenspor, M. (1989). Photoperiod and thermoregulation in vertebrates: Body temperature rhythms and thermogenic acclimation. *Journal of Biological Rhythms, 4*(2), 139—153. https://doi.org/10.1177/074873048900400211

Hoffman, C. L., Ladha, C., & Wilcox, S. (2019). An actigraphy-based comparison of shelter dog and owned dog activity patterns. *Journal of Veterinary Behavior, 34*, 30—36. https://doi.org/10.1016/j.jveb.2019.08.001

von Holdt, B. M., Shuldiner, E., Koch, I. J., Kartzinel, R. Y., Hogan, A., Brubaker, L., Wanser, S., Stahler, D., Wynne, C. D. L., Ostrander, E. A., Sinsheimer, J. S., & Udell, M. A. R. (2017). Structural variants in genes associated with human Williams-Beuren syndrome underlie stereotypical hypersociability in domestic dogs. *Science Advances, 3*(7), Article e1700398. https://doi.org/10.1126/sciadv.1700398

Hughes, J., & Macdonald, D. W. (2013). A review of the interactions between free-roaming domestic dogs and wildlife. *Biological Conservation, 157*, 341—351. https://doi.org/10.1016/j.biocon.2012.07.005

Jean-Joseph, H., Kortekaas, K., Range, F., & Kotrschal, K. (2020). Context-specific arousal during resting in wolves and dogs: effects of domestication? *Frontiers in Psychology, 11*, Article 568199. https://doi.org/10.3389/fpsyg.2020.568199

Kaminski, J., Waller, B. M., Diogo, R., Adam Hartstone-Rose, A., & Burrows, A. M. (2019). Evolution of facial muscle anatomy in dogs. *Proceedings of the National Academy of Sciences, 116*(29), 14677—14681.

Kirilyuk, A. V., Kirilyuk, V. E., & Minaev, A. N. (2021). Daily activity patterns of wolves in open habitats in the Dauria ecoregion, Russia. *Nature Conservation Research, 6*(4), 95—109. https://doi.org/10.24189/ncr.2021.049

Klinghammer, E., & Goodman, P. A. (1987). Socialization and management of wolves in captivity. In H. Frank (Ed.), *Man and wolf: Advances, issues, and problems in captive wolf research* (pp. 281—304). W. Junk.

Kortekaas, K., & Kotrschal, K. (2019). Does socio-ecology drive differences in alertness between wolves and dogs when resting? *Behavioural Processes, 166*, 103877. https://doi.org/10.1016/j.beproc.2019.05.024

Kotrschal, K. (2018). How wolves turned into dogs and how dogs are valuable in meeting human social needs. *People and Animals: The International Journal of Research and Practice, 1*(1), 6. https://docs.lib.purdue.edu/paij/vol1/iss1/6.

Kubinyi, E., Viranyi, Z., & Miklósi, Á. (2007). Comparative social cognition: From wolf and dog to humans. *Comparative Cognition & Behavior Reviews, 2*, 26—46. http://cogs.indiana.edu/spackled/2008readings/comparat_cognition_Miklosi_2007.pdf.

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*). *Hormones and Behavior, 35*(1), 28—37. https://doi.org/10.1006/hbeh.1998.1493

Lazzaroni, M., Range, F., Backes, J., Portele, K., Scheck, K., & Marshall-Pescini, S. (2020). The effect of domestication and experience on the social interaction of dogs and wolves with a human companion. *Frontiers in Psychology, 11*, 785. https://doi.org/10.3389/fpsyg.2020.00785

Leonard, J. A., Wayne, R. K., Wheeler, J., Valadez, R., Guillén, S., & Vilà, C. (2002). Ancient DNA evidence for old world origin of new world dogs. *Science, 298*(5598), 1613—1616. https://doi.org/10.1126/science.1076980

Leonhard, C., & Randler, C. (2009). Sync with the family: Children and partners influence the sleep-wake circadian rhythm and social habits of women. *Chronobiology International, 26*(3), 510—525. https://doi.org/10.1080/07420520902821101

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*). *Behavioural Processes, 92*, 131—142. https://doi.org/10.1016/j.beproc.2012.10.009

Majumder, S. S., Bhadra, A., Ghosh, A., Mitra, S., Bhattacharjee, D., Chatterjee, J., Nandi, A. K., & Bhadra, A. (2014). To be or not to be social: Foraging associations of free-ranging dogs in an urban ecosystem. *Acta Ethologica, 17*(1), 1—8. https://doi.org/10.1007/s10211-013-0158-0

Majumder, S., Paul, M., Sau, S., & Bhadra, A. (2016). Denning habits of free-ranging dogs reveal preference for human proximity. *Scientific Reports, 6*(1), 32014. https://doi.org/10.1038/srep32014

Marshall-Pescini, S., Cafazzo, S., Virányi, Z., & Range, F. (2017). Integrating social ecology in explanations of wolf—dog behavioral differences. *Current Opinion in Behavioral Sciences, 16*, 80—86. https://doi.org/10.1016/j.cobeha.2017.05.002

Matuschek, H., Kliegl, R., Vasishth, S., Baayen, H., & Bates, D. (2017). Balancing type I error and power in linear mixed models. *Journal of Memory and Language, 94*, 305—315. https://doi.org/10.1016/j.jml.2017.01.001

Mech, L. D., & Boitani, L. (2003). *Wolves: Behavior, ecology, and conservation*. University of Chicago Press.

