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Brown bear behaviour in human-modified landscapes: The case of the endangered Cantabrian population, NW Spain

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ABSTRACT

Large carnivores are recolonizing parts of their historical range in Europe, a heavily modified human landscape. This calls for an improvement of our knowledge on how large carnivores manage to coexist with humans, and on the effects that human activity has on large carnivore behaviour, especially in areas where carnivore populations are still endangered. Brown bears *Ursus arctos* have been shown to be sensitive to the presence of people and their activities. Thus, bear conservation and management should take into account potential behavioural alterations related to living in human-modified landscapes. We studied the behaviour of brown bears in the Cantabrian Mountains, NW Spain, where an endangered population thrives in a human-modified landscape. We analysed bear observations video-recorded over a 10-year period to try to identify human and landscape elements that could influence bear behaviour. Neither the occurrence nor the duration of vigilance behaviour in Cantabrian bears seemed to be influenced by the proximity of human infrastructures and activity. Our findings suggest that the general pattern of human avoidance by bears is adapted to the human-modified landscape they inhabit. Bears generally avoid people, but close presence of human infrastructures or activity did not seem to trigger an increased bear behavioural response. Coexistence between large carnivores and humans in human-modified landscapes is possible, even when human encroachment is high, provided that carnivores are not heavily persecuted and direct interactions are avoided. Further research should also document the potential existence of

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other responses to human presence and activity, e.g., hunting, traffic noise, and measuring stress levels with physiological indicators.

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1. Introduction

Large carnivores are recolonizing parts of their historical range in Europe (Chapron et al., 2014), in so-called human-modified landscapes (Kuijper et al., 2016), i.e. areas characterised by a widespread presence of people and infrastructures. This phenomenon is thus bringing wild animal populations closer to humans, in areas where habitats are fragmented and encroached on by towns, villages, roads, and a variety of human activities (Lowry et al., 2012; Venter et al., 2016; Watson et al., 2015).

Theoretically, the close coexistence of large carnivores and humans could produce human-driven disturbances that can affect species behaviour (Gaynor et al., 2018; Geffroy et al., 2015). Disturbance can alter space use and distribution (Hebblewhite et al., 2005; Leblond et al., 2013), food habits (Newsome et al., 2016; Valeix et al., 2012), and fitness-related behaviours like mating or nursing cubs (Ditchkoff et al., 2006; Frid and Dill, 2002; Higham and Shelton, 2011), potentially reducing survival rates (Basille et al., 2013; Shannon et al., 2017). Human disturbances can also be perceived by animals in a similar way to predation risk (Frid and Dill, 2002). Even apex predators display anti-predator behaviour in response to human presence (Clinchy et al., 2016; Ordiz et al., 2011; Parco Naturale Adamello e Brenta, 2007).

Studying animal behaviour is often the first approach to determine wildlife reactions to human-induced environmental changes and species' capacity to adapt to areas where animals and humans have to coexist (Tuomainen and Candolin, 2011). Animal behaviour can be a good indicator of the stress levels triggered by humans and can inform conservation and management of typically endangered species such as large carnivores (Dimitri and Longland, 2018). Moreover, the current expansion of these species in human-modified landscapes demands an improvement of our knowledge on how large carnivores manage to coexist with humans (Carter and Linnell, 2016), and what potential effects human presence and activities may have on their behaviour (Carter et al., 2012; Carter and Linnell, 2016; Elfström et al., 2014; Penteriani et al., 2018). This is particularly important in areas with increasing but still endangered populations (Treves and Karanth, 2003; Ordiz et al., 2013a).

Brown bears *Ursus arctos* are sensitive to human presence and activity (e.g., Ordiz et al., 2011). Bears change activity patterns to avoid encounters with people by becoming more nocturnal (Blankenheim, 2018; Cleverger AP, Francisco J. Purroy JP, 1990; Swenson et al., 2000; Tattoni et al., 2015), being less detectable when closer to human settlements (Oberosler et al., 2017), and avoiding roads (Bischof et al., 2017; Skuban et al., 2017), for instance. Besides, the brown bear is one of the most targeted species by wildlife tourism (Penteriani et al., 2017). Sharing the landscape with humans may be costly (Cooper and Frederick, 2007), and thus bear conservation and management strategies should take into account potential behavioural alterations related to living in human-modified landscapes, so as to favour the effectiveness of conservation practices (Treves and Karanth, 2003).

Brown bears in the Cantabrian Mountains (NW Spain) represent an example of an endangered large carnivore population in human-modified landscapes. It is a native bear population, which was never reinforced with relocations, officially protected since 1973. Most of their range is characterised by high human population densities (Penteriani et al., submitted), extensive agricultural livestock activities and urban development, connected by a diffuse network of transport infrastructures (Lamamy et al., submitted; Penteriani et al., submitted; Mateo-Sánchez et al., 2016), which have determined a reduction of continuous suitable habitat for this species (Martínez Cano et al., 2016). As a consequence, human activities and presence in the Cantabrian Mountains have the potential to cause stress to bears and, therefore, alter their behaviour. Additionally, brown bear viewing is nowadays a common practice in the Cantabrian Mountains (Ruiz-Villar et al., submitted; Penteriani et al., 2017). Generally, the places where brown bear viewing occurs (Ruiz-Villar et al., submitted; Penteriani et al., 2017) are not controlled or managed by local authorities and frequently appear randomly in the area inhabited by bears, e.g., when a female with cubs settles in a given place or several individuals congregate during hyperphagia (Ruiz-Villar et al., submitted). Such viewing spots can be close to bears, and thus bear viewing has the potential to negatively influence their behaviour. All of these factors might negatively impact the present positive trend of this endangered population, which is about 220 bears (Pérez et al., 2014).

We studied bear behaviour by analysing video recordings of direct observations during a 10-year period. In particular, we explored whether brown bear behaviours may be influenced in a human-modified landscape. We first analysed the time bears dedicated to different behaviours, namely walking, feeding, nursing and resting, in relation to the human features of the landscape they inhabit. Second, we studied whether human infrastructures may cause the appearance of vigilance/alert behaviour and influence its duration, and if that vigilance behaviour is affecting brown bear behaviour. As individual behaviour is the results of the complex interaction between internal (e.g. age) and external factors (natural habitat characteristics and season), we accounted for these effects when studying brown bear behaviour in human-modified landscapes. We hypothesised that, if brown bears are negatively influenced by the presence of humans, they should modify their behaviours, becoming especially vigilant when in closer proximity to people and/or human infrastructures. However, if brown

bears have adapted their behaviour to human presence, we should not find any difference in their behaviours as a function of the distance to human infrastructures.

