

Bachelor Thesis

What causes the European Bison to transition from travel to rest?

*An investigation into how sex, habitat and
microclimatic conditions/alterations influence the
traveling behavior of the European Bison*

A thesis

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Naomi van den Berg

Supervised by

Prof. Ferreira dos Santos



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Bison bonasus

“There is (they say) a wild beast in Peonia, which is called Bonasus, with a maine like an horse, otherwise resembling a bull: marie, his hornes bend so inward with their tips toward his head, that they serve him in no steed at all for fight, either to offend, or defend himselfe; and therefore, all the helpe that he hath, is in his good footmanship; and otherwhiles in his flight by dunging, which hee will squirt out from behind him three acres in length. This ordure of his is so strong and hot, that it burneth them that follow after him in chase, like fire, if haply they touch it. A strange thing it is, and wonderfull.”

These were the words of Plinius Secundus in his book *Naturalis Historia*, otherwise known as *Natural History*, which is one of the largest known works that dates back to the ancient times of the Roman Empire to have survived to this day. The *Bonasus*, as Plinius describes the ‘wild beast’ in the fifteenth chapter of the eighth volume, roamed the European continent (more specifically, North Macedonia) already at the time he wrote his manuscript in 77 AD. About two millennia later, the large herbivore can be found, among other areas, roaming in the Dutch nature reserve ‘Zuid-Kennermerland’, for which the enclosed ‘Kraansvlak’ is the special area dedicated to this majestic animal. However, the presence of the *Bison bonasus*, also known as the European Bison, has not been as forthright since the time Plinius wrote about them. The Bison have actually undergone some pretty rough patches in the centuries following their documentation, including an extinction in the wild.

Indeed, the Bison has been reintroduced. And successfully that is. The large herbivores have been roaming in the vast forests of the Polish nature reserve Bialowieza before they did so in the Netherlands. There is, however, a striking difference that makes the reintroduction of the Bison into Zuid-Kennemerland very intriguing to ecologists and conservationists. In Poland, the Bison lived in areas characterized by woody vegetation such as the mighty oak, spruce and hornbeam. There, they live off of tree bark, acorns and juicy leaves while occasionally nibbling on twigs, mushrooms and grasses. The dunes that characterize the Zuid-Kennemerland area are undeniably poorer in vegetation density, but grasses, shrubs and some trees flourish in the area nonetheless. So much so even, that conservationists and managers were starting to look for measures to curb the shrub encroachment that was corrupting the area. That is how the Bison came into play; partially as a strategy to avoid complete encroachment of the dunes, and also partially to extend the ‘re-bewilderment’ project of the European Bison to the Netherlands.

Academics as well as conservationists are actively involved in this pilot-project, and rightfully so: relatively little is known about the role of the bison in the ecosystems they now occupy. This lack of knowledge is not entirely unjustified when considering the fact that the animal has been absent from the wild for over a century (!) due to a regional extinction. A breeding program with merely a few dozen individuals that remained alive in captivity saved the species and provided the *bonasus* with a prospect of re-wilding the European continent. The herd present in the Kraansvlak is one of few that lives through the winter without supplementary feeding and is thus very independent from human interventions. Finally, the *Bison bonasus* are united with the wild again. The question is: will this union endure this time around?

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Introduction

Ecosystems are continuously undergoing changes in climate, nutrient loading, physical structures and biotic exploitation (Scheffer et al., 2001). How ecosystems deal with and adapt to such environmental changes on different spatial and temporal scales are among the primary current frontiers in Ecology (Hautier et al., 2015). Understanding ecosystem response to disturbances is of vital importance in an age defined by anthropogenic activity. Anthropogenic activities can either directly or indirectly interfere with ecosystem functioning (Crutzen, 2006). As a result of human-caused disturbances of ecosystems all over the world, global biodiversity is decreasing in a rate far beyond the background extinction rate (Bellard et al., 2012). Among the vulnerable species are large wild terrestrial herbivores due to developments such as habitat fragmentation, deforestation and global warming.

Large herbivores are often vital elements in ecosystem functioning (Wieren, 1995). As primary consumers, they redistribute nutrients by consuming plant biomass and excreting manure. Apart from accelerating nutrient cycling, large herbivores also play a vital role in the food web, as they provide a food source for higher (carnivorous) trophic levels (Augustine et al., 2003). Generally, large wild herbivores have a positive influence on the overall productivity, biodiversity and function of ecosystems, and the significance of their presence should therefore not be understated (Sandom et al., 2014).

In current and projected years, temperatures are expected to rise due to global warming (IPCC, 2015). This may pose a threat to large herbivores. Most large terrestrial herbivores are mammalian, and thus produce internal heat as a product of their metabolism. Higher metabolism ultimately means higher internal heat as byproduct of transforming consumed biomass into usable energy. Because of global warming, herbivores increase their metabolic rate and subsequently adjust their physiological activity (Dillon et al., 2010). An increase in metabolic rate requires an increase in energy input. When this input cannot be met and temperatures are high, the animal will be at risk of starvation and/or overheating.

Furthermore, most large herbivores exhibit sexual dimorphism, with the males being considerably larger in body size than the females. Consequently, males have a higher metabolism than females (White, 2003). Therefore, when looking into the physiological and behavioral responses to warming temperatures, it is relevant to differentiate between the sexes (Myserud, 2000). The greater body volume for males

is attributable to their higher muscle-to-fat ratio, and hence higher metabolism. This leads us to expect that males show greater amounts of transitions from travel to rest in their traveling behavior than do the females (Nagy, 1986). If it were the case that energy output for thermoregulation is higher than energy input through food intake, we may expect large herbivores to exhibit either of three strategies: A) resort to shaded areas, B) slow down traveling rate or C) transition from traveling to rest. We may expect the latter strategy to be exhibited especially among males in the herd during the summer months. Naturally, males have higher energy input requirements, possibly causing the trade-off between thermoregulating and feeding to be of a more critical importance for males than for females - with the predicted increase in temperature in mind (Dearing et al., 2008).

The reintroduction of the European bison in 2007 into a specific section of the Dutch nature reserve Zuid-Kennemerland – a coastal region with dune habitat – is expected to trigger environmental changes. This is because biotic communities as well as physical structures of the area are affected by the reintroduction; the former since the reestablishment of the bison embodies an additional primary consumer to the existing food web, and the latter since the animal alters the surface structure simply by its weighty body mass. The European bison is now the largest herbivore grazing on Dutch lands, and the animal's reintroduction offers several interesting ecological questions, such as to what extent the bison increases heterogeneity of the area and what species benefit from this (Fuhlendorf et al., 2001 & Cromsigt et al., 2015). Also of interest is understanding and learning how the bison responds to (gradual) changes in the environment induced by the species' own allogenic engineering role in the ecosystem, as the bison create microhabitats as a result of resting and wallowing behavior (Cromsigt et al., 2015). Furthermore, it is important to understand how the bison respond to changes caused by external anthropogenic processes such as global warming. The latter will be the focus of this thesis. As a consequence of climate change, warming summers might increasingly pose a strain on the bison's innate need to travel due to reasons related to their metabolism and thermoregulation (Owen-Smith et al., 2010). Due to the recency of the bison's reintroduction into the Kraansvlak, little is known about the particular behavior of the animal as a response to ecological/ environmental change in the area. Therefore, it is relevant to extend our knowledge on the matter.

