PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

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Cite this article: Conner JK, Lande R. 2014 Raissa L. Berg's contributions to the study of phenotypic integration, with a professional biographical sketch. *Phil. Trans. R. Soc. B* **369**: 20130250.
http://dx.doi.org/10.1098/rstb.2013.0250

One contribution of 14 to a Theme Issue 'Phenotypic integration and modularity in plants and animals'.

Subject Areas:
evolution, genetics, plant science

Keywords:
Raissa L. Berg, Lysenko, correlation pleiades, modularity, phenotypic correlations, floral integration

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Electronic supplementary material is available at http://dx.doi.org/10.1098/rstb.2013.0250 or via http://rstb.royalsocietypublishing.org.

Royal Society Publishing

Raissa L. Berg's contributions to the study of phenotypic integration, with a professional biographical sketch

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Raissa L. Berg had a remarkable career in many respects and an impact on the study of phenotypic integration that continues to increase over 50 years after the publication of her seminal paper in that area. She was born and lived most of her life in Russia, with most of her research focused on measuring spontaneous mutation rates in *Drosophila*. She was forced to abandon this work during the height of Lysenko's power in Russia, so she turned temporarily to the study of correlation patterns in plants; ironically, this work has had a more enduring impact than her main body of research. She showed that floral and vegetative traits become decoupled into separate correlation 'pleiades' in plants with specialized pollinators, but floral and vegetative traits remain correlated in plants that have less specialized pollination. Unfortunately, her plant work is often mis-cited as providing evidence for increased correlations among floral traits due to selection by pollinators for functional integration, a point she never made and one that is not supported by her data. Still, many studies of correlation pleiades have been conducted in plants, with the results mostly supporting Berg's hypothesis, although more studies on species with generalized pollination are needed.

1. Professional biographical sketch

Raissa L. Berg (1913–2006) was born and lived most of her life in Russia [1,2]. She completed graduate research supervised by the Nobel Prize-winning geneticist H. J. Muller, who spent 4 years in Russia (1933–1937), from which she published three papers in *Genetics* on sex-linked lethal and sterility mutations in *Drosophila melanogaster* [3–5]. Much of her lifelong research concerned measuring spontaneous mutation rates and temporal changes in them in natural populations. Her observations of mutation rate changes in natural populations of *D. melanogaster* may have been the first evidence of the worldwide spread of transposable P elements in that species (personal communication from James F. Crow to R. Lande, 1977).

In the 1920s and 1930s, Russia was one of the leading centres for the study of genetics and evolution, including the world famous figures N. I. Vavilov who studied the origins of crop plants and started the world's first seed bank and was one of only 50 foreign members of the Royal Society of London, and I. I. Schmalhausen whose belatedly translated book is considered one of the final contributions to the modern synthetic theory of evolution [6]. During the notorious period from the late 1930s until 1965, the Russian state under Stalin and Khrushchev, guided by their agriculture minister T. D. Lysenko, used Lamarckian ideas on the inheritance of acquired characters as an ideological basis for purging the entire field of genetics (and Darwinian evolution) from Russian science. This purge of genetics was motivated by the belief that the existence of hereditary variation among individual people was antithetical to their ability to be moulded to the ideals of communism.

During the Lysenko period, Raissa Berg became one of the leading figures championing genetics and evolutionary studies in Russia, although such studies were strictly prohibited. Their best geneticists were either forced to embrace Lysenkoism or were imprisoned with all trace of their work and even their name expunged from the libraries [1]. Vavilov starved to death in a Russian jail in 1943. Raissa Berg survived during this period because she was the daughter of a well-known scientist, ichthyologist Lev S. Berg, and because she was not sufficiently famous to be made an example and purged like Vavilov, but she had too much integrity and was too well established to be forced to testify against her superiors as were many junior scientists (personal communication from R. L. Berg to R. Lande, 1977). During her long and frustrating career in Russia, R. L. Berg knew and interacted with many of the leading scientists, mathematicians, artists and dissidents [1]. The recovery of Russian genetics and evolution after 1965 proceeded slowly. A major contribution by R. L. Berg was her decade-delayed co-authored publication of the first work on medical genetics, reestablishing the Mendelian basis of human diseases caused by recessive mutations. Even after the demise of Lysenko, her life was made intolerably difficult by individual jealousy and state antisemitism, involving closure of the institute of evolutionary genetics that she headed, destruction and confiscation of her private property, and withdrawal of her state pension. She was practically forced to emigrate, and in 1974 she moved to the USA to work at the University of Wisconsin and University of St. Louis, finally moving to Paris to be with her daughter during her last years [1,2].

In the darkest interval of the Lysenko period, when she was not allowed to study genetics or raise *Drosophila*, Raissa Berg turned to research on morphological variation and correlation in plants, and particularly the subject of developmental homeostasis and 'correlation pleiades', a concept that was earlier developed by leading Russian evolutionists P. V. Terentjev and I. I. Schmalhausen [1]. She published two papers on the subject in *Evolution* and *American Naturalist* [7,8] that belatedly stimulated substantial research in plant evolutionary ecology and continue to do so. In the USA, she co-authored research on mutations caused by transposable elements in *Drosophila* [9,10], works on changes in spontaneous mutation rates in natural populations, and her memoirs [1]. Despite an extreme and prolonged series of impediments, setbacks and persecutions, Raissa Berg maintained an indomitable positive spirit and unbreakable integrity, and made substantial contributions to genetics and evolution, not only in Russia but also the wider scientific community.

