



Barbastella barbastellus hibernation

24 product (correlation result) T and v, while a decrease in the size of the group occurs with
25 an increase in the products T and Rh, v and Rh as well as T, v and Rh.

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32 **Key words:** chiroptera; hibernation; thermoregulation; microclimate selection; western
33 barbastelle; quantile regression; clusters; thermal comfort; heat loss; roosting; grouping

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38 **1. Introduction**

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40 The phenomenon of grouping among bats is one of the important physiological
41 and ecological behaviours (Boyles et al. 2008). Although clustering aims mainly at
42 minimizing heat loss into the environment, it can also serve as protection against
43 predators or to maintain emotional and family ties, hierarchy in the herd, etc.

44 The hibernation process is precisely regulated and controlled (Thomas, 1995,
45 Janicki et al., 2006). The parameters characterizing metabolic changes in the state of
46 energy equilibrium during hibernation depend on constant factors (species, size, weight,



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47 gender, age of the individual) and variables (values of physical parameters of the
48 environment).

49 The process is characterized by a drastic reduction in body temperature and other
50 physiological functions, which can reduce energy consumption by up to 95% compared to
51 the cost of staying active during winter (Geiser, 2004). This state can last from several
52 hours to several months (Hoffman, 1964; Nelson, 1980; Lyman et al., 1982; Wang, 1987;
53 French, 1988; Storey and Storey, 1990; Geiser and Ruf, 1995). In particular, the bats can
54 decrease their body temperature almost to the ambient one (McNab, 1982) or in a short
55 time increase it significantly above this value (even up to 40°C at the air temperature of
56 only a few degrees) (Davydow, 2004).

57 It is widely known that in order to reduce energy consumption during hibernation,
58 in addition to the euthermic process, animals also use various behaviours, e.g. they form
59 dense clusters (aggregations). As it was noted by Ransome (1990), social
60 thermoregulation is of great importance during hibernation. The grouping of individuals
61 during wintering is variable both within the species and between species (Kłys, 2013).
62 Some bat species winter separately, some form small, "rare" clusters, while others gather
63 in dense groups (Смирнов et al. 1999; Томиленко, 2002; Kłys, 2013), numbering up to
64 several thousands of individuals (Betke et al., 2008). Dissimilar aggregation tendencies
65 are observed within the species also in the same winter accommodation. During winter,
66 bats may move and change their roosting place, which sometimes leads to change in the
67 size and composition of grouping in the hibernaculum (Орлова et al., 1983; Томиленко,
68 2002).

69 The study of bat hibernation is often limited to descriptive field observations (e.g.
70 when and where mammals have wintered) or physiological research in the laboratory (e.g.



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71 study of metabolism and endocrine system functions of animals), without the
72 environmental context. Initial studies assess the changes in the number of individuals
73 depending on the microclimate of the caves. Most of them concern the bat's
74 thermopreferendum (Gaisler, 1970; Baueroва and Zima, 1988; Boyles et al., 2019).
75 Currently, the description of the hibernation process is based on the measurements of
76 temperature (T) as the only parameter of the roost site microclimates (Harmata, 1969;
77 Boyles et al., 2019), and occasionally temperature and humidity (Kunz, 1982. Nagel,
78 Nagel, 1991; Visnovska et al., 2006; Boyles et al., 2008; Boratyński et al., 2012). Few
79 authors take into account the temperature, humidity, air velocity and thermal conductivity
80 coefficient of the substrate (λ) in the search for optimal values defining the so-called
81 thermal comfort of selected species (Kłys, 2004; Kłys and Wołoszyn, 2005; Kłys, 2008;
82 Kłys, 2013) Physiologists often define the conditions that minimize energy expenditure as
83 "optimal" (Day and Tomasi, 2014), the research and analysis of the hibernation process
84 should not be based on the determination of these conditions, but on predicting of bat
85 behaviour (Humphries et al., 2003; Boyles et al., 2019).

86 The authors chose for the study the western barbastelle *Barbastella barbastellus*
87 (Schreber, 1774) species which uses all available hibernation strategies (Kłys, 2013), both
88 individually and in clusters, sometimes up to several hundred individuals. The changes in
89 the roost site climate (Kłys and Wołoszyn, 2005) were analyzed through the changes in
90 the size of the roosting place parameters (temperature T and relative humidity Rh) and air
91 flow velocity v in the context of their influence on the formation of aggregation of this
92 species.

93 The aim of the study was the evaluation of the air temperature, its relative
94 humidity and air flow speed influence on bat aggregation during their winter hibernation.



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95 For this purpose appropriate model describing an influence of the air physical parameters
 96 on bats' grouping was constructed, analysis of the model would provide an outline of the
 97 relationship between grouping and the determined air parameters, and allow to find
 98 explanation of bats' behaviour.