As previously explained, a common response among large herbivores to warming temperatures is exhibited in their behavior. More specifically, as temperatures increase, certain energy-costly activities (such as traveling) will be increasingly replaced by activities that require lower energy investments (such as resting). The herd studied exhibits sexual dimorphism (Pape, 2014). Previous analysis of the data collected of the herd studied has shown that at around a temperature of 24 °C, traveling behavior sharply declines, whereas resting behavior peaks (Pape, 2014).

Habitat might also serve as an important predictor for traveling behavior exhibited by the European bison. The types of habitat in the Kraansvlak consist mainly of grasslands, shrublands, and deciduous as well as coniferous forests (Cromsigt et al., 2015)¹. In open (or semi-open) areas such as grasslands and shrublands, the bison are exposed to more direct solar radiation than in the closed areas that provide shade such as forests. Solar radiation is absorbed by the dark-colored fur of the bison, causing the surface of the bison to heat up depending on the radiation intensity. An increased surface temperature obstructs the loss of internal heat, and thus has a thermoregulatory relevance.

The focus of our study is to analyze whether the constant trade-off between energy intake in the form of grazing and energy output in the form of (primarily) thermoregulation and migration, is translated into the bison's traveling behavior and habitat use. On the one hand, one may expect that the bison exhibit greater continuous travel behavior in the closed habitat types, due to lower exposure to solar radiation and thus lower temperatures. Hence, in times of higher temperatures when thermoregulation requires large energy investments, and when traveling is also compulsory (which triggers higher metabolic rates and thus higher internal heat), traveling in areas with cooler ambient temperatures may be necessary to avoid overheating.

On the other hand, one may expect that the bison exhibit greater continuous travel behavior in the open habitat types, due to the trade-off between feeding and thermoregulating. In this line of reasoning, resting would be a lot less energy costly when done in closed habitat types, due to the lower energy investments needed for thermoregulation.

¹ The nature reserve also includes other types of habitat, such as bare sand (since it is a dune area) and reeds, but these occur in smaller relative quantities.

In this thesis, the investigation focuses on whether it is the case that higher temperatures induce the bison to cease traveling, and whether the transition from travel to rest is determined by a combination of different factors, namely sex of the individual and the type of habitat. These factors are relevant in order to investigate to what extent sexual dimorphism and habitat selection could also play a role in bison behavior.

Taking all of these factors into consideration, we will aim to answer the following research question in this thesis: *how and to what extent do microclimatic alterations, sex and habitat type influence the traveling behavior of the European bison?*

The general hypothesis examined in this thesis is as follows:

Male bison, having higher metabolic rates and thus higher internal heat than females (sex), are likely to A) exhibit greater amounts of transitions to rest in the warm(ing) summer months (temperature) and/or B) resort to different habitat types for rest (habitat) as strategies to thermoregulate.

The individual, more detailed hypotheses tested are the following:

H1: Males will exhibit a higher relative frequency in transitions from travel to rest than females, because they have larger body sizes and therefore have more thermoregulatory needs.

H2: As temperature increases, the bison will exhibit greater frequencies of transitions from travel to rest (especially in the summer months).

H3: Habitat types that provide shade will enhance fewer transitions between travel and rest compared to habitats that do not provide shade, because lower exposure to solar radiation in shaded areas gives continuous traveling in shaded habitat a thermoregulatory benefit.

H4: Habitat types that provide shade will enhance more transitions between travel and rest compared to habitats that do not provide shade, because resting in shaded habitat is less energy costly due to lower energy investments needed for thermoregulation.

Traveling behavior, in this thesis, is characterized by two transition types (see fig. 2). These transition types are mutually exclusive; the bison exhibits either A) continuous traveling or B) ceased traveling in order to rest. We will aim to investigate this thesis' research question with careful and thorough inquiry using statistical analysis of the dataset collected from the studied herd of bison residing in the Kraansvlak. The answer to this question might be of importance in formulating adequate management strategies to conserve the bison's presence.

Methodology

The studied herd of bison resides in the Dutch nature reserve Zuid-Kennemerland. More specifically, there is an enclosed area for the herd within this nature reserve called the Kraansvlak², which has an area of 226 ha and is located in the province of Noord-Holland (Oquinena Valluerca, 2011). The bison were introduced to the area in 2007, and since then the herd has increased in size from a few individuals to over a dozen (Santos et al., 2014).