2. Methods

2.1. Study area

Brown bear videos were recorded in the western sector of the Cantabrian Mountains (Fig. 1), which includes the west of Asturias and north of León Autonomous Provinces. The Cantabrian Mountains run parallel to the Atlantic coast of northern Spain and exhibit a mild and humid climate throughout the year (900–1900 mm, average total precipitation; Martínez Cano et al., 2016). Average elevation is around 1100 m (Martínez Cano et al., 2016; Naves et al., 2003). The main tree species are oaks (*Quercus petraea*, *Q. pyrenaica* and *Q. rotundifolia*), beech (*Fagus sylvatica*) and chestnut (*Castanea sativa*). Subalpine shrubland (*Juniperus communis*, *Vaccinium uliginosum*, *V. myrtillus* and *Arctostaphylos uva-ursi*) dominates mountain areas above the treeline (~1700 m; Martínez Cano et al., 2016). In some areas, former forests have been converted into pasture and brushwood (*Genista*, *Cytisus*, *Erica* and *Calluna*) through human activities (Naves et al., 2006, 2003). The main economic activities throughout the bear's range include livestock farming, mining, tourism, agriculture, and timber harvesting, with a generally low human population density (Blanco-Fontao et al., 2011). Surrounding areas have experienced extensive urban and agricultural development, and are fragmented by a network of main transport infrastructures (Mateo-Sánchez et al., 2016).

2.2. Behavioural analyses

Brown bears were recorded with the digiscoping technique (a telescope with a digital camera) over a period of 10 years, from 2008 to 2017. All the observations were done at a safe distance from bears (from several hundreds of meters to > 1 km) to avoid influencing bear behaviours. We assigned bear behaviours following ethograms established in other studies (Perdue, 2016), setting up 10 different classes: (1) feeding; (2) walking; (3) resting; (4) vigilance; (5) territorial marking; (6) conspecific aggression; (7) females nursing cubs; (8) mating; (9) social interaction; and (10) other behaviour (see Table 1). In particular, we focused on vigilance behaviour, which was taken as a response of individuals to human disturbances. We considered that bears were exhibiting vigilance behaviour when they were: (1) sniffing the air; (2) exploring their surroundings by intensively looking around; and (3) focusing attention in a given direction.

We measured the time bears spent on each behaviour with the free software BORIS (<http://www.boris.unibo.it/pages/download.html>), which allows quantifying the time dedicated to behaviours previously defined in an ethogram.

Specific characteristics of individuals, such as fur marks, colour and body morphology, allowed identification of some individuals during video recordings and over the years (Fagen and Fagen, 1996; Higashide et al., 2012). When possible, individuals were assigned to one of three bear age or sex related categories (hereafter, bear class), i.e., adult, subadult and

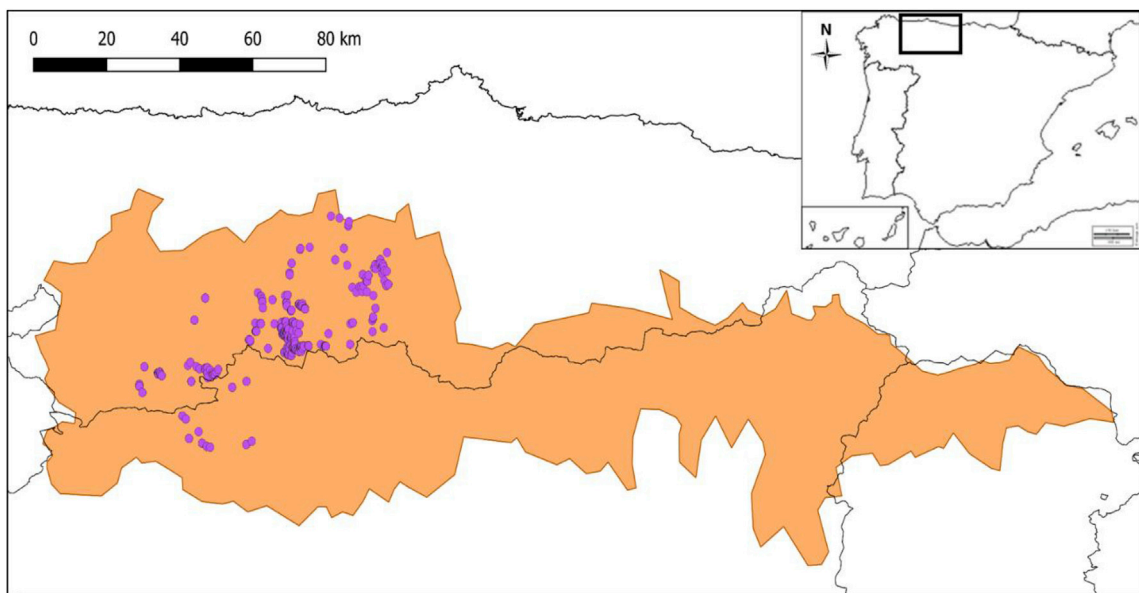


Fig. 1. The locations of the 3132 videos (78.5 h in total) of different brown bear behaviours associated with 167 adults, 42 subadults and 112 females with cubs, within the species distribution (orange shape) in the Cantabrian Mountains. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Ethnogram used to analyse brown bear behaviours in the Cantabrian Mountains.