99 2. Methods

100

101 The research was carried out in the underground systems of Poland: Forty Nyskie
 102 (Generalna ... 2014), Fortified part of Międzyrzecze (Nietoperek ... 2021) and Mopkow
 103 Tunel (Mopkow ... 2017). The data of the roost site climate was collected between the
 104 years 2002 and 2007 on the basis of the permits of the Provincial Nature Conservators
 105 and the Ministry of the Environment (DOPog-4201-04A-2/03 / al .; DOPog-4201-04A-
 106 6/04 / al .; DLOPiK-op / Ozgi- 4200 / IV.D-16/6568/06 / aj.) The most important criteria
 107 for selecting research sites were the large number of wintering specimens of the selected
 108 species.

109 Data was collected during the peak of hibernation (December - February). Due to
 110 the fact that the hibernating animals were not awakened, neither gender nor age was
 111 determined, in the places where bats hibernate, data was collected with use of measuring
 112 devices from SENSOTRON (Kłys 2013). Hibernation strategies were simplified in this
 113 work in relation, in order to illustrate the essence of the problem, what is more wintering
 114 was distinguished: individual and in groups (social) (Fig. 1, Fig. 2).

115 The influence of the air temperature (T), relative humidity (Rh) and flow speed (v) on
 116 bats' group formation was studied. Using explanatory variables T , Rh and v the bats'
 117 count n in the group was modelled. In calculation total number of 180 observations was
 118 used.



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3. Statistical methods

The aim of the statistical methods application was the construction of a model describing an influence of the air physical parameters on bats' grouping.

At the starting point of the analysis, the were studied the relationships between explanatory variables T , Rh and v . For this purpose the Principal Component Analysis (PCA) was used (Jolliffe 2002; Jackson 1991). Because the explanatory variables come from different units, before PCA they were centred with the mean column and scaled with the standard deviation.

Due to relatively low number of bats' clusters, the quantile regression (QR) model was used (Koenker et al., 2018; Davino et al., 2014) for the cluster size modelling. In quantile regression the conditional quantile τ of the response variable, for example median, was estimated.

QR model is an extension of the ordinary linear regression that is used when the conditions of linear regression are not met.

In the quantile regression model all determined explanatory variables and interactions between them were included. According to Chambers (Chambers and Hastie, 1993) the model is described by the mathematical formula below:

$$n \sim T * Rh * v \quad (1)$$

where “ \sim ” separates response variable on the left from the explanatory variables on the right. The “ $*$ ” operand adds interactions between variables to the model. For numerical variables it includes a point-wise product of the variables.



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141 In Eq. 2 the expanded, but equivalent to Eq. 1 form, is presented:

$$142 \quad n \sim T+Rh+v+T:Rh+T:v+Rh:v+T:Rh:v \quad (2)$$

143 where “+” separates predictor terms in an additive model, and “:” separates interacting
 144 terms.

145

146 The statistical computations were performed with use of R language (Team, 2020). For
 147 QR computation the R package quantile regression was used (Koenker, 2020).

148 **4. Results**

149

150 Tab. 1 Shows the summary of statistical parameters that describe the observations.

151 During observations the range of the temperature variations was 6.4 °C. But at most, the
 152 50% of temperatures changed in the interquartile range IQR ($IQR=q_{75} - q_{25}$) of the width
 153 1.62 °C. This value indicates stable temperature conditions during at least a half of bats’
 154 observation period. Changes in relative humidity exceeded 34 %. But, similarly as for T ,
 155 the predominating changes measured by IQR did not exceed 7%.The wind speed change
 156 fluctuated from nearly 0 up to almost 1.2 m/s. The corresponding IQR was 0.10. Group
 157 formation was not frequent. Starting from 91% quantile of n , bigger than 1 values were
 158 observed.

159 The structure and relationships between explanatory variables was assessed with use of
 160 the PCA method. The share of the first principal component (PC) in variability is 58 % of
 161 the total variance, and share of PC2 is 25 %. The first 2 PCs contain 83 % of the total
 162 variance.



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163 In Fig. 1 a biplot of the PC1 and PC2 is presented. There were no significant relationships
 164 between the parameters during the study. The points describing physical parameters form
 165 a relatively homogeneous structure, however, several outliers can be observed. Lack of
 166 tendency to grouping of observations and no common relationships among them
 167 promotes these variables for predictors in a regression model.
 168 Eq. 3 shows the expression describing relationship between 3 explanatory variables and
 169 response:

$$170 \quad n = \beta_0 + \beta_1 T + \beta_2 Rh + \beta_3 v + \beta_4 TRh + \beta_5 Tv + \beta_6 Rhv + \beta_7 TRhv \quad (3)$$

171 In the expression $\beta_i (i = \{1 \dots 7\})$ are structural parameters of the model.

172 For $\tau = \{0.925, 0.950, 0.975\}$ the values of the structural parameters and corresponding
 173 standard errors SE , and p -values for null hypothesis $H_0: \beta_i = 0$ were calculated. The
 174 standard errors were computed with use of the bootstrap method.