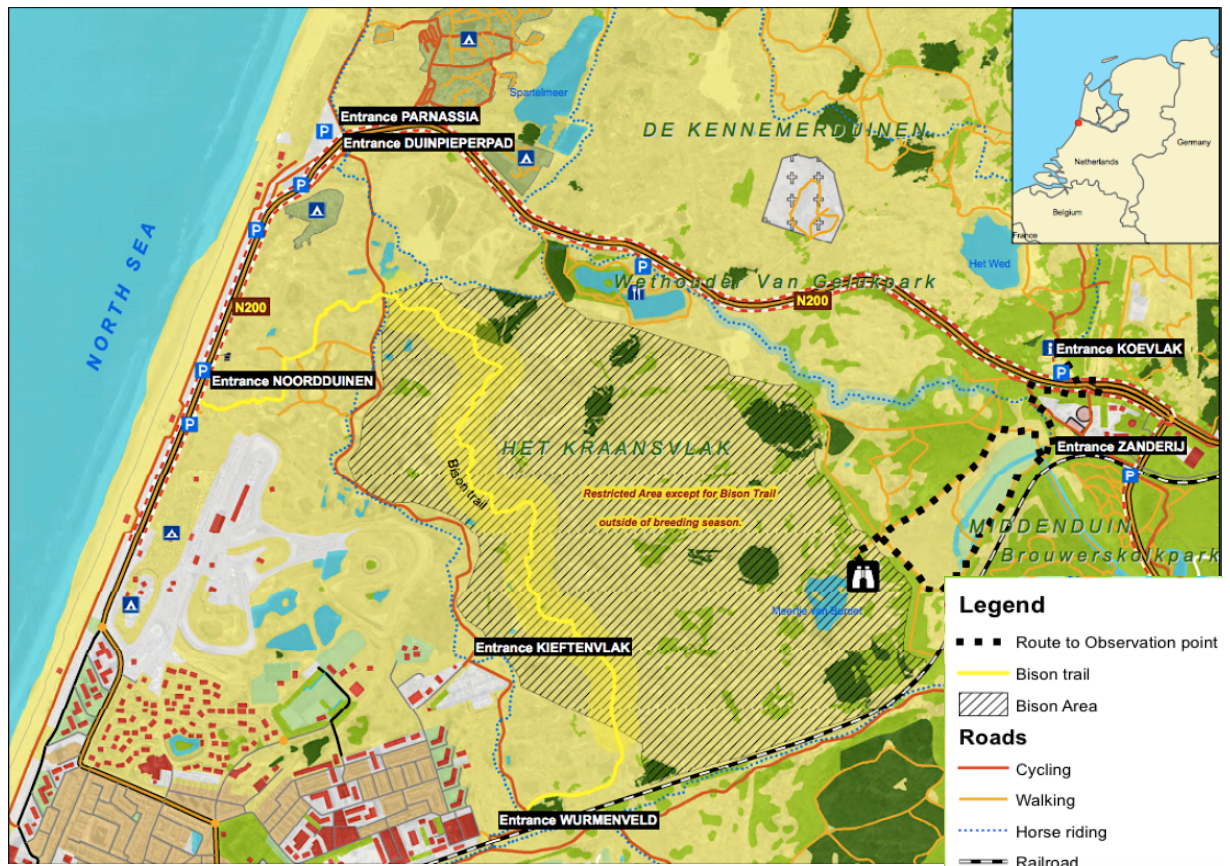


Fig 1 A map of the area. The area for the bison is indicated with diagonal lines. Source: PWN & Ark Natuurontwikkeling

As for data to test our hypotheses with, we will use a dataset collected in the years 2007 and 2009-2011 for individual bison in the herd inhabiting the Kraansvlak. The dataset contains a total of over 40.000 data points, each documented at specific time intervals ranging from 2 to 15 minutes, collected with GPS-collars. A maximum of four individuals could be collared at the same time.

² Coordinates of the Kraansvlak area: 52°23'17.03"N; 4°34'13.11"E.

At each location, there were a number of attributes being collected, namely:

- Date, time and season of documentation;
- Introduction date;
- The sex of the individual;
- A specific code that serves to identify the individual;
- Rotations and positions on X and Y-axes of the individual's head, from which type of movement and associated behavior is derived;
- Ambient temperature (ranging from -3 to 41°C);
- Habitat type, which has 9 categories (bare sand, coniferous forest, deciduous forest, dry grassland, paths, rosa, water and reeds, wet grassland and shrubland).

The dataset addressed throughout this thesis was collected by a team of academics of Utrecht University.³ Seven bison in total were tracked with a GPS collar, from which the data was collected.

The variables in the dataset that are of primary relevance for statistical analysis are the following: *Sex*, *Temp*, *Behavior*, *Habitat*. The variables *Introduction* as well as *Date* are also of interest for excluding data points collected in the first week after introduction, since variables such as behavior (and thus the traveling/resting patterns) are likely to be severely biased by the herd's acclimatization to a new environment. One may expect that the herd collectively exhibits atypical behavior as a response to elevated stress levels associated with the process of translocation and the subsequent release and reorientation in a new area (Jachowski et al., 2013). Assuming these elevated stress levels normalize after a week, all data points collected between 24-04-2007 and 30-04-2007 will not be included in the statistical analyses performed in this thesis. This means a total of 1766 data points will be excluded from further analysis and statistical testing on the basis of time since introduction. This reduces the size of the dataset from 41647 to 39881 points.

Since we are solely interested in traveling/resting types of behavior, we will remove all other data points that contain a different behavior type (these constitute feeding and wallowing) from further statistical testing. This means we further reduce the size of the dataset from 39881 to 32562 points. Since we defined traveling behavior as transitions, the data needs to be paired. The process of adequately pairing the data needs to be done in accordance with the time interval between each point. By removing a data point that is characterized by either feeding or wallowing behavior (e.g. removing the point corresponding to *feeding* from a series of consecutive points as

³ Consisting of: Maria J. Santos, Janneke van Kessel, Joris Cromsigt, Yvonne Kemp, Leo Linnartz, Esther Rodriguez Gonzalez, Chris Smit, Margje Voeten and Martin Wassen

follows: *traveling, feeding, resting*), one may create pairs eligible for targeted transitions which otherwise seemed ineligible. The points in our dataset are ordered in a chronological manner. The transitions between travel and rest have to follow each other up either *directly* within time interval x or *indirectly* in which the ‘undesired’ behavior lasts shorter than time interval x . The threshold value decided upon for this interval in which the transition has to take place is 30 minutes. This value is indeed arbitrary, but makes sense when taking into consideration the frequency of documentation of data by the GPS collars of the bison (in intervals of 2, 5 or 15 min). For example, if the behavior ‘feeding’ for a specific point between two points of the ‘desired’ behaviors is only documented to be 15 min long, the points of interest are still eligible for pairing (if meeting all other criteria, see below). Therefore, transitions that will be taken into account are *direct* or *indirect* follow-ups after travel, either by – again – travel (continuous migration) or by resting (ceased migration). Logically, in the process of pairing the data, it is of importance that transitions/pairs should always belong to one individual, and cannot consist of one data point that belongs to one individual, and one data point that belongs to another.

Since certain individuals in our dataset represent a far larger quantity of points than other individuals⁴, another additional criterion in the process of pairing the data is that each individual represents a number x of pairs. This threshold value of pairs of individuals will be 500 in order to secure equal representation and avoid bias. Four individuals in the dataset are able to meet the equal representation criterion, which would thus result in a dataset of 2000 points. In the results section, we will contrast the models derived from the dataset that *does* meet this criterion, with the dataset that *does not* meet this criterion in order to investigate the extent to which overrepresentation of certain individuals introduces bias.

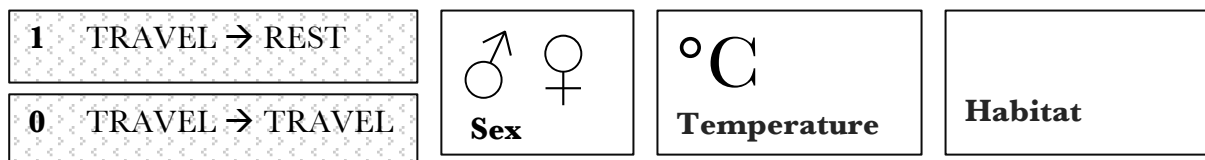


Fig 2 A conceptual diagram that shows the response variable and its predictor variables that we will address and evaluate throughout this thesis.

⁴ The distribution of collected points among individuals is noticeably disproportionate. There is an evident overrepresentation of the individuals Kaga1782RD and Kareta1781RD (see appendix A).

Of main interest in this thesis is the transition between travel to rest, which we will code as ‘1’ and henceforth refer to as a type 1 transition, where continuous travel is the alternative option, which we will code as ‘0’ and henceforth refer to as a type 0 transition. In the conceptual diagram shown in fig. 2, the dotted box indicates the response variable and its two levels. The response variable is binary in nature: one variant of this variable shows a transition from travel to rest; the other variant of this variable shows a transition from travel to travel⁵.

The original variable in the dataset on which we base our response variable is *Behavior*. This variable includes four categories: feeding, wallowing, resting and traveling. In order to create a binary variable suitable for our analysis, we transformed the variable *Behavior* into *Transition_type*. By pairing the data into transitions from travel to rest or from travel to travel (i.e. not rest to travel), we have organized the data into transitions of which the patterns we subsequently aim to explain through the three predictor variables shown in fig. 2.