Behaviour	Description
Feeding	The bear is actively searching for food or foraging.
Walking	The bear is moving in any direction with no apparent purpose, nor performing other behaviours at the same time.
Resting	The bear is in a still position laying down or sitting with its eyes open or closed (sleeping), and not exhibiting any other behaviour.
Vigilance	The bear is actively interested in some part of its environment, sniffing the air, moving the ears.
Marking	The bear is marking, e.g., on trees or shrubs.
Aggression	Contact or non-contact interaction with at least one conspecific, which includes chasing, biting, pawing at or slapping another animal with the paw.
Nursing the cubs	All interactions between a female with its cubs.
Mating	Mating behaviour, e.g., male and female interactions during the mating period.
Social interaction	Any interaction with at least one conspecific, except mating or aggression, e.g., eye contact with another individual, playing (usually between related subadults), observation of another close bear.
Other	Other behaviour not recognizable or not appearing in the list, e.g., grooming, scratching itself, preparing the den.

female with cubs. Beyond the fact that it was not possible to observe bears during the night, we consider that diurnal observations are best to detect bear reactions to humans because that is the time when humans are usually active, and there is greater potential for bear and human overlap. Each video was also classified seasonally, on the basis of the main bear cycle in the Cantabrian Mountains (Martínez Cano et al., 2016), including 'winter', when most bears, but not all, hibernate (January to mid-April), 'spring-early summer', when the mating season occur, (mid-April to June) and 'late summer and autumn', which includes the hyperphagia period when bears store fat for the next winter (July to December). In the Cantabrian Mountains, not all bears hibernate every year and hibernation may be relatively short (author's personal observations and Nores et al., 2010), and thus some bear observations (n = 90) were also recorded in winter.

2.3. Environmental variables

The location of each video-recorded bear was used to analyse the characteristics of the human and natural environment surrounding bear behaviour (Fig. 1) by using QGIS 3.0.2 (Quantum GIS Development Team, 2015). Bears generally moved only a short distance during the observations and the position of the bear when it was first observed and video-recorded was considered the location corresponding to each video.

For each video location, we measured human disturbance (i.e. human presence and activities) as the minimum bear distances to: (1) paved roads; (2) unpaved roads and trails; and (3) urban settlements. To obtain the minimum distance to roads and trails we used the transportation network information from CNIG (<http://centrodedescargas.cnig.es>), whereas for urban settlements we used the Base Topográfica Nacional BTN100. We also included a variable related to brown bear viewing activities, calculating the minimum distance from one of the six most common bear viewing points located in the Cantabrian Mountains to the location of the video.

Additionally, we evaluated natural habitat characteristics around bears by estimating the following parameters: (1) altitude; bear minimum distance to (2) forests; (3) shrubland; (4) natural open areas (grasslands and pastures) and (5) crops. Minimum distances to natural landscape variables were calculated using the Mapa Forestal de España MFE50 (<http://www.mapama.gob.es>). However, as the minimum distance to crops was highly correlated to urban settlements and trails, whereas altitude was so to roads (Pearson correlation coefficients > 0.6), we did not include minimum distance to crops and altitude in our statistical models.

2.4. Statistical analysis

To study brown bear behaviours in a human-modified landscape, we first explored the association between the duration of the recorded behaviours (i.e., walking, feeding, nursing and resting) and the environmental variables, season and bear class. In order to make behaviours recorded during different times comparable between them, we divided the time of each observed behaviour by the duration of the recorded video. As individual behaviours are intrinsically correlated, i.e. when a bear is walking is not resting, we constructed four separate covariance matrices with the dyads of walking and feeding, walking and resting, resting and feeding, and nursing and feeding. We run four separate bivariate models to quantify estimates of variance and covariance components between dyads of the behavioural traits considered (Doncaster and Davey, 2007). In these models, the explanatory variables were the environmental variables, season and bear class. In all models, year and individual identity were included as random factors. In order to test the significance of a covariance, we compared the models with and without the covariance set to 0 using a log-likelihood ratio test.

Second, to study whether human infrastructures may cause the appearance of vigilance/alert behaviour and also influence its duration, we built two separate generalized linear mixed-effects models (GLMMs). In the first model, we analysed the appearance of the vigilance behaviour (binomial variable: 0 = no vigilance behaviour showed by the individual; 1 = appearance of a vigilant behaviour) in relation to the presence of humans and their activities. To take into account that

brown bear behaviour also depends on other external and internal factors, we also included natural habitat features (forest, open habitat and shrubland), individual characteristics (i.e. bear class) and season. While the presence of humans and natural landscape characteristics were included as covariates, those related with individual characteristics and the variables related with time were included as factors. We then built a second general linear mixed-effect model to test whether the time bears spent alert (vigilance behaviour duration being normally distributed) depended on the proximity of different human structures (human settlements, roads, trails and bear tourism viewing points). Again, we included natural habitat landscape characteristics (forest, open habitat and shrubland), bear class and season. In these two models, we account for the intrinsic annual variability and for the fact that vigilance behaviour is more likely to last longer as the time recorded increases by including year as a random factor and the duration of the video as an offset, respectively. The offset is a structural predictor, whose coefficient is assumed to have the value 1; thus, the values of the offset are simply added to the linear predictor of the target (Bates and Sarkar, 2006). We selected the best models using the Akaike's Information Criterion, considering models with ΔAIC values lower than 2 as competitive. For each set of models, we employed model averaging on the 95% confidence set to derive relative importance values (RIV) and parameter coefficients of each variable using the full-model averaging approach (Burnham, K. P., & Anderson, 2002).

Finally, by returning to the bivariate analysis of variance explained above, we study whether brown bear behaviour (i.e., walking, feeding, nursing and resting) was influenced by the time individuals spend in alert behaviour. In this case, we analysed the covariance matrices described above against time alert behaviour, bear class and season as alternative explanatory variables.

All statistical analyses were performed using R 3.4.1 statistical software (R Core Team, 2013), using the MuMIn package (Barton, 2018) with lme4 package (Bates and Sarkar, 2006) and ASReml-R for bivariate models (Butler et al., 2009).

3. Results

We analysed 3132 videos, including 78.5 h of observed brown bear behaviours, of 167 adult bears, 42 subadults and 112 females with cubs (Table A2).