175 Tab. 2 Shows results of the computations.

176 The critical p -value = 0.05 was considered for rejection of the null hypothesis. The H_0
 177 hypothesis cannot be rejected for all structural parameters when $\tau = 0.95$. No statistically
 178 significant relationships between air parameters and bats' grouping were observed. Both
 179 for $\tau = 0.95$ and 0.975 the interaction terms occurred significantly different from 0,
 180 though for β_7 the critical value was slightly exceeded. The null hypothesis can be rejected
 181 also for the intercept β_0 .

182 5. Discussion

183



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184 The visible influence of T , Rh and v on grouping of the bats was not observed. The
 185 computation results indicate the influence of interactions between these parameters on the
 186 response. Interaction between the two numerical variables in regression model produces a
 187 new variable -the product of selected variables. Because interactions are products, their
 188 influence is important when both factors increase or decrease together. If the value of one
 189 factor increases and the value of the other decreases, their product changes only slightly
 190 and no influence on predictor is observed.

191 The main results from the quantile regression model application for bats' cluster size
 192 description can be summarised as follows:

- 193 • the negative value of β_4 indicates decrease in bats' group size with increasing T
 194 and Rh .
- 195 • the positive value of β_5 indicates increase in bats' group size with increasing T and
 196 v ,
- 197 • the negative value of β_6 indicates decrease in bats' group size with increasing v
 198 and Rh ,
- 199 • the negative value of β_7 indicates decrease in bats' group size with increasing T , v
 200 and Rh .

201

202 The purpose of hibernation is to minimize energy consumption during the
 203 unfavourable period of food shortage. This process is characterized by controlled
 204 reduction of metabolism and, consequently, body temperature (Wermundsen and
 205 Siivonen, 2010). Each species has its own optimal metabolic rate that guarantees it will
 206 survive the unfavourable period.



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207 Loss of energy can occur in various processes, including heat exchange with the
 208 environment or evaporation. Heat exchange with the environment can be regulated by
 209 hibernation strategies, which determine the participation of individual heat transport
 210 mechanisms between the bat's body and the air (convection) or between the body and the
 211 ground (conduction) (Kłys, 2013).

212 The formation of clusters causes the reduction of ratio in the surface area to body
 213 weight and, consequently, a smaller evaporation and heat exchange (giving up). This ratio
 214 is of great importance especially in small animals. It is commonly believed that clusters
 215 can facilitate energy saving, e.g. by reducing water losses in the body (Studier, 1970;
 216 Procter and Studier, 1970; Stapp et al., 1991; Canals, 1998; Brown, 1999; Jefimow et al.
 217 2011; Wojciechowski et al., 2011; Boratyński et al., 2012) or compensate for energy
 218 losses (Boyles et al., 2008). Often the effect of hydration is more important than
 219 nutritional status. Even in conditions of high air humidity (90-98%), the loss of moisture
 220 can be significant, depending on the intensity of metabolic processes, which in turn
 221 depend on the rate of heat loss to the environment, individuals may also have negative
 222 effects, such as extending the hibernation time or mutual awakening.

223 The amount of energy consumed depends on the microclimate, and more specifically
 224 on the roost site climate in which the bat hibernates. In favourable conditions of the
 225 climate, bats should hibernate individually, while in unfavourable conditions (causing too
 226 high consumption of energy) they should form clusters or leave the hibernacula.

227 Our own observations show that, unlike other species, *Barbastella barbastellus* bats
 228 hibernate at a relative air humidity that rarely exceeds 90%. Approaching the upper limit
 229 of the humidity range causes the aggregation of individuals into clusters, which is
 230 confirmed by the studies of other authors (Ransome, 1990; Thomas and Cloutier, 1992;



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231 Thomas, 1995), while there is no reference to the correlation of the values of other air
232 parameters.

233 The work of Wermundsen and Siivonen 2010 verified the belief that some bat species
234 prefer thermally stable habitats, while others choose conditions that vary in terms of
235 temperature. The authors of this article observed that bats (*Eptesicus nilssonii*, *Myotis*
236 *brandtii/mystacinus*, *Myotis daubentonii* and *Plecotus auritus*) in the initial period of
237 hibernation chose places with the highest air temperature and humidity, and in the last
238 stage, places with the lowest values of these parameters, although the range and extremes
239 of temperatures were similar throughout all hibernation period.