Moreover, in order to analyze the potentially significant difference in traveling behavior between males and females in our data⁶, we need to examine the significance of the predictor variable *Sex* in association with *Transition_type*. The variable *Sex* was transformed into *Sex_numerical*, which has two numerical levels; 1 for females and 0 for males. We will perform a chi square test for independence in order to establish whether there is statistical evidence to support the hypothesis that sex is a significant factor in what causes the bison to transition from travel to rest.

Furthermore, it is of interest whether or not a change in temperature triggers the bison to cease traveling and start resting. Therefore, we have transformed the variable *Temp* to *Temp_diff*, which indicates the unit change in temperature from one data point to the following⁷. We expect that a positive difference between data, i.e. temperature increase, yields more type 1 transitions than a negative difference between data, i.e. temperature drop, does. This expectation is formulated in the hypothesis stating that an increase in temperature triggers the bison to transition from

⁵ There is an abundance of traveling behavior over resting behavior. We may thus expect, in general, that the transitions from travel to travel will be more numerous than the transitions from travel to rest (see appendix D).

⁶ The dataset includes far more points collected from females than from males (see appendix B). However, since the points collected from males are still so numerous ($n > 8000$) we do not have to question the reliability of the results of a model (that does not meet the equal representation criterion) assessing to what extent sex can predict traveling/resting behavior.

⁷ The data for the variable *Temp* seems to be normally distributed and so is the data for the transformed variable *Temp_diff* (see appendix C & H).

travel to rest. As for the statistical tool suitable to analyze the potentially significant (univariate) relationship between temperature and traveling behavior, a logistic regression analysis is suitable.

The variable *Habitat*, the third predictor variable we will include in the logistic regression analysis, is expressed in several different categories (wet grassland, dry grassland, etc.). However, we will need to transform this variable into having merely two (numerical) levels: shade-providing habitat, which we will code with 1, and habitat that does not provide shade (open habitat), which we will code with 0. It should be noted that there is a clear abundance of points collected from bison residing in open habitats. This abundance is in part due to the fact that the Kraansvlak is composed of dune lands, in which the majority of the habitats are open and not closed (see appendix E).

Of interest is whether the bison exert intentional/purposeful habitat selection between shaded and not shaded areas. The coniferous forest and deciduous forest habitat types were transformed to 1 (providing shade) in the *Habitat_shade* variable. Although both forest types have a different degree of canopy density, and thus a different degree of shade-provision, we will nonetheless sort them in the same category. The remaining habitat types (dry grassland, rosa, shrubland, water and reeds, wet grasslands and paths) were transformed to 0. For the univariate analysis, a chi square test for independence is the appropriate statistical tool to examine whether the association between *Habitat_shade* and *Transition_type* is significant. Consequently, a logistic regression may establish the direction of this association, which is decisive in differentiating between the hypotheses of *hIII* & *hIV*.

Besides the univariate models of each predictor, it is of interest to formulate a multivariate model including all predictor variables as well as their interaction terms. In order to attain a full model including all three predictor variables as well as their interaction terms, we will perform a multiple regression analysis.

Including a full model with all three predictor variables and their interaction terms will thus provide us with the closest approximation of what (combination of factors) causes the bison to transition from travel to rest, and can only then have the potential to be of use for formulating adequate management strategies or valid predictions.

Results

After removing the irrelevant behaviors, as well as pairing the data for each individual, 26248 points for females and 6314 points for males remain present in our dataset.

The chi-square test confirms that the relation between *Sex* and *Transition_type* is not significant, $\chi^2(1, N=24541) = 1.984, p = 0.159$. We thus fail to reject the H_0 . The relationship between sex and traveling behavior is independent; hence sex is not a significant predictor for the transitions between travel and rest.

Employment of the critical value of 500 transitions per individual (equally divided over all seasons recorded in order to secure equal representation of seasons as well) yields a model in which the four individuals able to meet this criterion (Kaga1782RD, Katarina1781RD, Kramian1782RD and Kras1781RD) are represented equally (each of the individuals representing 25% of the transition pairs), and the variable *Sex* is represented equally (50% of the pairs belong to either sex)⁸. The chi square test performed on this dataset provides us with an even stronger statistical confirmation that the association between the variables *Sex_numerical* and *Transition_type* is not significant, $\chi^2(1, N=2000) = 0.471, p = 0.493$.

Following our expectations, testing *hII-hIV* with the dataset including all individuals yields significant results. Both *Temp_diff* ($p = 0.000$) and *Habitat_shade* ($p = 0.000$) are statistically significant predictors for the response variable. The individual regression equations are as follows: $\ln(\text{ODDS}) = -1,810 + 0,180\text{Temp_diff}$ and $\ln(\text{ODDS}) = -1,746 - 0,222\text{Habitat_shade}$ respectively.

A univariate logistic regression yields the following results for the interaction term *Habitat_shade*Temp_diff*: $\chi^2 = 128.358, df = 1, 95\% \text{ CI } [0.943, 1.135], p = 0.475$. We may thus conclude that this interaction term is not statistically significant in predicting the transition behavior of the bison.

⁸ By setting the critical level of 500 pairs per individual, the following individuals were excluded from further analysis due to not meeting this number: Kareta1781RD, Lelystad11782RD and Lelystad21784RD. Per individual, the 500 pairs were (for as far possible) equally divided over the number of seasons recorded for that individual to ensure equal representation of the seasons as well. This will strengthen the validity of tests concerning the relationship between temperature and traveling behavior. However, we should note that perfect equality in representation of seasons is not possible, due to the fact that the data points for each individual were collected from only two or three out of four seasons.

Interestingly, performing a univariate logistic regression with the interaction term *Sex_numerical*Temp_diff* yields the following results: $\chi^2 = 106.717$, $df = 1$, 95% CI [0.786, 0.967], $p = 0.010$. Thus, these results imply that this interaction term is a statistically significant predictor variable.

The full model composed of all three predictor variables and their interaction terms is presented in table 1. Intriguingly, there are some crucial differences in results comparing the dataset including all individuals with the dataset that is limited in magnitude by the equal representation criterion.

Table 1
Logistic Regression Analysis for Variables Predicting Transition Type by Temperature Difference, Presence/Absence of Shade and Sex. All individuals (n = 24369) & Equal representation (n=1995).

Predictor	<i>All individuals (dataset 1)</i>			<i>Equal representation (dataset 2)</i>		
	<i>B</i>	<i>SE B</i>	<i>e^B</i>	<i>B</i>	<i>SE B</i>	<i>e^B</i>
Sex_numerical	0,047	0,053	1,049	-0,078	0,142	0,93
Habitat_shade	-0,238***	0,048	0,788	0,131	0,207	1,14
Temp_diff	0,210***	0,022	1,233	0,130**	0,079	1,14
Sex_numerical*Habitat_shade	0,052	0,120	1,053	0,021	0,302	1,02
Habitat_shade*Temp_diff	-0,035	0,047	0,966	0,051	0,142	1,05
Temp_diff*Sex_numerical	-0,143**	0,053	0,867	-0,074	0,118	0,93
χ^2	136,991			5,968		
<i>df</i>	6			6		
% Transition type 1 (travel to rest)	85,8			84,9		

Note: e^B = exponentiated *B*. The left column ‘all individuals’ represents the results from the logistic regression performed on the dataset that does *not* meet the equal representation criterion; the right column ‘equal representation,’ however, does. See appendix I & J for SPSS output.