2. Berg's impact on the study of phenotypic integration

Berg published a total of four papers on correlation patterns in plants, the first two in Russian [11,12] and the last two in English [7,8]. The 1959 paper, 'A general evolutionary principle underlying the origin of developmental homeostasis', was three pages long and was essentially an abstract of her basic thesis. She argued that in plants with more specialized pollinators, floral dimensions should be under stabilizing selection so that flowers within a population match each other and their pollinators for effective pollen transfer. This would lead to lower correlations between floral traits and vegetative traits, so that floral size stays constant across individuals with different vegetative sizes. In plants pollinated by the wind or very unspecialized insects, there would not be this reduction in correlation between floral and vegetative traits. This process of decoupling of two groups of traits into modules was later termed parcellation by Wagner & Altenberg [13]. Note that Berg's hypothesis does not imply that floral traits in more specialized plants would have higher correlations as is often assumed (see below).

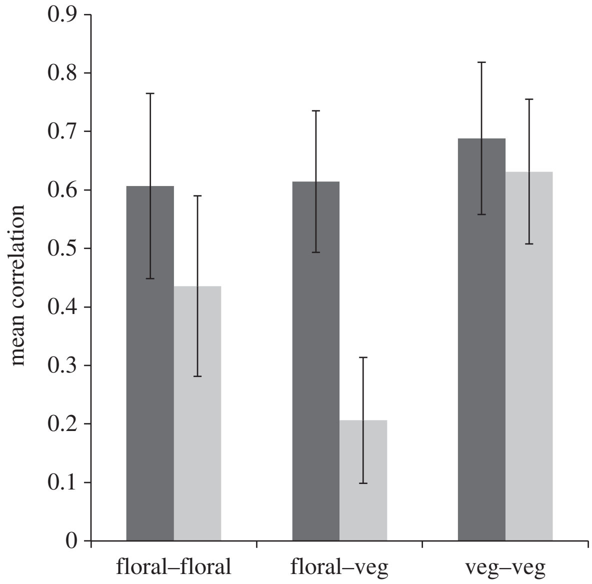

Figure 1. Mean correlations ± 95% CI from data in Berg [8,11,12]. Black bars are means for species designated by Berg as having generalized pollination, and grey bars are means for species with more specialized pollination. Floral–floral are correlations among floral traits, veg–veg correlations among vegetative traits and floral–veg are correlations between floral and vegetative traits. Confidence intervals are two times the standard error of the means, calculated as the standard deviation divided by the square-root of the number of species represented.

The word pleiades in the title of the 1960 paper, 'The ecological significance of correlation pleiades' [8] was Terentjev's [14] term for modules, that is, a cluster of correlated traits (referring to the cluster of stars named for the seven daughters of Atlas) that were uncorrelated with other clusters of traits. In the 1960 paper, Berg provides correlation data from three species with unspecialized pollination and three with specialized pollination that support her thesis. We compiled a database including all the correlations published in the three papers that include data [8,11,12]. The database consists of 198 correlations among eight vegetative and 12 floral traits from seven species Berg characterized as having generalized pollination and 11 species with more specialized pollination; note that we have used Berg's own categorization of species as specialized or generalized to focus on clarifying what her paper said.

In all cases, floral traits are positively correlated with each other, as are vegetative traits, in both specialized and unspecialized species (figure 1). In species with unspecialized pollination the cross-group (i.e. floral–vegetative) correlations are of similar magnitude to the within-group correlations, so the two groups are not separated into modules. On the other hand, the mean floral–vegetative cross-group correlations are significantly lower in the species with more specialized pollination; only in these species, there is evidence for separate floral and vegetative modules. Note that floral trait correlations are considerably *lower* in species with specialized pollination

