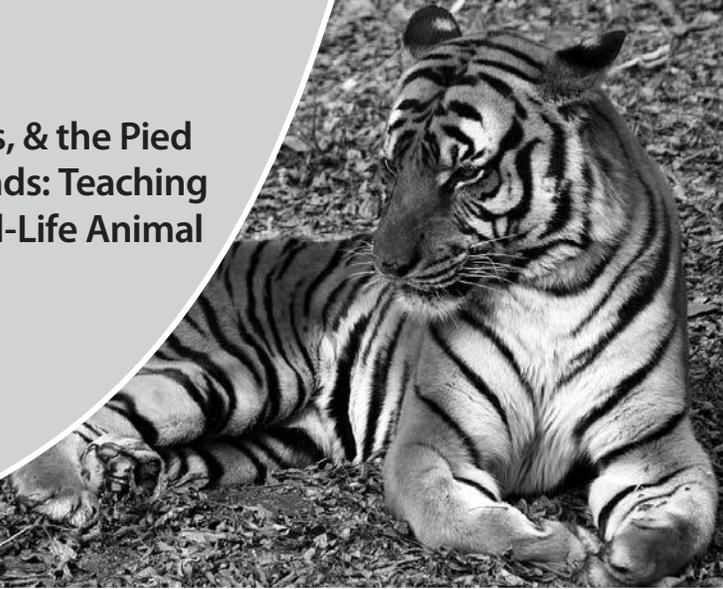


Blue Tigers, Black Tapirs, & the Pied Raven of the Faroe Islands: Teaching Genetic Drift Using Real-Life Animal Examples

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ABSTRACT

Genetic drift is a concept of population genetics that is central to understanding evolutionary processes and aspects of conservation biology. It is frequently taught using rather abstract representations. I introduce three real-life zoological examples, based on historical and recent color morphs of tigers, tapirs, and ravens, that can complement classical models.

Key Words: Genetic drift; Hardy-Weinberg principle; black tapirs; blue tigers; pied raven; teaching examples.

○ Introduction

Population genetics is of prime importance for understanding and discussing evolutionary processes and core aspects of conservation biology. It encompasses several key concepts that can be challenging to teach. These include the Hardy-Weinberg principle and genetic drift. The Hardy-Weinberg principle states that allele frequency within a population remains constant over generations unless evolutionary influences have an impact, assuming an infinite population size with random mating and no selection, mutation, or migration (Stern, 1943). It is often taught as a basis for introducing genetic drift (Wright, 1929).

The concept of genetic drift explains nonadaptive genotypic changes within populations. It states that allele frequency within a population can be subject to change as a consequence of random, nonselective events that alter the population size. These events can be any that result in a smaller subset of interfertile, interbreeding individuals separate from the original main population. One example would be migration and subsequent establishment of individuals in a new, often isolated habitat as founders of a new population. A second example would be the extermination of the main population, with a small number of individuals surviving and having offspring. Either case can be considered in an explanatory model as a random “sampling” process.

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According to the concept of genetic drift, it is likely that alleles in the “sample” or “shrunk population” are not represented in the same ratio as in the original population. The rarest alleles may even be missing entirely from the “sample” of survivors and their offspring. For its impact on the genetic structure of small, often founder populations, genetic drift is crucial for understanding evolutionary processes. Both the “founder” and the “survivor” examples of a shift of population size and consequent changes in allelic diversity lend themselves further as a basis to introduce the concepts of the bottleneck effect and the founder effect in due course.

It is important to note that the alleles in question may be recessive. They can thus be present in the population but lead to a discernible phenotype in only a very small number of homozygous individuals. For successful work in class using the examples introduced below, it is therefore important that students are familiar with classical Mendelian genetics.