240 Encarnacao et al., (2012), in studies on the influence of the habitat on the strategy
241 of the *Myotis daubentonii* bats hibernation, observed the occupation of more favourable
242 habitats by reproductive females, and less favourable by males. Males from different
243 habitats showed different hibernation strategies that depended, among others, on air
244 parameters. In less favourable conditions of the habitat, they observed the grouping of
245 males into clusters, which they explained as an energy-saving strategy. They used
246 temperature and air humidity measurements to determine the conditions of the roost site
247 climate.

248 The basic parameters characterizing the microclimate are temperature (T_a),
249 humidity (R_h) and air velocity (v) (Pawński et al., 1995; Paszyński et al., 1999).

250 During the analysis of the influence of two parameters (variables) on the Western
251 *Barbastellus* hibernation strategy, it was noticed that the increase of the T_a product causes
252 clustering of *Barbastella barbastellus*. Increasing T_a causes an increase in T_b , which in
253 turn causes an increase in the metabolic rate of the bat, so that it uses up energy stores
254 faster in the form of accumulated fat. The temperature of bats usually oscillates around



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255 the ambient temperature (Geiser, 2004; Dunbar and Tomasi, 2006; Boyles et al., 2008;
 256 Kłys, 2013), regardless of whether the animals hibernate individually or in aggregation.

257 The speed of the air flow has a decisive influence on the intensity of the heat
 258 exchange process in the convection mechanism. It determines the type of flow (laminar,
 259 transitional, turbulent), which determines the thickness of the laminar (Prandtl) layer that
 260 forms around the bat's body. The (Prandtl) film has the main resistance to heat penetration
 261 because it conducts heat which is much less efficient compared to heat transfer in a
 262 turbulent area. The greater the velocity values, the smaller the Prandtl film thickness and
 263 the more intense the heat transfer.

264 The T_a increase also increases the evaporation of water from the bat's organism,
 265 which simultaneously increases energy loss (Wermundsen and Siivonen, 2010). The
 266 increase in air R_h , on the other hand, reduces water loss. It is then possible to hibernate
 267 individual individuals.

268 An increase in the air flow velocity (v) increases the reception of moisture from
 269 the bat's organism to the environment or increases evaporation due to the transport of
 270 warmer or drier air, displacing the moist, cool air surrounding the bat (Wermundsen and
 271 Siivonen, 2010). At the same time, the higher the degree of air saturation with water
 272 vapor, the more difficult it becomes to collect heat by evaporation (Thomas and Cloutier,
 273 1992; Thomas, 1995; Paksuz et al., 2007).

274 However, analysing the changes in two parameters does not present a full picture
 275 of the thermal comfort of a hibernating bat.

276 When taking into account three variables, hibernation of individual animals was
 277 observed in the conditions of simultaneous increase in T_a , R_h and v values or a
 278 simultaneous decrease in the values of these parameters.



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279 With an increase in T_a and R_h , the metabolic rate increases, and heat transfer
280 occurs mainly by convection. Increasing the air velocity v allows to receive heat and
281 moisture from the body, and this in turn allows you to maintain optimal energy
282 expenditure.

283 When the values of all parameters are decreasing simultaneously, the metabolic
284 rate decreases and the evaporation intensity decreases, so low air velocities are sufficient
285 for the heat dissipation.

286 In this study, the authors did not take into account the heat transfer between the
287 bat's body and the ground, taking place through heat conduction. The intensity of heat
288 transfer in this mechanism depends on the value of the thermal conductivity coefficient of
289 the substrate (λ), which determines the heat conductivity and is characteristic for a given
290 material. In the conducted research, bats on the same basis adopted different strategies
291 (they hibernated separately or formed aggregations).

292

293 **6. Conclusion**

294

295 It was found that the clustering of bats is closely associated with the analysed
296 parameters. The statistical analysis using the quantile linear regression method showed
297 that the interactions between the parameters T , v and R_h are significant.

298 In the case of the *Barbastella barbastellus* species, the formation of clusters and an
299 increase in the size of the group of bats with an increase in the products T and v were
300 observed. These conditions can be described as less favourable for hibernation, which
301 may result in too high rate of heat transfer to the environment. The decrease in the
302 number of clusters indicates more favourable conditions for hibernation and it is followed



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303 by an increase in the products of T and Rh, v and Rh, and a simultaneous increase or
304 decrease in the values of the three parameters: T, v and Rh.

305

306 **Data availability**

307 Data and/or code are provided as private-for-peer review via the following link:

308 <https://repo.uni.opole.pl/info/researchdata/UO30dbd9c5ed004e7eae780273fdb8c917/Szczeg%25C3%25B3%25C5%2582y%2Brekordu%2B%25E2%2580%2593%2BDane%2Bba dawcze%2B%25E2%2580%2593%2BUniwersytet%2BOpolski?r=researchdata&ps=20&tab=&lang=pl&pn=1&cid=1706867>
311

312 Upon acceptance, Data will be provided via Knowledge Base of the University of Opole
313 via the link provided above.