Mech, L. D., & Peterson, R. O. (2003). Wolf-prey relations. In L. David Mech, & L. Boitani (Eds.), *Wolves: Behavior, ecology, and conservation* (pp. 131—160). University of Chicago Press.

Merrill, S. B., & Mech, L. D. (2003). The usefulness of GPS telemetry to study wolf circadian and social activity. *Wildlife Society Bulletin, 31*(4), 947—960.

Miklósi, Á., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. (2003). A simple reason for a big difference: Wolves do not look back at humans, but dogs do. *Current Biology, 13*(9), 763—766.

Nieuwenhuis, R., Grotenhuis, H. F. te, & Pelzer, B. J. (2012). *influence.ME: Tools for detecting influential data in mixed effects models*. https://journal.r-project.org/archive/2012/RJ-2012-011/index.html.

Packard, J. M. (2003). Wolf behavior: Reproductive, social, and intelligent. In L. David Mech, & L. Boitani (Eds.), *Wolves: Behavior, ecology, and conservation* (pp. 35—65). University of Chicago Press.

Pal, S. K. (2005). Parental care in free-ranging dogs, *Canis familiaris*. *Applied Animal Behaviour Science, 90*(1), 31—47. https://doi.org/10.1016/j.applanim.2004.08.002

Parker, H. G., Dreger, D. L., Rimbault, M., Davis, B. W., Mullen, A. B., Carpintero-Ramirez, G., & Ostrander, E. A. (2017). Genomic analyses reveal the influence of geographic origin, migration, and hybridization on modern dog breed development. *Cell Reports, 19*(4), 697—708. https://doi.org/10.1016/j.celrep.2017.03.079

Paul, M., Sen Majumder, S., Sau, S., Nandi, A. K., & Bhadra, A. (2016). High early life mortality in free-ranging dogs is largely influenced by humans. *Scientific Reports, 6*(1), 19641. https://doi.org/10.1038/srep19641

Piccione, G., Marafioti, S., Giannetto, C., Di Pietro, S., Quartuccio, M., & Fazio, F. (2014). Comparison of daily distribution of rest/activity in companion cats and dogs. *Biological Rhythm Research, 45*(4), 615—623. https://doi.org/10.1080/09291016.2014.884303

Price, E. O. (1999). Behavioral development in animals undergoing domestication. *Applied Animal Behaviour Science, 65*(3), 245—271. https://doi.org/10.1016/S0168-1591(99)00087-8

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/.

Randler, C., Díaz-Morales, J. F., & Jankowski, K. S. (2018). Synchrony in chronotype and social jetlag between dogs and humans across Europe. *Time & Society, 27*(2), 223—238. https://doi.org/10.1177/0961463X15596705

Range, F., Kassis, A., Taborsky, M., Boada, M., & Marshall-Pescini, S. (2019a). Wolves and dogs recruit human partners in the cooperative string-pulling task. *Scientific Reports, 9*(1), 1—10. https://doi.org/10.1038/s41598-019-53632-1

Range, F., Marshall-Pescini, S., Kratz, C., & Virányi, Z. (2019b). Wolves lead and dogs follow, but they both cooperate with humans. *Scientific Reports, 9*(1), 3796. https://doi.org/10.1038/s41598-019-40468-y

Range, F., Ritter, C., & Virányi, Z. (2015). Testing the myth: Tolerant dogs and aggressive wolves. *Proceedings of the Royal Society B: Biological Sciences, 282*(1807), 20150220. https://doi.org/10.1098/rspb.2015.0220

Range, F., & Virányi, Z. (2015). Tracking the evolutionary origins of dog-human cooperation: the "canine cooperation hypothesis. *Frontiers in Psychology, 5*, 1582. https://doi.org/10.3389/fpsyg.2014.01582

Range, F., & Virányi, Z. (2014). Wolves are better imitators of conspecifics than dogs. *PLoS One, 9*(1), Article e86559. https://doi.org/10.1371/journal.pone.0086559