○ Theoretical Models & Real-life Examples in Teaching

The teaching of genetic drift typically makes use of the Bayesian urn model, often with some pedagogical modifications, such as the use of playing cards (Oliver, 1975) or colored candy (Lauer, 2000; Staub, 2002) as representations of alleles or individuals of a population. These and related models involving theoretical representations of species, such as hypothetical “fish” in multiple shapes and colors (Journet, 1986; Winterer, 2001; Young & Young, 2003) or “aliens” with phenotypes of either round or pointy ears (Ortiz et al., 2000), have merits as a playful first introduction. However, not being linked to “real science,” they may lack one important

factor that significantly enhances student motivation: authenticity (Lombard, 2011).

Among the tools for overcoming this problem are real-life examples. For genetic drift or related principles, examples are often chosen

that go back to scenarios in the species' distant evolutionary past and are reflected in difficult-to-conceive molecular parameters. Oxford (1993) presents a real-life model of morph frequency patterns in a spider. Its use in teaching and as a learning activity, however, involves time-consuming fieldwork and extensive data collection. It therefore has its limitations for a quick introduction. Bringing life to the topic without fieldwork requires an easily told "story" of real-life phenotypes that are easy imaginable, memorable, and unusual enough to stir epistemic curiosity. At times, the best explanatory examples are found in species that may be unfamiliar to the learner (Robischon, 2014). In the examples presented here, the charm of the exotic may also turn out to be a bonus in attracting student interest. They also offer an alternative to case studies of the prevalence of certain human genetic conditions in small populations that are frequently used to illustrate the phenomenon. These more medically oriented cases may fail to catch the attention of students who are mostly interested in the organismic biology of animals and who do not consider zoology and genetics as an ancillary discipline to human medicine. In particular, the strong link to conservation biology in the examples chosen here accommodates students who are intrinsically motivated to learn specifically about nonhuman organisms.

In all three examples presented in the following – three rare color morphs of a tiger, of the Malayan tapir, and of a subspecies of northern raven – a striking phenotype is described that was once found in a given taxon but has disappeared or become exceedingly rare as a population underwent a severe reduction in numbers of individuals. In all three cases, the phenotype addressed here is likely attributable to a rare and recessive allele and is assumed to not result in negative natural selection, at least in a natural environment and the in absence of human impact. They are genuine, authentic cases for which only incomplete data are available. No "complete story" is therefore delivered to the learners, but several activities help students develop a hypothesis based on the concept of genetic drift.

Blue Tigers: A Lost Color Morph within a Vanishing Taxon

Domestic cats (*Felis catus*) sporting a slate-gray hue are typically referred to as "blue" or "Maltese" cats. Similar blue morphs also occur in large felines such as tigers. Historically, most sightings of "Maltese" tigers are reported in the subspecies of the South China tiger (*Panthera tigris amoyensis*) from Fujian province, China. The South China tiger has, in its normal form, a vividly colored coat (Figure 1B). The bluish-gray form is known exclusively from historical descriptions, such as the one by American missionary Harry Caldwell (1924), who upon sighting a blue tiger in the

early 1900s in Fujian reported that "The markings of the animal were marvelously beautiful. The ground color seemed to be a deep shade of maltese, changing into almost deep blue on the under parts. The stripes were well defined, and so far as I was able to make out similar to those on a tiger of the regular type." Other witnesses described the reverse, "saying it was black with Maltese markings, putting the thing just backward. Hunters say it appears black at a distance, but upon coming closer the lighter markings begin to show plainly." Tiger hair of bluish-Maltese coloration was reported to have been repeatedly

