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Original article

Ecoclines in the Near East along 36° N latitude in *Apis mellifera* L.

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(Invited paper)

Abstract – The ideas examined and the results presented in the last unfinished manuscript of Friedrich Ruttner have been further developed. Within the 6 populations of the Near East distinguishable by morphometry, the bees of Massandaran in Iran occupy an important position due to their large size. Even sea-level bees exceed the size of the bees of the elevated region of Central Iran, which seems to contradict Bergmanns' s rule. An extended study had revealed that this population, clearly belonging to the subspecies *Apis mellifera meda,* shows a very distinct size increase from the Caspian Sea to the northern slope of the Elbrus Mountains, rising to 2 200 m in elevation. A similar but less pronounced ecocline with a marked increase in size can be found reaching up from the Mediterranean coast to the elevated Central Iranian region. The general pattern within *A. m. meda* in the region along 36° N latitude thus generally confirms Bergmann's rule, thus providing a fine example of an ecoclinal structure. However, size differences between the extremes, i.e., the Mediterranean and the coast of the Caspian Sea remain marked, which indicates an additional genetic component linked to a different history of the populations. This might prove to be an interesting aspect, as the area covered by *A. meda* is suspected to have played a major role in the evolution of *A. mellifera.*

***Apis mellifera meda* / morphometry / ecocline**

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1. INTRODUCTION

1.1. Preliminary remarks

In his last year, Professor Friedrich Ruttner handed me (S. Fuchs) an unfinished manuscript with the comment that his health would not allow him to complete it, but he indicated how much he would appreciate having this material published. On the occasion of this special issue, I therefore feel that this might be the most opportune moment to submit this material both for its inherent interest, but also as a tribute to F. Ruttner, to whom honeybee biogeography owes so much. He had included a summary, which will follow in the form of an unaltered introduction. In this, he presents a general outline of his argument. In reevaluating the evidence for Ruttner's hypothesis, I considered it to be of interest to include some additional samples which meanwhile have become available, and to reassess the statistics according to my preferences.

1.2. Ruttner's outline

Surprisingly, in the morphometric analysis of the honeybees of Iran it was found that the bees along the coast of the Caspian Sea (Massandaran) were substantially larger than those of the Iranian highlands [17]. This was contradictory to Bergmann's rule, which has been confirmed in other populations of *A. mellifera*. There was no doubt about the position of the Massandaran population, as the bees (5 samples) clustered close to the center of the whole *A. m. meda* group.

Given this contradictory result, it was proposed to M. Pour Elmi, who was familiar with this particular region and looking for a thesis to complete his studies, that he collect more samples from varying altitudes (50–2200 m) in the Elbrus Mountains. The morphometric analysis of these samples carried out in cooperation with the Oberursel Institute provided a simple solution to the problem: the colonies of the Caspian bee population known so far represent only a part of a Massandaran population, extending from sea level up the Elbrus slopes to the tree borderline (2 200 m). Within this population, a clear correlation between body size and altitude exists, conforming to Bergmann's rule. The bees at higher altitudes correspond in size to the large bees of Central and Northern Europe. Separated from the bees of Central Iran by the high mountain chains of the Elbrus, the Massandaran population represents a separate and distinct group with a different scale of variation.

The bees of the highlands of Iran belong to a quite different cline, which also starts at sea level, but at the Mediterranean at Latakya (Syria) with very small bees, and extends with increasing body size and altitude through Syria and Iraq as far as Teheran. The data on altitude are not as precise as those on the slopes of the Elbrus (which were measured individually for each collection site with an altimeter), but were characterized only by the approximate altitude of the town on the map next to the collection sites. These data may be rather imprecise: the altitude of the railway station at Teheran is 1 160 m, but the town now extends up the mountain to 1 700 m. Although no exact correlation can be calculated for this second cline, the continuous increase in size is very clear. One feature of this region of variation is especially interesting: the variation between the Mediterranean and the Caspian Sea occurs almost precisely at the 36th parallel. This means that the influence of geographic latitude can be almost excluded. The climate at the southern coast of the Caspian Sea is more humid than in the Eastern Mediterranean, but the temperatures are very similar. The two bee populations at sea level represent the respective bottom lines of the two climate-dependent clines of body size. The considerable differences between them, therefore, can most likely be attributed to their genetic setup. So far, in no other region has this discrimination been shown in such a clear fashion.