3.1. Non-alert behaviours

Feeding was the behaviour in which bears spent more time (54% of the total amount of time recorded) (Table A1). Together with subadults in 'late summer and autumn' (Table A2), females with cubs were the bear group that spent more time feeding in all seasons (especially during 'spring-early summer': 5.45 ± 7.62 min, range = 0–47.5 min). Looking at the mean distance to human structures among bear classes (Table A3), adults were further away from urban settlements during 'spring-early summer' and 'late summer and autumn' than females with cubs or subadults (see also Fig. 2). Incorporating the covariance of

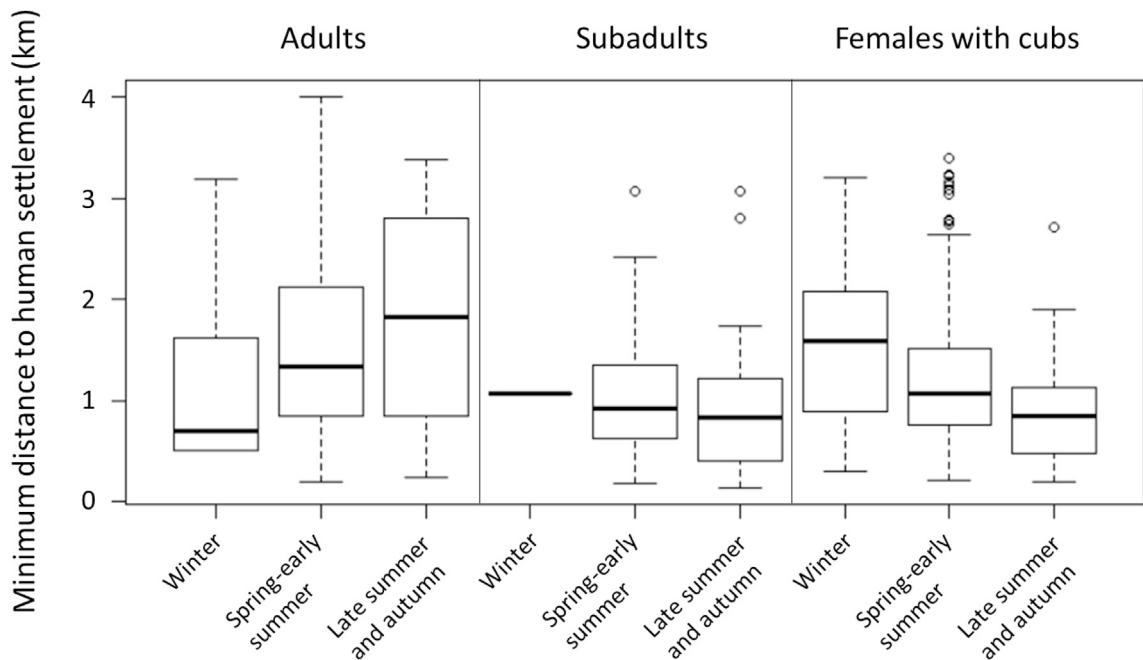


Fig. 2. Distribution of the minimum distance (km) to human settlements (town and villages) of all brown bear observations among the different bear classes (adults, subadults and females with cubs) in each season ('winter', 'spring-early summer' and 'late summer and autumn').

behaviour explained a significant proportion of variance compared with models in which covariance was not included (Table A4 and A5). Regarding the covariance between dyads of behaviour and environmental factors, we found that only the dyad between feeding and nursing was associated with human variables (Table A5). Specifically, we found a negative covariation between feeding and nursing associated with human settlements and a positive covariation with viewpoints. These results suggest that individuals tend to change from feeding and nursing to the other of these two behaviours as they get closer to urban settlements. In addition, our analyses suggest that around viewpoints, individuals were more often feeding and nursing.

3.2. Appearance of vigilance behaviour and its duration

We found that the appearance of vigilant behaviours was related to bear class and video duration (all RIV = 1; Table 2). In particular, the appearance of vigilance behaviour was less likely in adult bears than in subadults and females with cubs. The appearance of vigilance behaviour was never strongly related to any of the human elements or natural habitat variables (although their RIV values were above 0.56) (Table 3), suggesting that the appearance of vigilance behaviour was neither related to the natural habitat variables where bears inhabit.

The duration of vigilance behaviour was related to the season and the video duration (Table 4). The amount of time bears appeared vigilant mostly differed among seasons (Table 3), spending less time in vigilance during 'late summer and autumn' than in the other periods. Among all combinations of behavioural types explored, we found that alert duration was negatively associated with the covariance of multiple dyads of behaviour (Table A4). Specifically, we found that alert duration was negatively associated with the covariance of feeding-resting, feeding-walking and nursing-feeding (Table A4). This suggests that as alert duration increased, individuals choose to follow one or another behaviour. Conversely, in situations where alert duration was minimal, individuals were more likely to display both behaviours.

4. Discussion

Our results show that neither the appearance nor the duration of vigilance behaviour in Cantabrian brown bears seemed to be influenced by the closeness of any of the human structures and activities that we took into account in this study, i.e., roads, trails, urban settlements, and viewing points. Populations of bears and other carnivores that have been facing human persecution for centuries are more elusive, e.g., more crepuscular and nocturnal, than their counterparts inhabiting remoter areas (Ordiz et al., 2011; Zedrosser et al., 2011). Bears that have coexisted with humans for many generations seem to have adapted their behaviour to human presence and activities, especially if they cannot easily hide from humans (Skuban et al., 2018), and none of the habitat or human variables that we analysed seemed to increase or decrease the time that bears spent alert.

Human activities can trigger detectable behavioural changes in brown bears. In northern Europe, where bears are hunted, bears become even more nocturnal when hunting season starts (Ordiz et al., 2012) and after encounters with people in the forest (Ordiz et al., 2013b). Bears also seek more concealed daybeds following seasonal increases in human activity levels (Ordiz et al., 2011). However, the flight responses of experimentally approached bears were not dependent on the densities of human populations and roads inside the bears' home ranges, or the distances from the bears to roads and settlements when encountered (Moen et al., 2018). Consistency in bear behavioural responses regardless of proximity to human infrastructures, both in our study and in northern Europe, likely reflects the fact that bears living in human-modified landscapes have

Table 2

Model averaged coefficients and relative importance values (RIV) for vigilance appearance in relation to the human environment, habitat composition and individual characteristics (i.e., bear class). Vigilance appearance is a binary variable indicating whether there is any vigilance behaviour recorded (1) or not (0).