314 **Author contributions**

315 GK, JMF and ZZ developed the research questions, experimental design, and methods.

316 GK conducted the fieldwork and lab work and led data analysis with input from GK,

317 JMF and ZZ wrote and edited the manuscript. ZZ carried out a statistical analysis.

318 **Competing interests**

319 The contact author has declared that neither of the authors has any competing interests.

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324 **References**

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Barbastella barbastellus hibernation

- 326 Bauerova, Z., Zima J.: Seasonal changes in visits to a cave by bats. *Folia Zoologica*. 37,
 327 97-111, 1988.
- 328 Betke, M., Hirsch, D.E., Makris, N.C., McCracken, G.F., Procopio, M., Hristov, N.I.,
 329 Teng, S., Bacchi, A., Reichard, J., Horns, J.W., Crampton, S., Cleveland, C.J.,
 330 Kunz, T.H.: Thermal imaging reveals significantly smaller Brazilian free-tailed bat
 331 colonies than previously estimated. *Journal of Mammalogy*. 89 (1), 18-24, 2008.
- 332 Boratyński, J., Rusiński, M., Kokurewicz, T., Bereszyński, A., Wojciechowski, M.:
 333 Clustering behavior in wintering greater Mouse-eared bats *Myotis myotis* – the
 334 effect of micro-environmental conditions. *Acta Chiropterologica*. 14 (2), 417-424,
 335 2012.
- 336 Boyles, J. G., Johnson, J.S., Thomas, A.B., Lilley, M.: Optimal hibernation theory.
 337 *Mammal Review*. 50 (1), 91-100, 2019.
- 338 Boyles, J.G., Storm, J.J., Brack, V.Jr.: Thermal benefits of clustering during hibernation:
 339 a field test of competing hypotheses on *Myotis sodalis*. *Functional Ecology*. 22,
 340 632– 636, 2008.
- 341 Brown, P.E.: California leaf-nosed bat *Macrotus californicus*. In (D. E. Wilson and S.
 342 Ruff, eds.) *The Smithsonian Book of North American Mammals*. Smithsonian
 343 Institution Press, Washington D. C., 74-75, 1999.
- 344 Canals, M.: Thermal energetic of small animals. *Biological Research*. 31, 367-374, 1998.
- 345 Смирнов Д. Г., Курмаева Н. М., Вехник В. П.: Динамика численности и
 346 пространственное распределение зимующих рукокрылых (Chiroptera,
 347 Vespertilionidae) в одной из штолен Самарской Луки, // *Plecotus et al.* - № 2. -
 348 С. 67-78, 1999.



Barbastella barbastellus hibernation

- 349 Chambers, J.M, Hastie, T.J.: Statistical Models in S. Chapman & Hall Computer Science
350 Series. New York. 1993.
- 351 Davino, Q.C., Furno, M., Vistocco, D.: Quantile Regression. Wiley Series in Probability
352 and Statistics. Chichester. West Sussex. Wiley, Hoboken. 2014.
- 353 Davydow, A.F.: Energetics and Thermoregulation in Chiroptera. Journal of Evolutionary
354 Biochemistry and Physiology. 40 (3), 241-249, 2004.
- 355 Day, K.M., Tomasi, T.E.: Winter energetics of female Indiana bats *Myotis sodalis*.
356 Physiological and Biochemical Zoology. 87, 56– 64, 2014.
- 357 Dunbar, M.B., Tomasi T.E.: Arousal patterns, metabolic rate, and an energy budget for
358 eastern red bats (*Lasiurus borealis*) in Winter. J. Mammal. 87, 1096-1102, 2006.
- 359 Encarnação, J.A., Reiners, T.E.: Erratum to: Mating at summer sites: indications from
360 parentage analysis and roosting behaviour of Daubenton's bats (*Myotis*
361 *daubentonii*). Conserv Genet. **13**, 1433. 2012.
- 362 French, A.R.: The patterns of mammalian hibernation. Am. Scient. 76. 569-575, 1988.
- 363 Gaisler, J.: Remarks on the thermopreferendum of Palearctic bats in their Natural
364 Habitats. Bijdragen tot de Dierkunde. 40, 33-36, 1970.
- 365 Geiser, F.: Metabolic rate and body temperature reduction during hibernation and daily
366 torpor. Annual Reviews of Physiology. 66, 239–274, 2004.
- 367 Geiser, F., Ruf, T.: Hibernation versus daily torpor in mammals and birds: physiological
368 variables and classification of torpor patterns. Physiological Zoology. 68 (6), 935-
369 966, 1995.
- 370 Generalna Dyrekcja Ochrony Środowiska 2014.: Obszary Natura 2000.
371 <http://natura2000.gdos.gov.pl/wyszukiwarka-n2k> (accessed 2 December 2021).
372 2014.