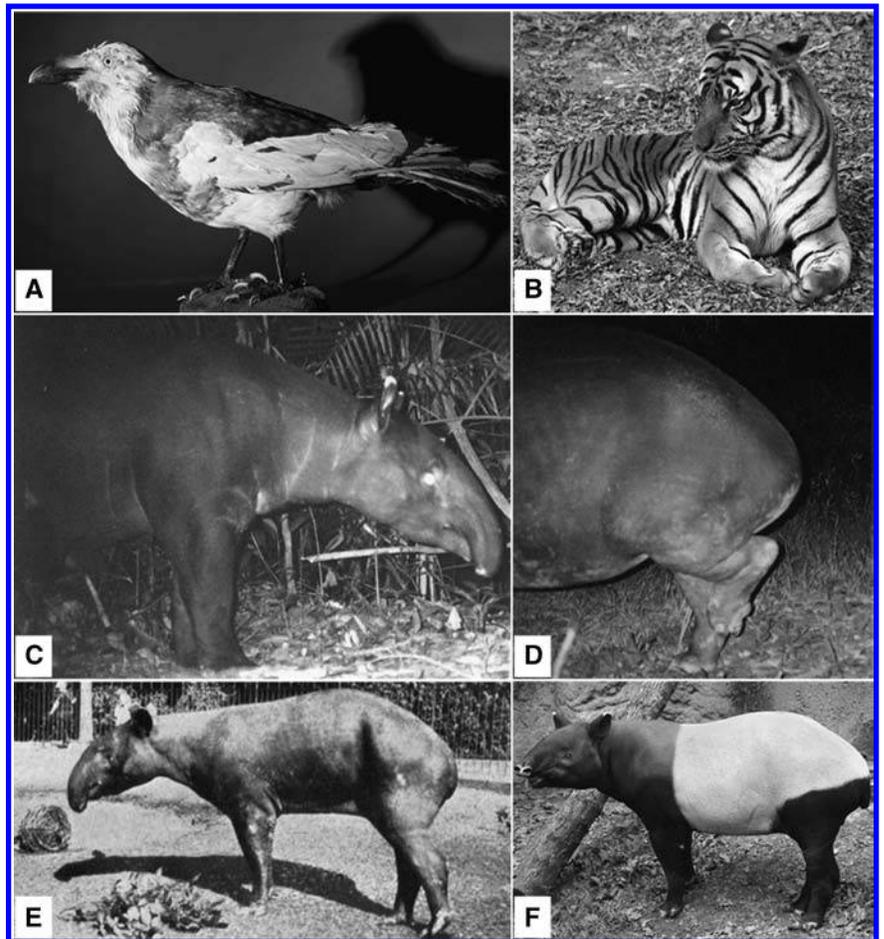


Figure 1. (A) A stuffed specimen of the Faroese pied morph of the North Atlantic raven *Corvus corax varius* morpha *leucophaeus*. Picture courtesy of Dr. J.-M. Ilger, Staatliches Naturhistorisches Museum Braunschweig, Germany. (B) A normally colored individual of the South China tiger. It shows the vivid coloration typical for the subspecies *Panthera tigris amoyensis*. No images of the "blue" form or tissue samples of any kind are known to exist in collections. Picture: J.P. Fischer, Wikimedia Commons. (C) An image taken by a camera trap showing an all-black Malay tapir. The white margin of the ears, typical for all tapirs, are visible. Photo courtesy of Mohd-Azlan J. Azad (Azad, 2002). (D) A second image, likely showing a different animal taken by camera trap. Although the camera trap did not catch the head or upper body of the animal, the absence of the white saddle is obvious. Photo courtesy of Mohd-Azlan J. Azad (Azad, 2002). (E) A black Malay tapir, further described as *Tapirus indicus brevetianus*. This individual came from Sumatra in 1924 to Rotterdam Zoo, The Netherlands. The absence of the white "saddle blanket" area in the coat is apparent. The ears may show the white margin typical of all tapirs. Picture taken from Kuiper (1926) with permission of Wiley Online Library. (F) A normally colored Malay tapir. The white "saddle blanket" and margins of the ears are clearly visible. Picture: T. Shears, Wikimedia Commons.