Dependent variable	Explanatory variable	Model-averaged coefficients and relative importance values			
		β	SE	P	RIV
Vigilance appearance	Intercept	0.716961	0.3137528	0.02249	-
	Duration (offset)	-	-	-	1
	BearClass1: Subadults	1.0642677	0.3514813	0.00251	1
	BearClass2: Females with cubs	0.8900139	0.2232919	6.94E-05	1
	Forest	0.2460338	0.1496288	0.1005	0.87
	Open habitat	0.205616	0.1381372	0.13702	0.83
	Human settlement	-0.122839	0.1344691	0.36138	0.62
	Shrubland	0.1004674	0.1258915	0.42524	0.56
	Season1: Spring-early summer	-0.2443475	0.3334388	0.46405	0.49
	Season2: Late summer and autumn	-0.0715122	0.2623352	0.78554	0.49
	Trail	0.0393377	0.0895955	0.66098	0.36
	Road	0.0093458	0.0635365	0.88325	0.29
	View point	-0.0001425	0.0611096	0.99814	0.28

P value and RIV of the variables with a significant effect ($p < 0.05$) are highlighted in bold.

Table 3

Comparison of the competing models built to explain the (a) appearance and (b) duration of brown bear vigilance behaviour in relation to the human environment variables, habitat composition and intrinsic bear characteristics. Vigilance appearance is a binary variable indicating whether there is any vigilance behaviour recorded (1) or not (0) and vigilance duration is a variable which represents the time in seconds each bear spent performing any vigilance behaviour.

Dependent variable	Competing models	df	AIC	Δ AIC	Weight	R ²
Vigilance appearance	BearClass + Forest + OpenHabitat + Shrubland + Duration	7	681.75	0	0.05	0.1292167
	BearClass + Season + Forest + OpenHabitat + HumanSettlement + Duration	9	682.13	0.38	0.04	0.1349776
	BearClass + Forest + OpenHabitat + HumanSettlement + Shrubland + Duration	8	682.15	0.41	0.04	0.1352757
	BearClass + Season + Forest + OpenHabitat + Shrubland + Duration	9	682.33	0.59	0.03	0.1338969
	BearClass + Forest + OpenHabitat + HumanSettlement + Shrubland + Trail + Duration	9	682.38	0.64	0.03	0.1370742
	BearClass + Season + Forest + OpenHabitat + HumanSettlement + Shrubland + Duration	10	682.71	0.96	0.03	0.1395005
	BearClass + Forest + OpenHabitat + HumanSettlement + Duration	7	683	1.25	0.02	0.1272648
	BearClass + Season + Forest + OpenHabitat + Duration	8	683.08	1.33	0.02	0.1258817
	BearClass + Season + Forest + OpenHabitat + HumanSettlement + Trail + Duration	10	683.15	1.4	0.02	0.1361518
	BearClass + Forest + OpenHabitat + Shrubland + Trail + Duration	8	683.21	1.47	0.02	0.1287212
BearClass + Season + Forest + OpenHabitat + HumanSettlement + Shrubland + Trail + Duration	11	683.35	1.61	0.02	0.1416621	
Vigilance duration	Season + Duration	5	5262.13	0	0.06	0.0721443
	Season + Viewing point + Duration	6	5262.69	0.55	0.04	0.07451133
	Season + HumanSettlement + Duration	6	5263.69	1.56	0.03	0.0732944
	Season + Forest + Duration	6	5263.89	1.76	0.02	0.07280913
	Season + Shrubland + Duration	6	5264.01	1.88	0.02	0.07179663
	Season + OpenHabitat + Duration	6	5264.12	1.99	0.02	0.07237139
	Season + Road + Duration	6	5264.13	1.99	0.02	0.07232507

Table 4

Model averaged coefficients and relative importance values (RIV) for vigilance duration in relation to the human environment, habitat composition and intrinsic bear characteristics. Vigilance duration is a variable that represents the time in seconds each bear spent performing any vigilance behaviour.

Dependent variable	Explanatory variable	Model-averaged coefficients and relative importance values			
		B	SE	P	RIV
Vigilance duration	Intercept	115.66585	16.15628	<2e-16	
	Season1: Spring-early summer	-42.45055	16.51049	0.01031	0.97
	Season2: Late summer and autumn	-57.19988	19.63053	0.00364	0.97
	Duration (offset)	-	-	-	0.90
	Viewing point	2.85842	4.91055	0.56110	0.43
	Human settlement	-1.06782	3.55456	0.76437	0.30
	Forest	0.94335	3.21050	0.76939	0.30
	Shrubland	0.64219	3.24819	0.84366	0.28
	Open habitat	0.56046	2.99271	0.85182	0.28
	Road	0.55080	2.99957	0.85467	0.28
	Trail	-0.08571	2.92292	0.97667	0.26
	BearClass1: Subadults	-1.82044	8.05437	0.82154	0.16
	BearClass2: Females with cubs	0.83250	5.00716	0.86827	0.16

P value and RIV of the variables with a significant effect ($p < 0.05$) are highlighted in bold.

developed a solid pattern of human avoidance. Most bears move away after a direct encounter with a person, both in Fennoscandia (Moen et al., 2018; Ordiz et al., 2013b), where bears are hunted, and in Spain (authors' personal observations), where they are legally protected. However, behavioural responses of bears do not seem to be dependent on the mere presence of human infrastructures in generally encroached landscapes, and this applies to both hunted (e.g., Fennoscandia) and non-hunted (e.g., Spain) bear populations.

Season seemed to have some effects on brown bear behaviour. That is, bears spend less time alert during 'late summer and autumn', when they focus on feeding prior to hibernation and cubs are no longer at risk of infanticide (Bellemain et al., 2006; Steyaert et al., 2013). Bears also appeared closer to human settlements in this period, probably due to the high availability of attractive food resources like fruit trees or crops (Libal et al., 2011; Skuban et al., 2018). During the 'spring-early summer' period, when the need to protect offspring is crucial due to the high risk of infanticide, females with cubs spend more time on vigilance behaviours compared to other seasons (Table A4). Then, alert behaviours of females with cubs may reflect the potential risk driven by males rather than by humans and their activities. Adult males and single females are often the most elusive bear classes, using areas further away from human settlements (Elfström et al., 2014; Smith et al., 2005). However, females with cubs may use proximity to human presence as a shield strategy (Skuban et al., 2018; Steyaert et al., 2016), and subadult bears also use areas closer to people, which are generally avoided by adult bears (Nellemann et al., 2007). Our results confirm this general pattern (Fig. 2), which reflects the interface between intraspecific avoidance of the most vulnerable bear

classes (Bellemain et al., 2006; Steyaert et al., 2016, 2013) and varying tolerance or adaptation of different bear classes to human presence (Elfström et al., 2014; Nellemann et al., 2007). Indeed, even if levels of vigilance are not generally high, a few individuals may conserve high alertness due to the individual variations in brown bears' behaviours (Milleret et al., 2018).