Barbastella barbastellus hibernation

- 373 Harmata, W.: The thermopreferendum of some species of bats (Chiroptera). Acta
 374 Theriologica. 14, 49–62, 1969.
- 375 Hoffman, R.A.: Speculations on the regulation of hibernation. Ann Acad Sci Fenn. Set A
 376 4. 71, 199–216, 1964.
- 377 Humphries, M.M., Thomas, D.W., Kramer, D.L.: The role of energy availability in
 378 mammalian hibernation: a cost-benefit approach. Physiological and Biochemical
 379 Zoology. 76, 165–179, 2003.
- 380 Jackson, J. E.: A User's Guide To Principal Components. John Wiley & Sons. New York,
 381 43, 1991.
- 382 Janicki, B., Cygan-Szczegielniak, D.: Hibernacja zwierząt. Medycyna weterynaryjna.
 383 366–369, 2006.
- 384 Jefimow, M., Głębska, M., Wojciechowski, M.S.: Social thermoregulation and torpor in
 385 Siberian hamster. Journal of Experimental Biology. 214, 1100–1108, 2011.
- 386 Jolliffe, I.T.: Principal Component Analysis. 2nd ed. New York. Berlin. Heidelberg:
 387 Springer. 2002.
- 388 Kłys, G.: Przyroda Podziemi Tarnogórskich. Pyrzowice-Sosnowiec PTG. 2004.
- 389 Kłys, G.: Wybrane aspekty hibernacji nietoperzy, in. Kłys, G., Wołoszyn, B.W., Yagt-
 390 Yazykova, E., Kuśnierz, A. (Eds.), Wpływ środowiskowych warunków na wybór
 391 hibernaculum przez nietoperze. ZPW Plik Bytom. 2008.
- 392 Kłys, G., Wołoszyn, B.: The influence of weather and interior microclimate on the
 393 hibernation of common long-eared bats (*Plecotus auritus*). Nature Journal. 38, 57-
 394 68, 2005.



Barbastella barbastellus hibernation

- 395 Kłys, G.: Multifactor Analysis of Refugioclimate in Places of Hibernation of Chosen Bat
 396 Species. T. 8 Studia Chiropterologica. Chiropterological Information Center, Insti-
 397 tute of Animal Systematics and Evolution, Polish Academy of Sciences. 2013.
- 398 Koenker, R.: Quantreg: Quantile Regression. R Package Version 5.67 (version 5.67). R.
 399 <https://CRAN.R-project.org/package=quantreg>. 2020.
- 400 Koenker, R., Chernozhukov, V., He, X., Peng, L.: Handbook of Quantile Regression.
 401 Chapman & Hall/CRC Handbooks of Modern Statistical Methods. Boca Raton:
 402 CRC Press. Taylor & Francis Group. 2018.
- 403 Kunz, T.H.: Age estimation and post-natal growth in the bat *Myotis lucifugus*. Journal of
 404 Mammalogy. 63 (1), 23-32, 1982.
- 405 Lyman, C.P., Willis, J.S., Malan, A., Wang, L.H.C.: Hibernation and torpor in mammals
 406 and birds. Academic Press, New York. 1982.
- 407 McNab, B.K.: Evolutionary alternatives in the physiological ecology of bats, in Kunz,
 408 T.H. (Eds.), Ecology of bats. Plenum Press, New York, London, pp.151–200, 1982.
- 409 Mopkowy tunel koło Krzystkowic 2017.: Centralny rejestr form ochrony przyrody.,
 410 Regionalna Dyrekcja Ochrony Środowiska w Gorzowie Wielkopolskim.
 411 <http://crfop.gdos.gov.pl/CRFOP/widok/viewnatura2000.jsf?fop=PL.ZIPOP.1393.N>
 412 [2K.PLH080024.H](http://crfop.gdos.gov.pl/CRFOP/widok/viewnatura2000.jsf?fop=PL.ZIPOP.1393.N) (accessed 2 December 2021). 2017.
- 413 Nagel, A., Nagel, R.: How do bats choose optimal temperatures for hibernation?. Corp.
 414 Biochem. Physiol. 99A (3), 323-326, 1991.
- 415 Nelson, R.A.: Protein and FAT metabolism, in hibernating bears. Federation Proceedings.
 416 39, 2955-2958. 1980.