* $p < ,05$. ** $p < ,01$. *** $p < ,001$.

The distinct differences between the two datasets demonstrated in the full model may lead us to believe that the equal representation criterion has a large influence on the eventual outcome of the analyses. Evidently, the two dataset vary a lot and this may be due to the fact that the first has a clear domination by Kaga1781RD and

Katarina1782RD, whereas the latter is not dominated by these two individuals. Hence, a part of the significant outcomes gained in the first analysis (performed on the dataset including all individuals) may be attributable to the significance provided by these individuals alone, overwhelming the statistical analysis and overshadowing the contribution of ‘minor’ individuals present. The second dataset, however, guarantees against dominance of certain individuals, as it meets the equal representation criterion of 500 transition pairs per individual, also equally distributed over the seasons registered per individual. The only statistically significant outcome is that of the predictor *Temp_diff*, with $p < 0.01$. The strength of this statistical significance, however, is slightly weaker compared to the first dataset ($p < 0.001$). In the second dataset, transitions were more equally distributed among seasons as well, including a larger proportion of transitions in the winter months compared to the first dataset.

Another interesting feature about the results of the full model is that there is a very strong significance for the predictor *Habitat_shade* in the first dataset, whereas that is not the case in the second dataset. The coefficient for *Habitat_shade* in the first dataset is negative, from which we may conclude that the significance of this predictor lies in the statistically justifiable preference exhibited by the bison to transition to rest in open habitats. This outcome confirms the alternative hypothesis of *hIII*. However, it seems that this statistical significance is again attributable to the dominant presence of Kaga1781RD and Katarina1782RD. When equal representation is secured, the significance of *Habitat_shade* as a predictor disappears, as is shown in the results for the second dataset.

Additionally, using the dataset that meets the equal representation criterion, we may more closely examine the precise differences between the sexes when it comes to the bison’s use of habitats (see appendix *K*). Males use the habitat type coniferous forest considerably less than females (n= 30 and n=62 respectively). However, the contrary is the case for shrublands; males roam this habitat type more often than females (n=198 and n=150 respectively). This difference in habitat use between the sexes turns out to be statistically significant. For the coniferous forest habitat type, the results of a logistic regression analysis (taking *Sex_numerical* as the binary variable) are as follows: $\chi^2 = 45.910$, $df = 1$, 95% CI [0.003, 0.260], $p = 0.002$. As for shrubland: $\chi^2 = 45.910$, $df = 1$, 95% CI [0.157, 0.896], $p=0.027$.

After examining the results of the full model including all individuals and all three predictor variables as well as their interaction terms, we will now more closely examine the two major individuals present in the dataset: namely Kaga1782RD and

Katarina1781RD. These two individuals make up over 75% of all points collected. Whether the results for these individuals seem to be analogous or rather dissimilar may aid in understanding the degree of variance present in the full model (especially when it turns out these individuals show very disparate results)⁹.

Table 2

Cross tabulation depicting the amount and type of transitions per individual

	<i>Individual</i>						
	<i>Kaga178 2RD</i>	<i>Kareta178 1RD</i>	<i>Katarina 1781RD</i>	<i>Kramian 1782RD</i>	<i>Kras178 1RD</i>	<i>Lelystad1 178RD</i>	<i>Lelystad21 784RD</i>
Transition							
type 0	9939	112	7316	1794	1518	259	137
type 1	1663	24	1135	298	228	78	40
Total	11602	136	8451	2092	1746	337	177

Kaga1782RD

For the individual Kaga1782RD, about 10% of the transitions take place from travel to rest (see appendix F). The majority of the transitions (about 66%) take place from travel to travel. The missing points, making up about 23%, indicate irrelevant sequences, which are either A) resting followed by resting or B) resting followed by traveling.

The results of a univariate logistic regression testing the association between *Temp_diff* and *Transition_type* are as follows: $\chi^2 = 50.035$, $df = 1$, 95% CI [1.151, 1.284], $p = 0.000$. The odds-ratio of 1,216 indicates that there is indeed a positive relationship present between temperature difference and the odds of a type 1 transition. The resulting regression equation is: $\ln(\text{ODDS}) = -1,795 + 0,195\text{Temp_diff}$.

Furthermore, the chi-square test confirms that the relation between *Habitat_shade* and *Transition_type* is significant, $\chi^2(1, N=11521) = 8.633$, $p = 0.000$. The H_0 stating the relationship between habitat and traveling behavior is independent may be rejected. However, of interest is to establish the direction of this relationship. Therefore, we performed a logistic regression, for which the results are as follows: $\chi^2 = 8.788$, $df = 1$, 95% CI [0.746, 0.943], $p = 0.003$. The resulting regression equation is: $\ln(\text{ODDS}) = -1,732 - 0,176\text{Habitat_shade}$. Since $p < \alpha$, we can state that the variable

⁹ That applies for tests performed with the dataset including all individuals *without* the equal representation criterion

Habitat_shade is a statistically significant predictor for the variable *Transition_type*. Since the odds-ratio is smaller than 1 (namely 0.839), we may establish that the relationship between the predictor and the response variable is negative in nature: when the predictor variable increases with one unit between points (so from no-shade to shade providing habitat), the odds of a transition type 1 decrease. Hence, it appears that open habitats (coded with 0 in the transformed variable) trigger a relatively greater frequency of type 1 transitions than shade-providing habitats do. Kaga1782RD seems to prefer resting in open habitats to resting in the forests.

Katarina1781RD

For the individual Kaga1782RD, about 10% of the transitions take place from travel to rest (see appendix G). The majority of the transitions (about 67%) take place from travel to travel. The missing points make up about 23%. One may note the strong similarity with Kaga1782RD in the distribution of transition types.

The results of the logistic regression test assessing to what extent *Temp_diff* acts as a predictor for *Transition_type* are as follows: $\chi^2 = 53.743$, $df = 1$, 95% CI [1.166, 1.306], $p = 0.000$. The odds-ratio of 1,216 indicates that there is indeed a positive relationship present between the predictor variable and the odds of a type 1 transition. The resulting regression equation is: $\ln(\text{ODDS}) = -1,872 + 0,210\text{Temp_diff}$. We may thus conclude that also for Katarina1781RD, temperature is a statistically significant predictor for traveling behavior: a unit increase in temperature increases the odds of a type 1 transition.