In the Cantabrian Mountains, brown bear mortality associated with roads is rare and illegal poaching, the most common driver of human-induced bear deaths (Palomero et al., 2007), may have declined in recent decades, resulting in the positive trends exhibited by this population (Gonzalez et al., 2016). Lower rates of human-induced mortality in recent times might have improved bear-to-human tolerance, as may have happened in other populations where bears are not persecuted (Smith et al., 2005). A previous study in the Cantabrian range documented that bear behaviour associated with vigilance was not different inside and outside natural parks (Naves, 2016), which perhaps might have been different if there were areas where bears were hunted and areas where they were fully protected.

Brown bears have largely coexisted with humans in Europe, including northern Spain (Clevenger et al., 1987), where the bear population is increasing (Gonzalez et al., 2016). If the positive trend persists, brown bears would have to expand into even more encroached landscapes, although suitable areas are still available in the Cantabrian Mountains (Zarzo-Arias et al., submitted). Human activities and infrastructure do not seem to provoke acute behavioural responses in the brown bears of the Cantabrian Mountains, but physiological reactions of bears to human presence, i.e., stress responses, should also be investigated, because they do not necessarily need to manifest visible behavioural changes and can have a cost on disturbed animals (Støen et al., 2015).

Certain levels of tolerance from both humans and large carnivores, which are reflected in behavioural patterns, seem crucial to facilitate persistence and eventual recovery of bears and other carnivores in human-modified landscapes, even where human encroachment is high, but management agencies must ensure that direct interactions between human and animals are not likely to occur. For instance, some authors have proposed that good brown bear tourism practices and the minimization of human-bear conflicts can improve and enhance the conservation of this species (Herrero et al., 2005; Penteriani et al., 2017; Smith et al., 2005). Finding that bears tended to change from feeding and nursing to the other of these behaviours as they were closer to urban settlements may suggest bear awareness, whereas finding that bears more often feed and nurse near viewpoints (Table A5) likely reflects the fact that these points are located where it is easiest to see bears. This highlights that effective management of bear viewing is necessary to ensure that tourists do not interact with bears (Penteriani et al., 2017), and the same concern should apply in general to other human activities in areas that are inhabited by large carnivores, thus avoiding any potential change in carnivore behaviour.

Finally, it is noteworthy that the goodness of fit (R^2) of our models was usually quite low, which is understandable because of underfitting, i.e., other important variables might not be in the models. Evidently, not all the external factors acting on the recorded individuals might have been recorded, and we also lack of information on what bears may have experienced just before our recording, as well as on the health state of individuals and on their behavioural traits (e.g., shy vs. bold individuals).

5. Conclusions

Our results suggest that the general pattern of human avoidance by bears is adapted to the human-modified landscape they inhabit. Bears generally avoid people, but close presence of human infrastructures or activity did not seem to trigger an increased bear behavioural response. Coexistence between large carnivores and humans in human-modified landscapes is possible, even when human encroachment is high, provided that carnivores are not heavily persecuted and direct interactions are avoided. Further research should also document the potential existence of other responses to human presence, e.g., hunting, traffic noise, and measuring stress levels with physiological indicators.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2018.e00499>.

Appendices

Table A1

Total time dedicated and percentage of each behaviour by each bear class (adults, subadults and females with cubs) in each season to the different behaviours included in the ethogram.

Age	Adults						Subadults				Females with cubs					
	Winter		Spring-early summer		Late summer and autumn		Spring-early summer		Late summer and autumn		Winter		Mating		Late summer and autumn	
Behaviour	Seconds	%	Seconds	%	Seconds	%	Seconds	%	Seconds	%	Seconds	%	Seconds	%	Seconds	%
Duration	17 545	-	58 571	-	27 761	-	12 356	-	12 939	-	11 956	-	93 918	-	22 016	-
Vigilance	4334	25	5376	9	3927	14	1263	10	2101	16	1905	16	15 581	17	3714	17
Feeding	5879	34	23 174	40	14 442	52	9984	81	8972	69	8392	70	54 216	58	13 833	63
Walking	893	5	3385	6	5062	18	569	5	955	7	997	8	3511	4	1133	5
Resting	2807	16	2147	4	733	3	439	4	301	2	102	1	6326	7	2700	12
Marking	72	0	480	1	114	0	57	0	0	0	332	3	1085	1	40	0
Aggression	0	0	452	1	0	0	0	0	49	0	0	0	219	0	0	0
Nursing	0	0	61	0	197	1	0	0	14	0	134	1	9065	10	433	2
Spring-early summer	690	4	22 974	39	0	0	0	0	0	0	0	0	3429	4	24	0
Social interaction	281	2	36	0	3246	12	39	0	521	4	89	1	35	0	105	0
Other	2591	15	487	1	40	0	5	0	26	0	6	0	451	0	33	0

Table A2

Mean, standard deviation (SD), minimum (Min) and maximum (Max) duration (in sec) of all the brown bear behaviours during the three seasons ('winter', 'spring-early summer' and 'late summer and autumn') of the bear cycle (see text for more details) for adults (A), subadults (B) and females with cubs (C).^a There is only one observation for subadults in this period.