Barbastella barbastellus hibernation

- 417 Nietoperek PLH 080003 NATURA 2000.: - standard data form 2021.
 418 <https://natura2000.eea.europa.eu/Natura2000/SDF.aspx?site=PLH080003> (accessed
 419 2 December 2021). 2021.
- 420 Орлова, Н.Г., Дмитриев, В.Е., Рыбаков С.А.: Условия и места зимовок рукокрылых
 421 на восточном склоне Кузнецкого Алатау. Экология наземных позвоночных
 422 Сибири. Томск. ТГУ, 53-59, 1983.
- 423 Paksuz, S., Ozkan, B., Postawa, T.: Seasonal changes of cave-dwelling bat fauna, and
 424 their relationship with microclimate in Dupnisa Cave System (Turkish Thrace).
 425 Acta zoologica cracoviensia. 50 A (1-2), 57-66, 2007.
- 426 Paszyński, J., Miara K., Skoczek, J.: Wymiana energii między atmosferą a podłożem jako
 427 podstawa kartowania topoklimatycznego. Dokumentacja Geograficzna 14. IG i PZ
 428 PAN. Warszawa. 1999.
- 429 Pawiński, J., Roszkowski, J., Strzeziński, J.: Przewietrzanie Kopalń. Śląskie
 430 Wydawnictwo Techniczne, Katowice. 1995.
- 431 Procter, J. W., Studier, E.H.: Effects of ambient temperature and water vapor pressure on
 432 evaporative water loss in *Myotis lucifugus*. Journal of Mammalogy. 51, 799–804,
 433 1970.
- 434 Ransome, R.D.: The natural history of hibernating bats. Christopher Helm, London. 1990.
- 435 Stapp, P., Pekins, P.J., Mautz, W.W.: Winter energy expenditure and the distribution of
 436 southern flying squirrels. Canadian Journal of Zoology. 69 (10), 2548–2555, 1991.
- 437 Storey, K.B., Storey, J.M.: Facultative metabolic rate depression: molecular regulation
 438 and biochemical adaptation in anaerobiosis, hibernation and aestivation. Quarterly
 439 Review of Biology. 65, 145-174, 1990.



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- 440 Studier, E.H.: Evaporative water loss in bats. *Comparative Biochemistry and Physiology*.
 441 35, 935–943, 1970.
- 442 Team, R.C.: R: A Language and Environment for Statistical Computing. R Foundation
 443 for Statistical Computing. Vienna. Austria. <http://www.R-project.org>. 2020.
- 444 Thomas, D.W.: Hibernating Bats Are Sensitive to Nontactile Human Disturbance. *Journal*
 445 *of Mammalogy*. 76, (3), 940–946, 1995.
- 446 Thomas, D.W., Cloutier, D.: Evaporative water by hibernating little brown bats, *Myotis*
 447 *lucifugus*. *Physiological Zoology*. 65, 443–456, 1992.
- 448 Томиленко, А.А.: Зимовка рукокрылых (Vespertilionidae) в Новосибирской области.
 449 *Plecotus. et al., pars spec*, 99–106, 2002.
- 450 Visnovska, Z.: Spatial distribution of hibernating bats (Chiroptera) in relation to climatic
 451 conditions in the Demanovska ice cave (Slovakia). *Proceedings of the 2nd*
 452 *international workshop on ice caves, Demanovska Dolina, - Slovak Republic*.
 453 *Liptovsky Mikulas*, 87–97, 2006.
- 454 Wang, L.C.H.: Mammalian hibernation. In: Grout B. W. W., Morris G. J. eds. *The Effects*
 455 *of Low Temperature on Biological Systems*. London, Edward Arnold.: 349–386,
 456 1987.
- 457 Wermundsen, T., Siivonen, Y.: Seasonal variation in use of winter roosts by five bat spe-
 458 cies in south-east Finland. *Central European Journal of Biology*. 5 (2), 262–273,
 459 2010.
- 460 Wojciechowski, M., Jefimow, M., Pinshow, B.: Heterothermy, and the Energetic
 461 Consequences of Huddling in Small Migrating Passerine Birds. *Integr. Comp. Biol*.
 462 51 (3), 409–418, **2011**.
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Table 1. The statistical parameters of the data collected during observation. The *min* and *max* are the minimum and maximum values in the data, q_{25} and q_{75} are respectively the lower and upper quartile, *median* is the median (q_{50}) value, *mean* is the arithmetic average, and *SD* stands for the standard deviation.

parameter	$T[^{\circ}\text{C}]$	$Rh[\%]$	$v[\text{m/s}]$	$n[-]$
<i>min</i>	6.00	56.4	0.01	1
q_{25}	8.28	74.5	0.05	1
<i>median</i>	9.05	78.4	0.12	1
q_{75}	9.90	81.3	0.15	1
<i>max</i>	12.40	91.8	1.17	220
<i>mean</i>	8.87	77.7	0.19	4.5
<i>SD</i>	1.29	6.8	0.25	18.9