2. MATERIALS AND METHODS

2.1. Sources of data

Bees from Massandaran (Massandaran cline) were sampled from 29 colonies, each from a different location ranging from 50 to 2 200 m in altitude from the slopes of the Elbrus Mountains. Samples were preserved in ETOH and analyzed morphometrically using the techniques and characters described in Ruttner [14, 15] and Ruttner et al. [16] on at least 15 bees per colony. A total of 38 characters were measured using a stereomicroscope and a PC-based video measuring system developed by Meixner [9]. More detailed information on these samples is given in [10]. For the western cline, data were extracted from the morphometric data bank in Oberursel which had been measured by the same methods. Samples were included if their collection site was located between 34 and 38° latitude and 34 to 56° longitude, and if they had been assigned $P = 0.99$ a posteriori probability to one of the races as described by Ruttner [14]. This resulted in 37 samples either attributed to *A. m. meda* or *A. m. syriaca*. For analysis, colony means were averaged for the locations, thus resulting in 22 data points each from a different location. Altitudes were inferred from sample locations either by location descriptions and maps provided by the collectors, or by using altitudes from nearby towns. Locations and altitudes of both data sets are mapped in Figure 1.

2.2. Statistical analysis

For characterization of the bee colony or location, means were subjected to factor analysis, and sample scores on the first two principal component analysis (PCA) axes were plotted. Samples were grouped into the three a priori groups: *A.m. syriaca*, *A. m. meda* (except Massandaran) and *A. m. meda* from Massandaran, and group assignment was evaluated by discriminant analysis. The allocation of Massandaran samples was investigated by discriminant analysis.

For evaluation of ecoclines, all samples ranging from the Mediterranean coast to the southern slopes of the Elbrus Mountains were put into one group (western cline, including *A. m. syriaca* and *A. m. meda*), and those ranging from the Caspian Sea up the Elbrus Mountains into the other (Massandaran cline). Each morphological character was plotted against altitude. Sample sets were subjected to analysis of covariance (ANCOVA), with the two groups as fixed factor, and with altitude and longitude as covariates. In addition, linear regression for altitude was calculated separately within both data sets. All calculations were performed using the statistical package SPSS 8.0.

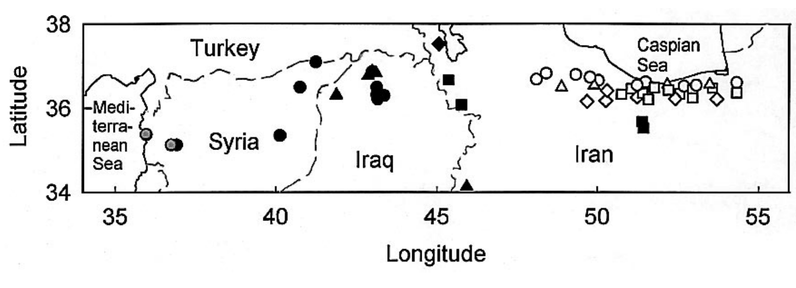

Figure 1. Map of sample locations. Open symbols: Massandaran cline of *A. mellifera meda*. Filled symbols: western cline, black: *A. m. meda;* grey: *A. m. syriaca*. Sample altitudes: circles: < 500 m; triangles: 500 to < 1 000 m; squares: 1 000 to < 1 500 m; diamonds: > 1 500 m.

3. RESULTS

3.1. Factor analysis and discriminant analysis

Seven principal components with eigenvalues > 1 were extracted, which explained 78.7% of the data variation. The first component explained 36.3% of the variation, and was preferentially loaded by size measurements (> 0.5 in 11 out of 13 size measurements, but also wing venation angle E19, pigmentation on labrum 2, on tergite 2 and on tergite 3). The second component explained 9.5% of the variation and loaded preferentially on coloration (pigmentation on labrum 1, on tergite 3, on tergite 4, but also on wing venation angle K19). The other 5 factors explained 25.3% of the variation, with a prevalence of wing venation characteristics. Figure 2 gives a plot of the sample scores on the first two factors, which represents clearly the higher size values of the Massandaran bees on axis 1. The separate position of these bees was confirmed by discriminant analysis, which allocated all samples to their correct group (Massandaran, *A. m. syriaca*, other *A. m. meda*) with a high a posteriori probability (*P* > 0.99), except for two samples from Massandaran which were allocated to the western cline *A. m. meda.*