Robert, S., Dancosse, J., & Dallaire, A. (1987). Some observations on the role of environment and genetics in behaviour of wild and domestic forms of *Sus scrofa* (European wild boars and domestic pigs). *Applied Animal Behaviour Science, 17*(3), 253—262. https://doi.org/10.1016/0168-1591(87)90150-X

Schielzeth, H., & Forstmeier, W. (2009). Conclusions beyond support: Overconfident estimates in mixed models. *Behavioral Ecology, 20*(2), 416—420. https://doi.org/10.1093/beheco/arn145

Schultz, J. T., & Young, J. K. (2018). Behavioral and spatial responses of captive coyotes to human activity. *Applied Animal Behaviour Science, 205*, 83—88. https://doi.org/10.1016/j.applanim.2018.05.021

Scott, J. P., & Fuller, J. L. (1965). *Genetics and the social behavior of the dog*. University of Chicago Press.

Smith, T. D., & Van Valkenburgh, B. (2021). The dog—human connection. *Anatomical Record, 304*(1), 10—18. https://doi.org/10.1002/ar.24534

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., … Wayne, R. K. (2013). Complete mitochondrial genomes of Ancient canids suggest a European origin of domestic dogs. *Science, 342*(6160), 871—874. https://doi.org/10.1126/science.1243650

Theuerkauf, J. (2009). What drives wolves: Fear or hunger? Humans, diet, climate and wolf activity patterns. *Ethology, 115*(7), 649—657. https://doi.org/10.1111/j.1439-0310.2009.01653.x

Theuerkauf, J., Gula, R., Pirga, B., Tsunoda, H., Eggermann, J., Brzezowska, B., Rouys, S., & Radler, S. (2007). Human impact on wolf activity in the Bieszczady Mountains, SE Poland. *Annales Zoologici Fennici, 44*(3), 225—231.

Troxell-Smith, S. M., Tutka, M. J., Albergo, J. M., Balu, D., Brown, J. S., & Leonard, J. P. (2016). Foraging decisions in wild versus domestic *Mus musculus*: What does life in the lab select for? *Behavioural Processes, 122*, 43—50. https://doi.org/10.1016/j.beproc.2015.10.020

Trut, L. N., Plyusnina, I. Z., & Oskina, I. N. (2004). An experiment on fox domestication and debatable issues of evolution of the dog. *Russian Journal of Genetics, 40*, 644—655. https://doi.org/10.1023/B:RUGE.0000033312.92773.c1

Trut, L. N., Oskina, I., & Kharlamova, A. (2009). Animal evolution during domestication: the domesticated fox as a model. *Bioessays, 31*(3), 349—360. https://doi.org/10.1016/j.cpnec.2021.100100

Vanak, A. T., & Gompper, M. E. (2009). Dogs *Canis familiaris* as carnivores: Their role and function in intraguild competition. *Mammal Review, 39*(4), 265—283. https://doi.org/10.1111/j.1365-2907.2009.00148.x

Vasconcellos, A. da S., Virányi, Z., Range, F., Ades, C., Scheidegger, J. K., Möstl, E., & Kotrschal, K. (2016). Training reduces stress in human-socialised wolves to the same degree as in dogs. *PLoS One, 11*(9), Article e0162389. https://doi.org/10.1371/journal.pone.0162389

Vilà, C., Urios, V., & Castroviejo, J. (1995). Observations on the daily activity patterns in the Iberian wolf. In L. N. Carbyn, S. H. Fritts, & D. R. Seip (Eds.), *Ecology and conservation of wolves in a changing world* (pp. 335—340). Canadian Circumpolar Institute.

Wandeler, A. I., Matter, H. C., Kappeler, A., & Budde, A. (1993). The ecology of dogs and canine rabies: A selective review. *Revue Scientifique et Technique (International Office of Epizootics), 12*(1), 51—71. https://doi.org/10.20506/rst.12.1.663

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. https://doi.org/10.1534/genetics.114.165423

Wirobski, G., Range, F., Schaebs, F. S., Palme, R., Deschner, T., & Marshall-Pescini, S. (2021a). Endocrine changes related to dog domestication: Comparing urinary cortisol and oxytocin in hand-raised, pack-living dogs and wolves. *Hormones and Behavior, 128*, 104901. https://doi.org/10.1016/j.yhbeh.2020.104901