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found on tiger trails in the region and around the time of this sighting (Caldwell, 1953). Given that there was apparently more than one animal (Caldwell, 1953; Perry, 1965), it is likely that the coloration had a heritable genetic basis. Caldwell was “sure the Blue Tiger was a freak of melanism, though if there were more than a single animal, as the mountain people maintained, this explanation was not entirely satisfactory” (Caldwell, 1953). The last documented witness of the blue variant contributed to the demise of the species. A review of his book points out that “Mr Caldwell, one may be permitted to say, went about his work with a Bible in one hand and a rifle in the other – the latter being for any game he might encounter” (Anonymous, 1926). In fact, he probably killed no less than forty-eight of the regular-colored South China tigers (Caldwell, 1953).

In the 1950s, the total population of the South China tigers was still thought to comprise more than 4000 animals. By the 1980s, the estimated population size had plummeted to between 150 and 200 (Lu & Sheng, 1986), and it declined further to about 30 to 40 over that decade. Less than 20 were believed to be left in the wild by the late 1990s. No reliable sighting in the wild of any South China tiger of any coat color has been confirmed since the early seventies (Tilson et al., 2004). The subspecies may be extinct in the wild (Nyphus, 2008). The blue morph disappeared much earlier and has not been reliably reported since Caldwell’s time. None of the zoo-kept survivors, who all descend from only six animals, show the “blue” phenotype (Tilson et al., 2004).

Black Tapirs: A Rare Variety of an Endangered Species

In its normal form, the Malayan tapir, a large ungulate native to Southeast Asia, shows a striking whitish-gray “saddle blanket” region on its coat (Figure 1F). This characteristic feature is absent in a rare morph known as Brevet’s black Malayan tapir (*Tapirus indicus* var. *brevetianus*). It first came to the attention of zoologists in the 1920s, when a Dutch captain, K. Brevet, sent two all-black tapirs from Sumatra to the Rotterdam Zoo (Kuiper, 1926). The picture of one of the Rotterdam specimens (Figure 1E) appears to show the white margin on the ears that is typical of all tapirs. Kuiper (1926) described one of the two animals that was brought to the zoo as a calf, with a normal juvenile coloration, but maturing into an all-black adult with “a small grey stripe on the median line of its belly.” These animals therefore were not likely to be fully melanistic individuals. Kuiper (1926) considered these two specimens as individuals of a new emerging “variety.” However, no more specimens were documented until the early 2000s, when two black individuals were photo-trapped on the Malay Peninsula (Azad, 2002; Figure 1C, D). Both photographs show a uniform black animal. No trace of the white “saddle blanket” is visible in either animal. However, the picture published by Azad (2002), in which the black tapir’s head is visible, appears to show the white ear margin. The numbers of Malayan tapirs have gone down significantly since the time when the black morph was first described. Malayan tapirs are now considered an endangered species, and their number has been steadily declining for decades (Lynam et al., 2013).

The Pied Raven of the Faroe Islands: The Extinction of an Endemic Avian Color Morph

The Faroe Islands are home to the North Atlantic subspecies of raven, *Corvus corax varius*, which is also found on Iceland. Exclusively on the Faroe Islands, a black-and-white “pied” color morph of this subspecies has been reported. It has been known to occur in this

location for several centuries (Ebels, 1996). It was apparently always present in smaller numbers than the common black “nominant” form. An author named Hans Christopher Müller stated that

One does find it at times mated with common raven. Some individual couples of black raven have every year one or several pied chicks. A few years back I received on an annual basis 1 or 3 pied chicks from a place where a couple of black raven were nesting, in recent years however the aerie contained only black chicks. (Droste, 1869)

In these couples, both birds must have been heterozygous carriers of the recessive “pied” allele. Ornithologist Julius Graba (1830), as quoted by Darwin (Stauffer, 1975), witnessed “that the pied birds are persecuted & driven away by the common ravens” – which suggests that mating between the color morphs may have been less common than within a color morph.