The results of a chi square test for independence indicate that also for Katarina1781RD, the degree of shade provided per habitat type has a statistically significant association with traveling behavior: $\chi^2(1, N=10954) = 17.171$, $p = 0.000$. The results of a univariate logistic regression are as follows: $\chi^2 = 17.979$, $df = 1$, 95% CI [0.608, 0.837], $p = 0.000$. The resulting regression equation is: $\ln(\text{ODDS}) = -1,786 - 0,338\text{Habitat_shade}$. As $p < \alpha$, we can state that the variable *Habitat_shade* is a statistically significant predictor for the variable *Transition_type*. With an odds-ratio of 0,713, we may establish that also for Katarina1781RD open habitats trigger a relatively greater frequency of type 1 transitions than shade-providing habitats do. Therefore we may conclude that Katarina1781RD too seems to have a preference for resting in open habitats.

Discussion

In general, our results are consistent with the predictions based on the hypothesis that an increase in temperature (i.e. greater exposure to solar radiation) triggers a transition from travel to rest, most likely for thermoregulatory purposes. When temperature rises, the odds of the bison transitioning from traveling to resting become greater. These results are consistent with other studies examining thermoregulatory responses by ruminants, which also state that daily and seasonal traveling behaviors are often a result, at least in part, of the intensity of solar radiation (Norris & Kunz, 2012). Indeed, especially in summer months, temperature may pose a constraint on the overall energy budget of the bison, as investments in thermoregulation are necessary (Aublet et al., 2009). Since our dataset collected from the bison herd in the Kraansvlak did not include specifics on physiological processes of the bison, we were not able to test the physiological responses to increasing temperatures. However, we aimed to study the decisive forces behind the traveling behavior of the bison, and found statistical evidence from the herd studied in the Kraansvlak that thermoregulation seems to be an important driver in the bison's traveling behavior (following the underlying assumption that the intensity of radiation is a decisive factor in whether or not the bison decides to cease traveling and starts resting).

We picked three predictor variables to investigate; sex, temperature and habitat. It turned out that the latter two were significant, with habitat being transformed into being defined by the presence/absence of shade. Sex, however, turned out to be insignificant in relation to traveling behavior. However, we were limited in testing the precise statistical presence of sexual dimorphism in the dataset, since we restricted our analysis to examining the capacity of the three mentioned variables to predict traveling behavior. Also, the response variable, traveling behavior, can be expressed in various ways, not exclusively in the two transition types we chose to define traveling behavior with (travel to travel & travel to rest).

Another clear limitation in the dataset, as the full model shows, is the unequal representation of the individuals. Most data belongs to the two prevalent individuals Kaga1782RD and Katarina1781RD – both are females, both have no data in the winter months. This disproportionate representation might interfere with the validity of the test results.

Applying the equal representation criterion fixes this problem. However, consequently, the size of the dataset reduces considerably, causing the statistical power and the reliability of the statistical tests performed on this dataset to become lower.

Unequal representation was also evident in the distribution of data points collected over the seasons. For the purpose of our research question, the overrepresentation of data points in the summer months was not necessarily detrimental to the validity of our analysis, since the relevance of thermoregulation in traveling behavior is predominantly noticeable in the summer months. However, the overall reliability of the dataset could be improved by A) collecting a fairly equal amount of data per individual studied and B) collecting data over the complete annual seasonal (and thus temperature) continuum.

In this thesis, we have studied the control of ambient temperature on the bison's traveling behavior, which turned out to be significant with our without meeting the equal representation criterion. However, the strength of the significance was not equal in both instances. The dataset meeting the equal representation criterion contains a larger proportion of data collected in the winter. This may have led to the somewhat reduced strength in significance for the predictor *Temp_diff* (from $p < 0.001$ to $p < 0.01$). After all, winter months are colder; leading to fewer type 1 transitions that correlate with an increase in temperature, as there is still no thermoregulatory need to rest when the temperature rises, for example, from -5 °C to -3°C. The thermoregulatory necessity to rest is primarily present in the warmer months, which is statistically represented in our full model.

Additionally, there was a limitation in the way ambient temperature was measured for the bison. Due to the fact that the GPS collar was located near the surface of the bison, the ambient temperature it measured may have been a mix of internal and external temperature. However, this limitation does not seem to have disturbed the data to an evident extent, since the data for temperature still showed to be normally distributed.

The disappearance of the significance in *Habitat_shade* shown in the full model is rather peculiar, since the dataset containing all individuals exhibited strong significance for this variable. This difference in results may also be because the dataset meeting equal representation includes a larger proportion of transitions collected in the winter months. In the winter, the degree of shade as a means to mitigate exposure to radiation is not yet relevant, as only in the summer months the difference in shade provision starts to have a thermoregulatory purpose. After all,

exposure to radiation is overall lower in winter months. Therefore, in the winter months, the decision by the bison to rest in or out of a shaded area is more or less random rather than purposeful. It appears that random variation present in the relationship between habitat type and transition type increased to such an extent (when comparing with the complete dataset), that the variable *Habitat_shade* no longer constitutes as a significant predictor in the second dataset (that meets equal representation).

Interestingly, when we tested with the original habitat variable, which has nine categories instead of two¹⁰, the bison seems to exhibit statistically significant sex-specific behavior. This may be due to the sexual size dimorphism present in the bison. In line with the body-size hypothesis¹¹, we may explain the significance of the interaction between sex and habitat type by the fact that males aim to increase their dry matter intake rates (Myserud, 2000). When looking at per unit food efficiency (energy stored in biomass versus energy investment necessary to consume), shrubs provide a resourceful dry matter food source (Ginnett & Demment, 1997). Coniferous forests, however, provide a far less efficient food source. Coniferous forests presumably provide more protection¹², so we may prudently hypothesize that females – especially when with young – seek security in the more dense vegetation provided by forests compared to shrublands.

However, another factor that is of great importance when aiming to explain thermoregulatory responses exhibited by large ruminants is relative humidity (Luz et al., 2014). The greater the relative humidity, the greater the potential pressure that temperature can exercise on thermoregulatory and metabolic processes¹³. Therefore, to fully attribute the significance of temperature as a predictor predicting when the

¹⁰ *Habitat_shade*, as we have examined previously, turns out *not* to be a significant predictor for traveling behavior in the dataset meeting equal representation. This variable was transformed into a dichotomous one, sorting the habitat types into either shade (1) or non-shade (0) providing categories in order to examine the thermoregulatory relevance of the degree of shade. When combined with the variable *Sex_numerical*, it also became clear that *Habitat_shade* did not show sex-specific significance.

¹¹ This hypothesis predicts that males exhibit certain behaviors that fasten their rate of dry matter intake relative to females.

¹² Which spans all over the year, due to the fact that this type of forests is composed of predominantly evergreen trees.

¹³ The higher the relative humidity, the higher the ambient water vapor pressure, causing evaporation to be hampered → therefore, heat loss is hampered.

bison transitions from travel to rest, inclusion of an interaction term with a variable concerning relative humidity could complement the cogency of this research.

Conclusion

In this thesis, we aimed to answer the following question: *how and to what extent do microclimatic alterations, sex and habitat type influence the traveling behavior of the European bison?* In order to answer this question, we performed statistical analyses based on a dataset collected from the herd of bison that was reintroduced to the Dutch dune lands of the Kraansvlak, located in nature reserve Zuid-Kennemerland.