Wirobski, G., Range, F., Schaebs, F. S., Palme, R., Deschner, T., & Marshall-Pescini, S. (2021b). Life experience rather than domestication accounts for dogs' increased oxytocin release during social contact with humans. *Scientific Reports, 11*(1), 14423. https://doi.org/10.1038/s41598-021-93922-1
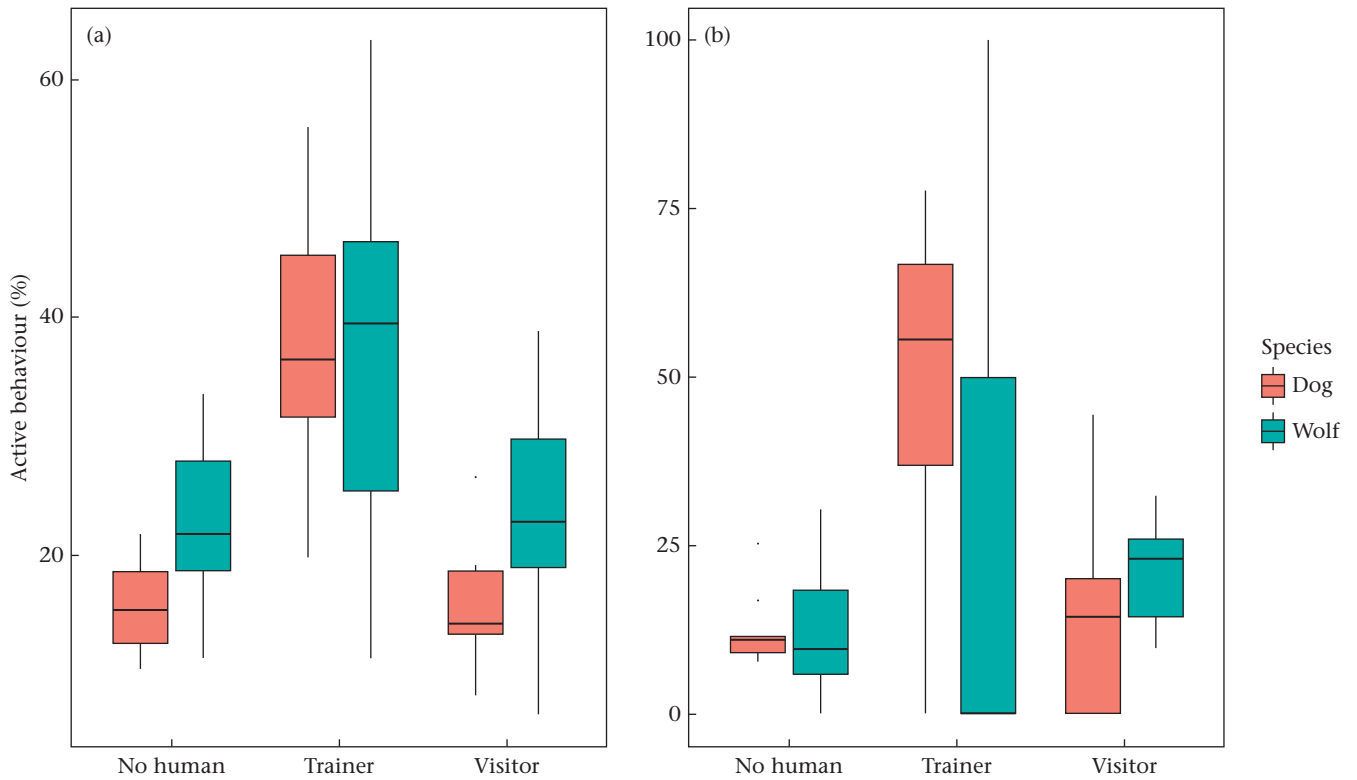
Appendix

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[1]		Human absent[1]	
	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	
	Count	%	Count	%	Count	%
Wolves						
Amarok	980	28.34	37	47.43	166	23.41
Aragorn	480	12.37	32	19.63	16	16.33
Chitto	619	21.57	22	29.33	244	31.16
Etu	1043	28.90	20	26.31	227	32.15
Geronimo	696	21.87	78	37.14	147	21.06
Kaspar	739	19.08	81	46.02	29	29.29
Kenai	816	22.84	50	63.29	166	21.40
Maikan	999	27.74	14	19.82	189	26.18
Nanuk	405	11.29	47	35.88	106	13.96
Shima	303	17.54	14	22.58	3	6.67
Taima	938	29.55	47	48.86	372	35.26
Tala	516	18.84	9	11.25	145	19.73
Tekoa	1067	29.55	51	54.84	404	38.80
Una	651	18.05	56	42.10	184	24.73
Wamblee	676	21.69	95	44.39	100	15.15
Yukon	868	27.36	86	41.95	150	22.15
Dogs						
Asali	679	16.03	102	41.63	9	8.11
Bora	915	21.80	105	46.46	30	26.55
Enzi	435	12.51	130	47.27	158	13.29
Gombo	182	10.76	19	35.18	25	14.20
Hiari	374	10.40	349	19.77	8	11.27
Imara	581	14.60	358	29.89	13	19.12
Layla	735	21.51	154	56.00	32	17.02
Meru	327	12.58	105	30.88	4	13.34
Panya	596	17.22	105	37.77	25	14.12
Zuri	657	18.99	103	33.77	55	19.16