Charles Darwin suggested that “The pied Raven of Faroe is a good case of an incipient local race, yet sometimes crossing with common [sic] form” and speculates that, if the pied variety was the majority “& crosses being thus prevented, it is probably that the pied colouring & other characters would become in the course of many generations more fixed and constant” (Stauffer, 1975). In fact, it wasn’t “incipient” but was, by this time, already on its way out. Historically, ravens of any coloration – including individuals that carried the recessive “pied” allele but did not show the phenotype – were relentlessly persecuted on the islands for attacking newborn lambs and, hence, being detrimental to sheep farming. Also, most ornithologists, private collectors, and museum curators who were interested in the pied raven in the 19th century and earlier collected specimens for taxidermy, accelerating their removal from the population. The last pied raven was seen – and shot – in 1902, at a time when the population of ravens on Faroe was at its lowest (van Grouw, 2014). Ravens of the normal black color are still found on the Faroe Islands, and their number has recovered since.

Learning Activities, Learning Tasks, Learning Operations

In the development of a classroom teaching arrangement for genetic drift, technical terms and basic concepts can be introduced using classical explanatory models, including those based on the Bayesian urn model. Terms such as *allele*, *genotype*, *phenotype*, *population*, and *subpopulation* are important to be defined in advance.

The three real-life examples given here can be introduced either in a teacher’s presentation or in reading pieces based on the above summaries and the literature referenced. Subsequently, students can be asked to prepare a presentation of their own, based on the case studies, using the appropriate genetic terms. As a successfully fulfilled learning task, this would involve mentioning

- The shrinking of populations that contain different phenotypes, a rare and a common one
- The putative genetic background of a rare and a common allele
- The predating of the disappearance of the “rare” phenotype of color morph to before the disappearance or lowest number of the “common morph”
- The absence (or presence) of a selective advantage or disadvantage of the phenotype

A third task is to compare the cases and discuss the potential implications in class. It is important to consider that the Hardy-Weinberg equilibrium is a theoretical model that assumes the conditions of an ideal population, which are not fulfilled in these, or any other real, cases. Therefore, the individual circumstances and aspects in which the real-life case differs from the model have to be included in the discussion.

In the example of the tiger, a putative rare allele leads to the “blue” phenotype. Cats’ breeding behavior does not seem to be affected by coat color, as evidenced by black leopards or jaguars, “white” tigers, or domestic cats. By deduction, it can be assumed that being “blue” did not lower a tiger’s breeding success. Neither is it likely that it lowered its chance of survival, given that hunters, upon sighting *any* tiger of *any* coloration, would have shot it *anyway*. The phenomenon of the blue tigers and their disappearance, followed by the entire population’s demise, thus suggests that it is a textbook case of genetic drift, with the rare allele being lost from a shrinking population and no carriers of this allele being left among the survivors. Assuming that the allele was recessive, the likelihood of two individuals that carried this recessive gene surviving and producing homozygous offspring that show the phenotype is even smaller.

The specific case of the “Maltese” tiger, however, offers another level of complexity because there may be more than one allele involved. In domestic cats, the “Maltese” phenotype occurs if two conditions are fulfilled: the animal has to have the genetic makeup necessary to have black fur and, further, it needs to be homozygous with a recessive allele, the d-gene, that “dilutes” the black coloration into the gray–Maltese color (Priour & Collier, 1984). In tigers, a black coloration – pseudomelanism – may be caused by a gene known as the “nonagouti gene.” The Maltese coloration may be caused, as in the domestic cat, by a dilution gene. With either of the two putative alleles being affected on its own by genetic drift in the shrinking population, the combination of both, and the expression of the blue phenotype, is hence extremely rare.

The fact that no more black tapirs were reported from Sumatra suggests that the rare “black” allele in the tapir population on that island had a fate similar to that of the “blue” allele in the South China tiger. Destruction of their forest habitat and poaching will affect tapirs of either morph indiscriminantly. In the tapir model, a selective pressure for or against either morph can be excluded, supporting the suitability of this example to explain genetic drift. The genetic basis of the black coloration is unknown. The fact that each time the phenotype was found it was in more than one animal suggests a heritable genetic basis rather than a de novo mutation.