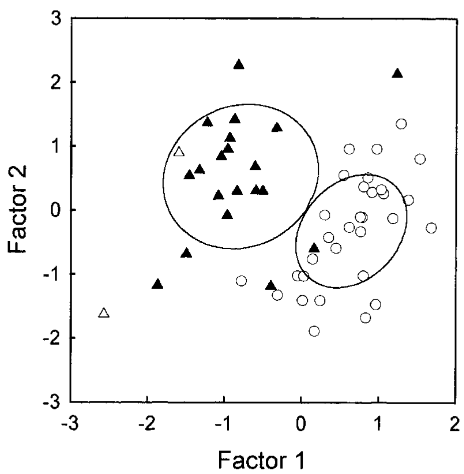

Figure 2. Sample scores on the first two principal components axis. Western cline, black triangles: *A. m. meda*; open triangles: *A. m. syriaca*. Massandaran cline, open circles. Ellipses circumscribe the 90% confidence area for the western cline and the Massandaran cline respectively for *A. m. meda*.

The Massandaran bee samples were individually allocated by discriminant analysis to 5 different *A. mellifera* subspecies in or close to the region (*A. m. mellifera, A. m. carnica, A. m. meda, A. m. anatoliaca, A. m. syriaca).* Twenty-six out of the 33 samples were allocated to *A. m. meda*, 3 to *A. m. armeniaca*, and 4 to *A. m. anatoliaca*.

3.2. ANCOVA and regression analysis

An ANCOVA was performed on the 39 measured characters and on the derived two composite measures and 7 indices. The two suspected cline groups, i.e., western cline and Massandaran cline were used as factors, and longitude and altitude were used as covariates. The distinctness of the Massandaran bees was confirmed, as 30 out of these 48 characters were significantly different between the two groups, 30 of these with $P < 0.05$, 27 with $P < 0.01$. Longitude as a covariate was significantly correlated with only 10 of these measurements (cubital vein 1 and 2, length of wax mirror, length and width of tarsus, width of forewing: $P < 0.05$; length of forewing, sternite 6, width of tomentum 1 and of sternite 6, length to width ratio of wax mirror: $P < 0.01$), thus determining only a weak overall explanative value. Altitude as a covariate was, however, significantly correlated with 20 of the characters. It was positively correlated with 11 of the 13 size measurements ($P < 0.05$; of these, 10 with $P < 0.01$) and with both composite size characters ($P < 0.005$), with the number of hooks ($P < 0.05$) and with hairlength ($P < 0.0005$). Altitude was negatively correlated with both tomentum measurements ($P < 0.05$) and with the pigmentation of scutellum 1. Figure 3a shows a plot of one of the size measurements (length of the forewing) against altitude.

Additionally, linear regressions were calculated for the two clines separately. In the western cline, 11 of the characters showed a significant increase with altitude. These were 6 of the size measurements (length and width of forewing and of sternite 6, width of wax mirror: $P < 0.01$; length of sternite 3: $P < 0.05$), hairlength ($P < 0.01$) and cubital index ($P < 0.05$). Three characters, pigmentation of scutellum 1 and 2 and length to width ratio of the metatarsus, depended negatively on altitude ($P < 0.01$, $P < 0.05$, $P < 0.05$ respectively). In the Massandaran cline, 18 of the characters increased with altitude. This included 12 of the 13 measurements of size ($P < 0.0005$, except the width of sternite 6: $P < 0.005$) and the two composite size characters ($P < 0.005$), number of hooks ($P < 0.05$), hairlength ($P < 0.0005$), and pigmentation of tergite 4 ($P < 0.05$), while the pigmentation of scutellum 1 decreased ($P < 0.05$).

Factor scores of PCA were also submitted to ANCOVA and regression analysis. Sample scores on the first factor, which represented mainly size measurements, differed between the two groups (western cline and Massandaran cline, $P < 0.0005$). Longitude as a covariate showed a weak influence ($P < 0.05$), but altitude was clearly positively correlated ($P < 0.0005$). Similarly, regression analysis showed a highly significant increase with altitude in both clines ($P < 0.0005$). A plot of factor 1 scores against altitude is given in Figure 3b. Factor 2 scores showed a similar but less pronounced distinction between the two groups ($P < 0.05$) and a significant increase with altitude ($P < 0.005$), which was confirmed by regression analysis in the Massandaran cline ($P < 0.0005$) but not in the western cline (NS).