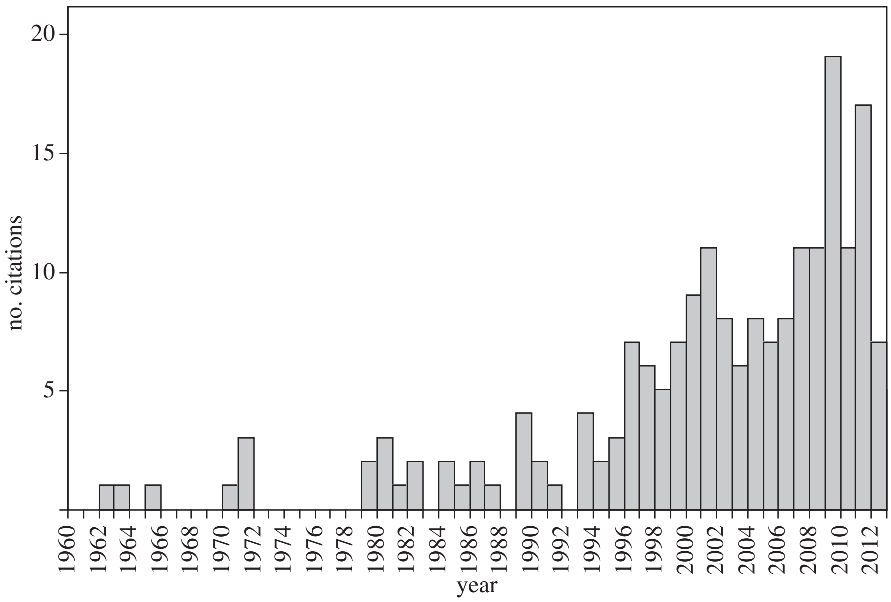

Figure 2. Citations of Berg [8] by year in the ISI Web of Science database on 13 July 2013.

(mean = 0.44) compared to floral correlations in unspecialized species (mean = 0.61) or vegetative traits in either group, although the 95% confidence intervals are broadly overlapping. The reason the 95% CI are overlapping is that the floral–floral correlations are based on a small sample size of only 30 correlations, 12 from unspecialized and 18 from specialized species. Further, the 12 correlations from unspecialized species were from only two species of primarily self-pollinating crop grasses, wheat and barley.

The 1960 paper has a remarkable history of citations (figure 2). As of 13 July 2013 it had been cited 200 times, but only nine of these were in the first two decades after it was published, and only two of these papers were about plants. Citations slowly increased in the 1980s and early 1990s, but since 1997 citations have increased rapidly and do not show much sign of levelling off. This far outstrips the citation numbers of any of her *Drosophila* papers—her 1980 *Science* paper had the next most citations at 72.

Unfortunately, much of this enduring impact of Berg's paper on evolutionary biology is based on a misunderstanding of what the paper said and what the data in it demonstrate. To document what we perceived as a pattern of mis-citation of Berg, we searched all 18 papers that cited Berg [8] through 1985 for those citations, and did the same for a stratified random sample of 20% of the papers in each 5-year period after that for a total of 54 papers, just over a quarter of all those citing Berg.

Over 60% of these papers (34; 19 of them on plants) cite Berg for the idea that functional relationships and selection should lead to correlation or integration. A careful reading of Berg's papers in English shows that she focuses exclusively on trait independence, not increased correlation—searching her 1960 paper reveals that she uses the words independence, independently, or independent 21 times, but the words integrate or integration never appear. Her view is encapsulated in this quote from the Summary: 'In all the instances of existence of pleiades it was the flower that had become free of the correlation interdependences within the plant organism'. In her scheme, stabilizing selection breaks down 'undesirable correlations' to create trait groups that are uncorrelated with each other, the opposite of correlational selection for functional integration increasing correlations. This is clearly a functional argument, but selection for effective pollination is reducing correlations rather than increasing them.

Some papers go further to cite Berg to support the idea that floral traits in species with specialized pollinators are more highly correlated than floral traits in species with unspecialized pollinators, or more highly correlated than vegetative traits, again suggesting selection by pollinators for functional integration. Not only did Berg not conclude this, but recall that the patterns in our reanalysis of Berg's data show that floral traits in plants with specialized pollination had lower correlations than floral traits in unspecialized species or vegetative traits (figure 1). Clearly, neither Berg's ideas nor data support functional integration in floral traits due to pollinator-mediated selection. The only hint of increased functional integration in the 1960 paper is in the discussion, where she notes that some of the plants with specialized pollinators in her dataset show 'reduction in number (oligomerization) and the rigid fixation of the number of homologous parts', which could be interpreted to imply higher floral correlation through trait fusion.

This is an all too common cautionary tale of the importance of carefully reading the original paper that is cited, which would prevent the propagation of mutated memes. The importance of this mistake goes beyond Berg's legacy to negatively impact plant evolutionary biology in general, because the idea that flowers are tightly integrated organs has become entrenched in the literature. However, the evidence is clear that flowers are not highly integrated organs [15,16].

Note that 24 of the papers we sampled correctly cited one or both of Berg's two main points—that specialized pollination should impose stabilizing selection on floral traits, and that this stabilizing selection decouples the floral traits and vegetative traits into separate correlation pleiades. It would be interesting to perform meta-analyses of the data that have been collected on these two points to determine the overall level of support. In general, negative quadratic selection gradients (necessary but not sufficient to establish stabilizing selection) are no more common than positive quadratic gradients [17,18], but whether this is true for floral traits has not been addressed to the best of our knowledge. Separation of floral and vegetative traits into separate modules in more specialized plants has usually been found [19,20], but more studies of wind-pollinated or highly unspecialized plants are needed to test for the lack of modularity Berg found. Rigorously categorizing the degree of pollinator specialization can be a difficult issue, however. Still, it is clear that Berg's ideas will continue to provide fertile ground for evolutionary biology in the years to come.

Acknowledgements. Thanks to Elena Litchman for translating some of Berg's tables from Russian.

Funding statement. J.K.C. was supported by NSF DEB 0919452, and R.L. was supported by a Royal Society Research Professorship. This is KBS contribution no. 1775.

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