A							
Age	Adults						
Season	Winter		Spring-early summer		Late summer and autumn		
Cases	39		160		90		
N° individuals	16		118		54		
	Mean ± SD	Min - Max	Mean ± SD	Min - Max	Mean ± SD	Min - Max	
Duration	450 ± 399	54 - 1737	366 ± 391	3 - 2162	308 ± 326	18 - 1594	
Vigilance	111 ± 158	0-605	34 ± 87	0-876	44 ± 71	0-348	
Feeding	151 ± 241	0-961	145 ± 268	0 - 2149	160 ± 261	0 - 1322	
Walking	23 ± 77	0-457	21 ± 49	0-243	56 ± 110	0-778	
Resting	72 ± 116	0-605	13 ± 48	0-383	8 ± 25	0-186	
Marking	2 ± 8	0-49	3 ± 22	0-257	1 ± 7	0-49	
Aggression	0 ± 0	0-0	3 ± 21	0-177	0 ± 0	0-0	
Nursing	0 ± 0	0-0	0 ± 3	0-33	2 ± 19	0-177	
Mating	18 ± 77	0-345	144 ± 301	0 - 1769	0 ± 0	0-0	
Social interaction	7 ± 37	0-226	0 ± 2	0-15	36 ± 136	0-884	
Other	66 ± 116	0-364	3 ± 21	0-190	0 ± 3	0-19	
B							
Age	Subadults						
Season	Winter	Spring-early summer		Late summer and autumn			
Cases	1	39		38			
N° individuals	1	23		27			
	Mean ^a	Mean ± SD	Min - Max	Mean ± SD	Min - Max		
Duration	130	317 ± 291	18 - 1123	340 ± 272	18 - 1068		
Vigilance	0	32 ± 52	0-225	55 ± 54	0-213		
Feeding	130	256 ± 262	0-889	236 ± 247	0-990		
Walking	0	15 ± 47	0-267	25 ± 56	0-315		
Resting	0	11 ± 33	0-141	8 ± 45	0-277		
Marking	0	1 ± 7	0-40	0 ± 0	0-0		
Aggression	0	0 ± 0	0-0	1 ± 8	0-49		
Nursing	0	0 ± 0	0-0	0 ± 2	0-14		
Mating	0	0 ± 0	0-0	0 ± 0	0-0		
Social interaction	0	1 ± 4	0-22	14 ± 45	0-235		
Other	0	0 ± 1	0-5	1 ± 3	0-18		

C						
Age	Females with cubs					
Season	Winter		Spring-early summer		Late summer and autumn	
Cases	50		166		43	
N° individuals	23		74		30	
	Mean ± SD	Min - Max	Mean ± SD	Min - Max	Mean ± SD	Min - Max
Duration	440 ± 432	8–2134	566 ± 740	16 - 6063	278 ± 304	1 - 1503
Vigilance	74 ± 107	0–450	94 ± 185	0 - 1707	44 ± 100	0–597
Feeding	277 ± 342	0 - 1386	327 ± 457	0 - 2850	195 ± 240	0–854
Walking	23 ± 47	0–261	21 ± 55	0–534	23 ± 49	0–190
Resting	54 ± 127	0–575	38 ± 165	0 - 1744	2 ± 12	0–79
Marking	1 ± 6	0–40	7 ± 68	0–854	8 ± 21	0–91
Aggression	0 ± 0	0–0	1 ± 17	0–219	0 ± 0	0–0
Nursing	9 ± 26	0–163	55 ± 140	0–919	3 ± 11	0–45
Mating	0 ± 3	0–24	21 ± 158	0 - 1769	0 ± 0	0–0
Social interaction	2 ± 15	0–105	0 ± 2	0–21	2 ± 10	0–59
Other	1 ± 5	0–33	3 ± 16	0–172	0 ± 1	0–6

Table A3

Mean, standard deviation (SD), minimum (min) and maximum (max) distance (in meters) to human structures and habitats during the three seasons ('winter', 'spring-early summer' and 'late summer and autumn') for adults (A), subadults (B) and females with cubs (C).

A						
Age	Adults					
Season	Winter		Spring-early summer		Late summer and autumn	
	Mean ± SD	Min - max	Mean ± SD	Min - max	Mean ± SD	Min - max
Trails	230 ± 161	4–698	335 ± 186	15–857	572 ± 372	0–988
Roads	503 ± 378	115 - 1884	658 ± 623	92 - 4085	561 ± 434	119 - 2060
Human settlements	1074 ± 714	502 - 3181	1618 ± 934	196 - 4705	1801 ± 1009	245 - 3380
Viewing points	5547 ± 3028	97 - 12 450	4842 ± 4287	97 - 16 428	2581 ± 3239	478 - 12 450
Forest	19 ± 44	0–189	46 ± 81	0–416	41 ± 95	0–442
Open habitat	965 ± 609	0 - 2447	915 ± 816	0 - 3195	1149 ± 748	0 - 3117
Shrubland	438 ± 301	0–693	152 ± 217	0–982	159 ± 192	0–784
B						
Age	Subadults					
Season	Winter	Spring-early summer		Late summer and autumn		
	Mean ^a	Mean ± SD	Min - max	Mean ± SD	Min - max	
Trails	273	224 ± 203	5 - 1068	297 ± 293	1–999	
Roads	130	448 ± 371	3 - 1196	614 ± 497	25 - 1932	
Human settlements	1064	1059 ± 610	181 - 3061	1019 ± 779	134 - 3064	
Viewing points	1093	3667 ± 3046	97 - 14 923	2696 ± 2429	478 - 9681	
Forest	0	65 ± 75	0–213	60 ± 87	0–403	
Open habitat	1391	1214 ± 788	16 - 2724	1224 ± 996	0–3003	
Shrubland	452	64 ± 134	0–592	102 ± 171	0–584	
C						
Age	Females with cubs					
Season	Winter		Spring-early summer		Late summer and autumn	
	Mean ± SD	Min - max	Mean ± SD	Min - max	Mean ± SD	Min - max
Trails	328 ± 193	22–948	336 ± 180	8–886	235 ± 179	11–712
Roads	418 ± 301	70–1429	624 ± 525	9–2230	490 ± 462	38–1769
Human settlements	1540 ± 767	297–3204	1252 ± 741	206–3387	913 ± 518	194–2715
Viewing points	5735 ± 3562	516–15820	5840 ± 4963	97–17285	4991 ± 4084	560–14774
Forest	33 ± 95	0–501	63 ± 82	0–359	49 ± 94	0–337
Open habitat	606 ± 412	0–1692	933 ± 782	0–3367	1059 ± 862	0–2956
Shrubland	200 ± 221	0–701	109 ± 180	0–693	189 ± 254	0–776

^a There is only one observation for subadults in this period.

Table A4

Association between the covariance of different behaviours and duration of stress response for brown bears in the Cantabrian Mountains (see 2. Methods for details on the models).