4. DISCUSSION

The results of reanalyzing the morphological characteristics of honey bees between the Mediterranean and the Caspian Sea, between the 34th and the 38th parallel, confirm the hypothesis that the seeming

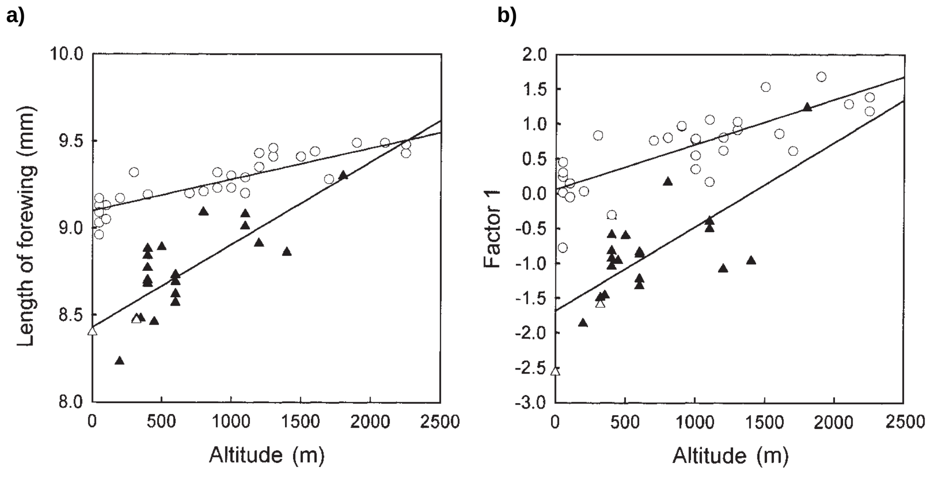

Figure 3. Relation of wing length (**a**) and sample scores on principal component axis 1 (**b**) to sample location altitude. Western cline, black triangles: *A. m. meda*; open triangles: *A. m. syriaca*. Massandaran cline, open circles. Lines show linear regression for both clines.

contradiction to Bergmann's rule of smaller bees in the Iranian highlands and larger bees around the Caspian Sea is resolved by the existence of two separate clines, one extending from the Mediterranean to the Iranian highlands, and a second cline extending from the Caspian shore to the high altitudes of the Elbrus Mountains. In accordance with this rule, both clines predominantly encompass size measurements, which fits with the different examples known of this rule applying to *A. mellifera*, both in relation to absolute geographic latitude [13, 14] and to altitude [5, 6, 13], and also to *A. florea* [17]. In particular, the Massandaran cline, which extends over a distance of only 100 km, is a particularly clear example of an ecocline which has been comparatively unaffected by human practices and transport.

In the second feature, i.e., hairlength, Rensch's observation [11] that in colder climates the hair tends to be longer is clearly corroborated, in accordance with the fairly clear-cut increase in hairlength observed from the Equator towards the poles [13] or in relation to altitude [7, 13]. Other biogeographical rules are not consistently satisfied. Gloger's rule, which predicts darker colors in warmer climates, seems to apply reversely to honey bees [13-15], but shows many exceptions [4, 14]. Darker coloration at higher altitudes seems to apply in the western cline but not in the Massandaran cline. Allen's rule [8, 12] predicts that body appendices become relatively shorter with altitude, but results show that wing size and leg size also increase leaving the relative proportions, as expressed by indices, fairly unaffected. In relation to wing size, an increase in wing area is likely to be necessitated to retain a favorable excess power index (EPI) [5] required for efficient flight at high altitudes. Concurrently, in an analysis of 7 African mountain systems, a clear increase in wing dimensions has been demonstrated by Hepburn et al. [6], and has also been found in the Yemen [7] and in *A. florea* [18]. In relation to leg size, again Allen's rule is not generally met in honey bees [15], or in the current data set. In a preliminary analysis on 728 *A. mellifera* samples from the Oberursel data bank, over the whole range of distribution the relation of wing length to body size, or of hindleg length to body size showed a statistically significant decrease with absolute latitude ($P < 0.0005$, regression analysis, unpubl. data). However, in relation to the absolute increase in size, this decrease was slight and unlikely to show up in small data sets.