In this thesis, the bison's traveling behavior is defined as being either A) continuous traveling, or B) ceased traveling followed by resting; the latter being the transition type of interest. As it was the focus of this thesis to find out what causes the bison to stop traveling in order to rest, the data was paired into transitions belonging to either type, resulting in the response variable that would be subjected to statistical testing (*Transition_type*). The three predictor variables that were examined in this thesis were: sex, temperature and habitat type. The first being relevant in order to examine the importance of sexual dimorphism in traveling behavior, the latter two being relevant in order to examine the relevance of temperature/exposure to solar radiation in leading the bison to stop traveling and start resting.

The results of our statistical analyses are in line with the hypothesis that large herbivores, including the European bison, exhibit behavior aimed to thermoregulate. In the case of the bison residing in the Kraansvlak, it seems that higher temperatures do indeed induce these animals to stop traveling in order to rest as a means to control thermoregulatory processes.

The relevance of this research lies in the projected increase in temperatures over the coming years. Global warming, apart from having numerous interspecific impacts, also has intraspecific impacts that may eventually pose a threat to the European bison. Warming in the winter months may be beneficial for the bison, as this would mean an increase of biotic productivity in the area. However, warming in the summer months will force the bison to deal with an increasing limit posed by the requirement to thermoregulate. As our results indicate, this need to thermoregulate is exhibited in traveling behavior, leading the bison to more frequently transition from travel to rest. It might thus be the case that, at a certain point, the rise in temperature and the subsequent increase in transitions from travel to rest interfere with population-scale processes such as overall herd migration and mating.

The European bison proves to be an important contributor to the increase of heterogeneity in the area. This increase in heterogeneity facilitates the settlement and maintenance of other species, which consequently increases the biodiversity of the area. Therefore, conserving the bison has ecosystem-scale relevance. Hence, further research in the bison's response to warming temperatures may aid in formulating conservation strategies that help the bison – when necessary – adequately adjust to warmer temperatures in the summer. In general, further research in the matter may aid in reaching a more conclusive overarching understanding of thermoregulatory behavior exhibited by large herbivores in an age defined by global warming.

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Appendix

Table A

Frequency distribution table belonging to fig 2 displaying the variable 'Individual' prior to pairing the data.

		Individual			
		Frequency	Percent	Valid Percent	Cumulative Percent
Valid	Kaga1782RD	18431	46,2	46,2	46,2
	Kareta1781RD	181	,5	,5	46,7
	Katarina1781RD	13140	32,9	32,9	79,6
	Kramian1782RD	3401	8,5	8,5	88,1
	Kras1781RD	3583	9,0	9,0	97,1
	Lelystad11782RD	679	1,7	1,7	98,8
	Lelystad21784RD	466	1,2	1,2	100,0
	Total	39881	100,0	100,0	

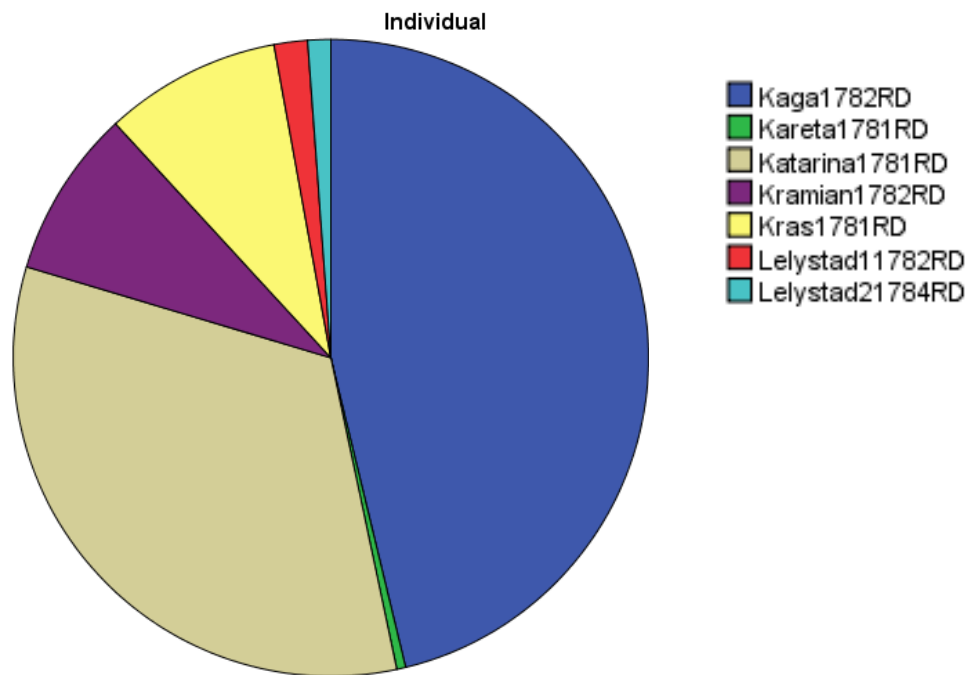


Fig A Pie chart displaying the distribution of data for the variable 'Individual' prior to pairing the data (i.e. prior to removal of 'undesired' behaviors from dataset).

Table B

Frequency distribution table belonging to fig 3 displaying the variable 'Sex' prior to pairing the data.

		Sex			
		Frequency	Percent	Valid Percent	Cumulative Percent
Valid	F	31752	79,6	79,6	79,6
	M	8129	20,4	20,4	100,0
Total		39881	100,0	100,0	

Table C

Statistics table belonging to fig 4 displaying the variable 'Temperature' prior to pairing the data.