	Variable	Estimate	df	Wald	P
Feeding-resting Sig cov: p = 0.001	Intercept		2	639.66	<0.001
	Stress duration	-0.234 ± 0.023	1	96.99	<0.001
	Age		2	8.66	<0.001
	Adult	0			
	Subadult	0.059 ± 0.018			
	Female with cubs	0.053 ± 0.012			
	Season		2	24.01	0.013
	Winter	0			
	Spring-early summer	-0.049 ± 0.016			
	Late summer and autumn	-0.049 ± 0.019			
Resting-walking Sig cov: p = 0.854	Intercept		2	108.203	<0.001
	Stress duration	-0.031 ± 0.023	1	1.657	0.198
	Age		2	3.087	0.213
	Adult	0			
	Subadult	-0.023 ± 0.018			
	Female with cubs	-0.020 ± 0.012			
	Season		2	7.842	0.01982
	Winter	0			
	Spring-early summer	-0.048 ± 0.017			
	Late summer and autumn	-0.041 ± 0.019			
Feeding-walking Sig cov: p = 0.002	Intercept		1	721.01	<0.001
	Stress duration	-0.256 ± 0.025	2	96.35	<0.001
	Age		2	15.35	<0.001
	Adult	0			
	Subadult	0.060 ± 0.022			
	Female with cubs	0.052 ± 0.015			
	Season		2	6.72	0.034
	Winter	0			
	Spring-early summer	-0.005 ± 0.019			
	Late summer and autumn	0.031 ± 0.022			
Nursing-feeding Sig cov: p = 0.060	Intercept		1	676.30	<0.001
	Stress duration	-0.110 ± 0.017	2	40.13	<0.001
	Age		2	75.47	<0.001
	Adult	0			
	Subadult	0.031 ± 0.013			
	Female with cubs	0.074 ± 0.008			
	Season		2	5.15	0.075
	Winter	0			
	Spring-early summer	0.024 ± 0.011			
	Late summer and autumn	0.012 ± 0.013			

Table A5

Association between the covariance of different behaviours and environmental variables for brown bears in the Cantabrian Mountains (see 2. Methods for details on the models).

Dependent variable	Explanatory term	Estimate	Df	Wald statistic	Pr(Chisq)
Feeding-resting Sig cov: p = 0.003	Estimate		2	647.52	<0.001
	Trail	0.000002377973 ± 0.00002817721	1	1.03	0.309
	Road	-0.00001422876 ± 0.00001319897	1	3.47	0.062
	Population	-0.000006698541 ± 0.000009335185	1	1.05	0.305
	Viewpoint	-0.0000008867574 ± 0.000001589525	1	0.02	0.898
	Forest	0.00004822027 ± 0.00007104066	1	0.81	0.366
	Open area	0.000001439187 ± 0.000007901669	1	0	0.957
	Shrub	-0.00001260678 ± 0.00003067264	1	0.08	0.779
	Age		2	10.48	0.005
	Adult	0			
	Subadult	0.03483288 ± 0.0200567	1.7367208		
	Female with cubs	0.03773566 ± 0.01353378	2.7882576		
	Season		2	8.83	0.012
	Winter	0			

(continued on next page)

Table A5 (continued)

Dependent variable	Explanatory term	Estimate	Df	Wald statistic	Pr(Chisq)
	<i>Spring-early summer</i>	-0.05123261 ± 0.01831624			
	<i>Late summer and autumn</i>	-0.05871958 ± 0.02108495			
Feeding-walking Sig cov: p = 0.006	Estimate		2	630.69	<0.001
	Trail	0.000007639117 ± 0.00003364863	1	0.04	0.842
	Road	-0.000006213665 ± 0.00001573358	1	0.01	0.941
	Population	0.00001358491 ± 0.0000112485	1	0.06	0.800
	Viewpoint	-0.00000422118 ± 0.000001928767	1	0.97	0.324
	Forest	0.0001156135 ± 0.00008264027	1	2.45	0.117
	Open area	0.00001685135 ± 0.000009398256	1	3.3	0.069
	Shrub	0.000009025442 ± 0.00003611364	1	0.05	0.817
	Age		2	8.31	0.016
	<i>Adult</i>	0			
	<i>Subadult</i>	0.04455599 ± 0.02478221			
	<i>Female with cubs</i>	0.04419866 ± 0.01677296			
	Season		2	3.37	0.186
	<i>Winter</i>	0			
	<i>Spring-early summer</i>	-0.004757785 ± 0.02132428			
	<i>Late summer and autumn</i>	0.02419377 ± 0.024599			
Resting-walking Sig cov: p = 0.001	Estimate		2	110.43	<0.001
	Trail	0.00001359865 ± 0.00002740033	1	1.536	0.215
	Road	-0.0000252366 ± 0.00001293281	1	2.442	0.118
	Population	0.00001467776 ± 0.000009149365	1	3.083	0.079
	Viewpoint	0.000001051238 ± 0.000001559227	1	0.023	0.879
	Forest	0.00003011914 ± 0.00006923074	1	0.038	0.845
	Open area	0.00001405256 ± 0.000007740065	1	3.15	0.076
	Shrub	-0.000001377284 ± 0.00002992615	1	0.304	0.581
	Age		2	1.771	0.413
	<i>Adult</i>	0			
	<i>Subadult</i>	-0.01969695 ± 0.01970204			
	<i>Female with cubs</i>	-0.01798043 ± 0.01339476			
	Season		2	6.616	0.037
	<i>Winter</i>	0			
	<i>Spring-early summer</i>	-0.04575061 ± 0.01778761			
	<i>Late summer and autumn</i>	-0.04034224 ± 0.02031587			
Feeding-nursing Sig cov: p < 0.001	Estimate		2	639.44	<0.001
	Trail	0.0000214035 ± 0.0000194367	1	0.01	0.922
	Road	0.000008253989 ± 0.000009096992	1	0.37	0.543
	Population	-0.000005231529 ± 0.000006411933	1	5.93	0.015
	Viewpoint	0.000001871871 ± 0.000001094458	1	10.05	0.002
	Forest	-0.000006007738 ± 0.00004929487	1	0.4	0.526
	Open area	0.000000125456 ± 0.000005432183	1	0.06	0.809
	Shrub	-0.000008901726 ± 0.00002111216	1	2.81	0.094
	Age		2	51.84	< 0.001
	<i>Adult</i>	0			
	<i>Subadult</i>	0.0187464 ± 0.01376408			
	<i>Female with cubs</i>	0.06531672 ± 0.009159461			
	Season		2	5.67	0.059
	<i>Winter</i>	0			
	<i>Spring-early summer</i>	0.025342 ± 0.01249231			
	<i>Late summer and autumn</i>	0.01041436 ± 0.01449922			

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