Bees of both clines differ considerably, again predominantly by their size. Bees of Massandaran are markedly bigger, and in overall size, measurements fall within the range of the bigger European bee races (Tab. I). Also, as regards most measurements of coloration, they are distinctly darker than the bees of the western cline.

Table I. Size measurements of body parts in 5 subspecies of *A. mellifera* and the Massandaran population of *A. m. meda*.

	Subspecies of *A. mellifera*						
	meda (Massandaran)	*mellifera*	*ligustica*	*caucasica*	*meda*	*anatoliaca*	*Syriaca*
Complete leg	8.18 ± 0.12	8.19 ± 0.13	7.99 ± 0.11	8.28 ± 0.12	7.84 ± 0.15	8.11 ± 0.11	7.83 ± 0.20
Length forewing	9.27 ± 0.14	9.29 ± 0.19	9.18 ± 0.10	9.33 ± 0.12	8.91 ± 0.23	8.15 ± 0.14	8.55 ± 0.19
Body size	4.54 ± 0.09	4.65 ± 0.09	4.42 ± 0.11	4.54 ± 0.08	4.38 ± 0.11	4.47 ± 0.08	4.28 ± 0.12
Width forewing	3.20 ± 0.07	3.11 ± 0.07	3.20 ± 0.05	3.13 ± 0.06	3.06 ± 0.08	3.10 ± 0.06	2.86 ± 0.08
Width sternite 6	3.27 ± 0.07	3.37 ± 0.11	3.12 ± 0.09	3.25 ± 0.07	3.09 ± 0.12	3.15 ± 0.10	3.01 ± 0.11

Numbers show means and standard deviations in mm.

Table II. Average temperatures at both coastal extremities of the respective *A. mellifera* clines. Data on climate for Latakia (Mediterranean coast, Syria) are averages of the years 1984 to 1994. Data on climate for Ramsar (Caspian Sea coast, Iran) are averages of the years 1956 to 1971, given in Ehlers [1].

Location	Mean temperature (°C)				Average yearly rainfall (mm)
	January	April	July	October	
Latakia (Mediterranean coast)	11.9	18.1	25.9	22.5	701.3
Ramsar (Caspian Sea coast)	8.0	12.6	24.7	17.9	1 197

Nevertheless, in an analysis including other bee subspecies, the Massandaran population is clearly part of the *A. m. meda* subspecies. These differences are unlikely to be based on ecological circumstances. Specifically, at the starting positions where the *A. m. meda* range reaches the Mediterranean coast [3] and the Caspian coast, climatic conditions are roughly similar, though somewhat cooler and distinctly more humid on the Caspian coast (Tab. II). Alternatively, they point to genetic differences which relate to the biogeographical history of the species. This is particularly interesting, as *A. m. meda* is likely to be in a position close to the presumed origin of the species in the Near East [2, 15, 17]. The current data set, covering a 1 000 × 2 300 km landstrip extending East-West at the same latitude, thus provides a clear example of the effect of altitude on morphological features in the honeybee. But this can be complicated by the presence of endemic biohistorical populations, separated by geographical barriers.

ACKNOWLEDGMENTS

We thank Prof. A. Ftayeh and Dr. Hartoum (Faculty of Agriculture, University of Damascus) for providing climatical data for Latakia.