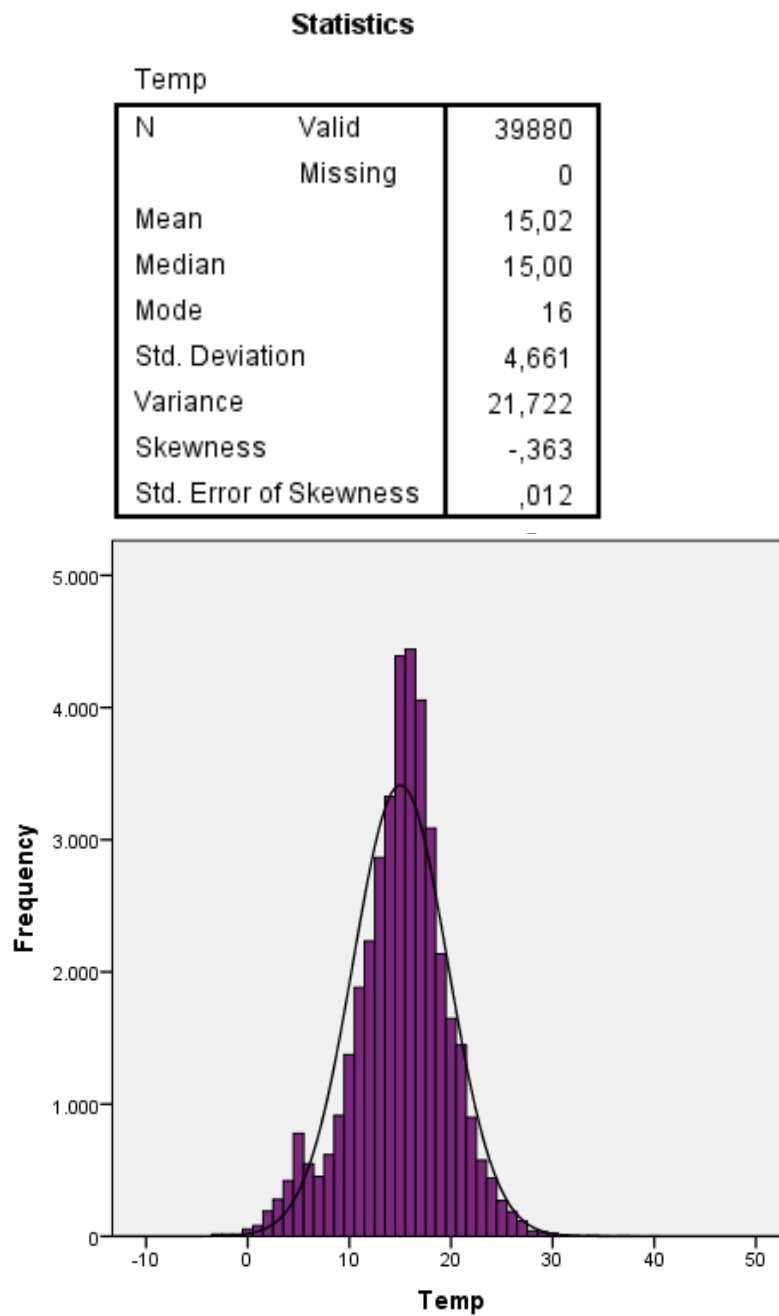


Fig C Histogram displaying the distribution of data for the variable 'Temperature'.

Table D

Frequency distribution table belonging to fig 5 displaying the variable 'Behavior' prior to pairing the data.

		Behavior			
		Frequency	Percent	Valid Percent	Cumulative Percent
Valid		4	,0	,0	,0
	feeding	6858	17,2	17,2	17,2
	Feeding	196	,5	,5	17,7
	Resting	8019	20,1	20,1	37,8
	Traveling	24592	61,7	61,7	99,5
	Wallowing	211	,5	,5	100,0
	Total	39880	100,0	100,0	

Table E

Frequency distribution table belonging to fig 6 displaying the transformed variable 'Habitat_Shade' prior to pairing the data.

		Habitat_shade			
		Frequency	Percent	Valid Percent	Cumulative Percent
Valid	no shade	30829	74,0	77,7	77,7
	shade	8858	21,3	22,3	100,0
	Total	39687	95,3	100,0	
Missing	System	1959	4,7		
Total		41646	100,0		

Table F

Frequency distribution table displaying the transformed variable 'Transition_Type' after pairing the data for Kaga1782RD.

		Transition_type			
		Frequency	Percent	Valid Percent	Cumulative Percent
Valid	0	9939	65,7	85,7	85,7
	1	1663	11,0	14,3	100,0
	Total	11602	76,7	100,0	
Missing	System	3524	23,3		
Total		15126	100,0		

Table G

Frequency distribution table displaying the transformed variable 'Transition_Type' after pairing the data for Katarina1781RD.

		Transition_type			
		Frequency	Percent	Valid Percent	Cumulative Percent
Valid	travel to travel	7316	66,8	86,6	86,6
	travel to rest	1135	10,4	13,4	100,0
	Total	8451	77,1	100,0	
Missing	System	2503	22,9		
Total		10954	100,0		

Table H

Cross tabulation displaying the distribution of points between 'Habitat_shade' and 'Temp_diff'.

		Habitat_shade		Total
		no shade	shade	
Temp_diff	-10.0	0	2	2
	-9.0	2	0	2
	-8.0	3	0	3
	-7.0	6	2	8
	-6.0	20	3	23
	-5.0	35	9	44
	-4.0	87	10	97
	-3.0	244	42	286
	-2.0	739	137	876
	-1.0	4588	1166	5754
	.0	13554	4394	17948
	1.0	4607	1426	6033
	2.0	741	178	919
	3.0	204	48	252
	4.0	59	15	74
	5.0	27	7	34
	6.0	8	1	9
	7.0	6	1	7
	9.0	2	0	2
10.0	1	0	1	
Total		24933	7441	32374

Table I

Multiple regression model displaying all predictor variables, as well as the interaction terms, for the dataset with all individuals included.

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)	95% C.I. for EXP(B)	
								Lower	Upper
Step 1 ^a	Sex_numerical(1)	,047	,053	,804	1	,370	1,049	,945	1,163
	Temp_diff	,210	,022	93,717	1	,000	1,233	1,182	1,287
	Habitat_shade	-,238	,048	24,238	1	,000	,788	,717	,866
	Sex_numerical(1) by Temp_diff	-,143	,053	7,245	1	,007	,867	,782	,962
	Temp_diff by Habitat_shade	-,035	,047	,537	1	,464	,966	,880	1,060
	Sex_numerical(1) by Habitat_shade	,052	,120	,184	1	,668	1,053	,832	1,332
	Constant	-1,758	,023	5618,824	1	,000	,172		

a. Variable(s) entered on step 1: Sex_numerical, Temp_diff, Habitat_shade, Sex_numerical * Temp_diff, Temp_diff * Habitat_shade, Sex_numerical * Habitat_shade.

Table J

Multiple regression model displaying all predictor variables, as well as the interaction terms, for the dataset that meets the equal representation criterion.

Variables in the Equation

		B	S.E.	Wald	df	Sig.	Exp(B)	95% C.I. for EXP(B)	
								Lower	Upper
Step 1 ^a	Sex_numerical(1)	-,078	,142	,305	1	,581	,925	,700	1,222
	Temp_diff	,130	,079	2,725	1	,099	1,139	,976	1,329
	Habitat_shade	,131	,207	,402	1	,526	1,140	,760	1,710
	Sex_numerical(1) by Temp_diff	-,074	,118	,395	1	,530	,929	,737	1,170
	Temp_diff by Habitat_shade	,051	,142	,130	1	,719	1,053	,796	1,391
	Sex_numerical(1) by Habitat_shade	,021	,302	,005	1	,946	1,021	,564	1,847
	Constant	-1,719	,100	295,633	1	,000	,179		

a. Variable(s) entered on step 1: Sex_numerical, Temp_diff, Habitat_shade, Sex_numerical * Temp_diff, Temp_diff * Habitat_shade, Sex_numerical * Habitat_shade.

Table K

Crosstabulation table displaying the interaction between sex and habitat type, in the dataset that meets the equal representation criterion.

Sex * HABITAT Crosstabulation

Count		HABITAT									Total	
		Bare sand	Coniferous forest	Deciduous forest	Dry grassland	Paths	Rosa	Shrubland	Water and reeds	Wet grassland		
Sex	F	0	1	62	157	496	0	70	150	41	23	1000
	M	5	12	30	162	485	1	65	198	34	8	1000
Total		5	13	92	319	981	1	135	348	75	31	2000