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Table 2. The structural parameters β_i values, their standard errors SE , and p-values for null hypothesis $H_0: \beta_i=0$

Structural parameter	value	SE	p -value
$\tau=0.925$			
β_0	10	14	0.474
β_1	-3.3	7.9	0.681
β_2	1.4	8.9	0.872
β_3	2	17	0.917
β_4	-3.5	6.2	0.573
β_5	4	12	0.763
β_6	-3	12	0.818
β_7	-1.8	7.0	0.802
$\tau=0.950$			
β_0	46	16	0.005
β_1	9	10	0.360
β_2	-13.6	10.0	0.176
β_3	35	19	0.065
β_4	-16.7	7.3	0.024
β_5	31	15	0.036
β_6	-29	13	0.033
β_7	-16.9	8.6	0.051



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	$\tau = 0.975$		
β_0	56	17	0.001
β_1	3	10	0.791
β_2	-9	11	0.441
β_3	28	19	0.133
β_4	-20.7	8.6	0.016
β_5	37	16	0.020
β_6	-29	13	0.031
β_7	-18.0	9.2	0.052

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493 Fig. 1. Wintering of a single individual *Barbastella barbastellus*

494 Fig. 2. Group wintering of *Barbastella barbastellus*

495 Fig. 3. The biplot containing projected scores in PC1 and PC2 coordinates.

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508 Fig. 1.

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512 Fig. 2.

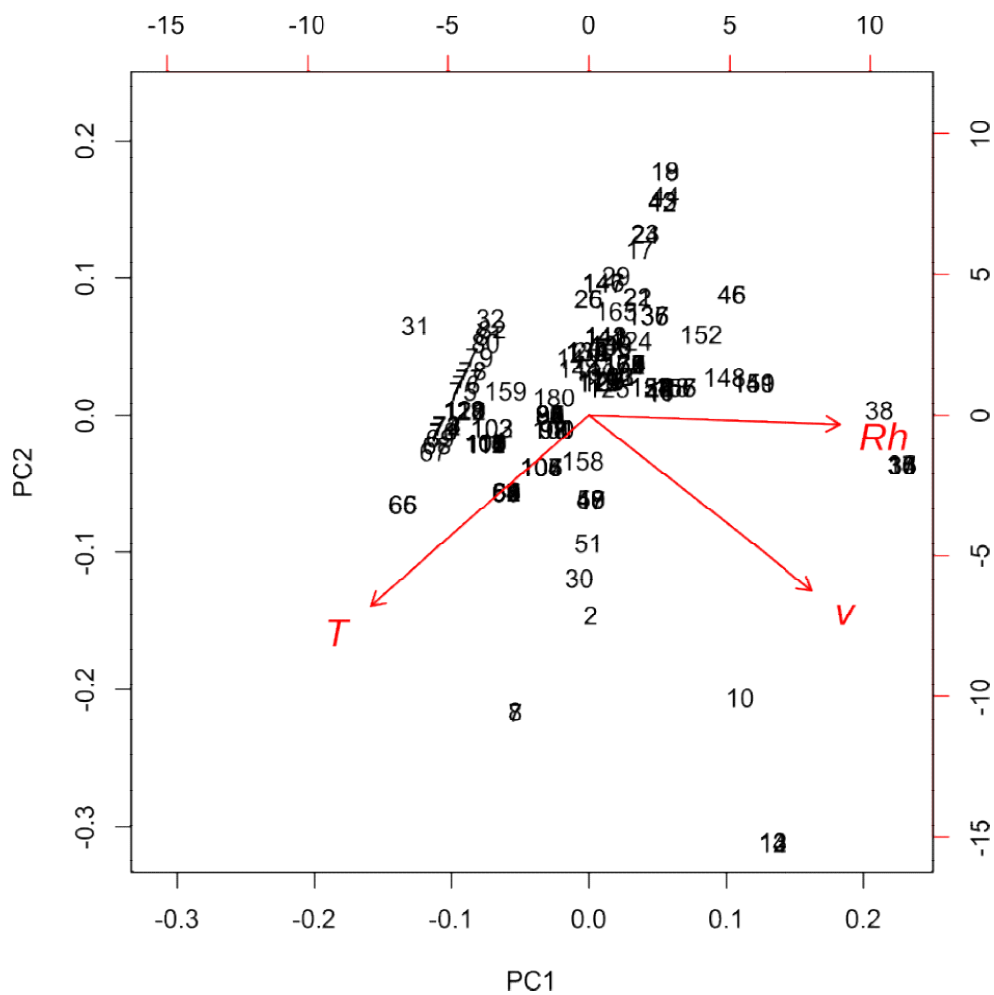
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517 Fig. 3.