Résumé – Ecoclines au Proche Orient le long du 36^e parallèle N chez *Apis mellifera*. Ce travail est basé sur les idées et les données que Friedrich Ruttner avait transmis dans un dernier manuscrit inachevé en demandant qu'il soit complété et remanié. À l'origine de la recherche était un rapport antérieur selon lequel les abeilles domestiques de la rive sud de la mer Caspienne (Massandaran) étaient nettement plus grandes que celles des massifs montagneux iraniens. Ceci était en contradiction avec la règle de Bergmann, qui stipule que la taille des abeilles augmente avec l'altitude. La présente étude analyse le volumineux matériel prélevé dans la population de Massadaran à différentes altitudes sur les pentes nord du Mont Elbrouz [10], ainsi que des données issues de la base de données morphométriques d'Oberursel. Les 66 échantillons provenaient d'une région comprise entre le 34^e et le 38^e degré de latitude Nord et le 34^e et le 56^e degré de longitude Ouest (Fig. 1). Le résultat des analyses morphométriques et statistiques montre que les abeilles de Massadaran présentent un cline très net avec des corrélations significatives pour la plupart des caractères de taille, ainsi que pour la longueur des poils. On a pu aussi mettre en évidence un second cline moins net, qui s'étend de la limite occidentale de l'aire d'*Apis mellifera meda* sur la mer Méditerranée (Latakia, en Syrie [3]) jusqu'au massif montagneux iranien et qui présente aussi des corrélations significatives pour de nombreux caractères de taille, pour la longueur des poils et pour la pigmentation (Fig. 3). En outre, l'ensemble des abeilles de Massadaran se distingue nettement des autres *A. m. meda* du point de vue morphologique, entre autres par la taille. Elles appartiennent pourtant incontestablement à cette sous-espèce. La contradiction d'origine par rapport à la règle de Bergmann a pu être résolue : il existe deux populations différentes d'*A. m. meda*, nettement distinctes par la taille, mais, au sein de chaque population, il existe une relation nette entre l'altitude et les caractères morphométriques. Pour les abeilles de Massadaran en particulier, le cline d'altitude peut être considéré comme un exemple particulièrement net de la validité de la règle de Bergmann chez les abeilles domestiques, puisque l'altitude varie du niveau de la mer à 2200 m sur une distance de 100 km seulement.

***Apis mellifera meda* / morphométrie / écocline**

Zusammenfassung – Ökoklinen bei *Apis mellifera* im Nahen Osten längs 36° nördlicher Breite. Die vorliegende Arbeit beruht auf Gedankengänge sowie Datenmaterial von F. Ruttner, die dieser in einem letzten unbeendeten Manuskript mit der Bitte um Vervollständigung und Überarbeitung übergeben hatte. Anlass der Untersuchung war der frühere Befund, nach dem die Honigbienen des am Südufer des Kaspischen Meeres gelegenen Massandaran durch ihre die Bienen des persischen Hochlandes übertreffende Gröβe der Bergmann'schen Regel zu widersprechen schienen. Hiernach wären in den höheren Berglagen gröβere Bienen zu erwarten gewesen. Die vorliegende Studie analysiert das umfangreiche Material aus einer Untersuchung des Massandaran bis in die Höhenlagen des nördlichen Elbrusgebirges [10], sowie Daten der morphometrischen Datenbank in Oberursel. Alle 66 Proben stammten aus einem Areal zwischen 34° bis 38° nördlicher Breite und 34° bis 56° westlicher Länge (Abb. 1). Im Ergebnis zeigte sich, daβ die Bienen des Massandaran eine sehr deutliche Kline mit signifikanten Korrelationen der meisten Gröβenmerkmale sowie der Behaarung aufwiesen. Zusätzlich konnte eine weitere etwas weniger deutliche Kline nachgewiesen werden, die von der westlichen Grenze der Verbreitung von *Apis mellifera meda* am Mittelmeer (Latakia, in Syrien [3]) bis in das Persische Hochland reicht und ebenfalls signifikante Korrelationen vieler Gröβenmerkmale, der Behaarung und der Pigmentierung zeigte (Abb. 3). Zusätzlich lieβen sich die gesamten Bienen des Massandaran morphometrisch deutlich von den übrigen *A. m. meda* abgrenzen, unter anderem durch ihre Gröβe. Dennoch sind sie eindeutig dieser Subspezies zuzurechnen. Der ursprüngliche Widerspruch zur Bergmann'schen Regel konnte hiermit aufgelöst werden – es bestehen zwei unterschiedliche Populationen von *A. m. meda* mit einem deutlichen Gröβenunterschied, innerhalb jeder dieser Populationen konnte aber eine deutliche Höhenabhängigkeit morphometrischer Merkmale nachgewiesen werden. Insbesondere für die Bienen des Massandaran kann diese Höhenkline als ein besonders ausgeprägtes Beispiel für die Gültigkeit der Bergmann'schen Regel bei Honigbienen angesehen werden, da der Anstieg von unter Meereshöhe bis in 2200 m Höhe innerhalb einer Entfernung von nur 100 km erfolgt.

***Apis mellifera meda* / Morphometrie / Ökokline**

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