However, it could be argued that there is a different reason for the emergence of the black animals: the existence of an as-yet-undescribed taxon. Kuiper (1926) considered the first two specimens of all-black Malayan tapirs as representatives of a new emerging variety, but he did not claim that the black tapir is a species in its own right. Interestingly, however, the IUCN (International Union for the Conservation of Nature) Red List states that “Further research is needed to investigate whether this taxon contains more than one species” (Lynam et al., 2013). The possibility of another as-yet-unrecognized species of tapir being present is particularly interesting in light of the recent description of *Tapirus kabomani* as a new species distinct from the Brazilian tapir (*T. terrestris*; Cozzuol et al., 2013).

In contrast to the tiger and tapir examples, in the case of the raven it can be assumed that targeted hunting of individuals of the pied morph added a factor of negative selection and contributed to extermination of the “white-pied” allele. Further, it is possible that the breeding success of a pied raven was lower than that of the “normal” form, another factor that could have accelerated the extinction of this color morph and the underlying alleles. This aspect makes the case of the pied raven a good example for testing whether the principle of genetic drift was fully understood by students.

Beyond their direct benefits to the teaching of population genetics, these instructional examples support content that is crucial for evolutionary and ecosystem thinking. They illustrate that biodiversity goes beyond the species or subspecies level. They help to establish that the shrinking of a population may alter the phenotypes and genetic diversity that are observed and, thus, alter adaptation and evolutionary processes. Use of these animal examples may also instill an appreciation of the beauty, uniqueness, and information content of unusual phenomena in living nature, fostering awareness of the importance of nature conservation.

References

- Anonymous. (1926). *Blue Tiger* by Harry R. Caldwell. *Geographical Journal*, 67, 365.
- Azad, J.M. (2002). Recent observations of melanistic tapirs in peninsular Malaysia. *Newsletter of the IUCN/SSC Tapir Specialist Group*, 11(1), 27–28.
- Caldwell, H.R. (1924). *Blue Tiger* (pp. 68–69). New York, NY: Abingdon Press.
- Caldwell, J.C. (1953). *China Coast Family* (pp. 60, 62). Chicago, IL: Henry Regnery.
- Cozzuol, M.A., Clozato, C.L., Holanda, E.C., Rodrigues, F.H.G., Nienow, S., de Thoisy, B. & others (2013). A new species of tapir from the Amazon. *Journal of Mammalogy*, 94, 1331–1345.
- Burkhardt, F. & Smith, S. (Eds.) (1992). *The Correspondence of Charles Darwin, vol. 7: 1858–1859* (p. 85). Cambridge, UK: Cambridge University Press.
- Droste, F. v. (1869). Vogelfauna der Färöer. Färöernes Fuglefauna af Sysselmaand Müller 1862. Aus dem Dänischen übersetzt und mit Anmerkungen versehen von Ferd. Baron von Droste. *Journal für Ornithologie*, 17, 381–390.
- Ebels, E.B. (1996). White raven. *Dutch Birding*, 18, 83–85.
- Graba, C.J. (1830). *Tagebuch, geführt auf einer Reise nach Färö im Jahre 1828* (pp. 51, 54). Hamburg, Germany: Perthes & Besser.
- Journet, A.R.P. (1986). Population genetics: a fishy process. *American Biology Teacher*, 48, 478–482.
- Kuiper, K. (1926). On a black variety of the Malay tapir (*Tapirus indicus*). *Proceedings of the Zoological Society of London*, 96, 425–426.
- Lauer, T.E. (2000). Jelly Belly jelly beans and evolutionary principles in the classroom: appealing to the students’ stomachs. *American Biology Teacher*, 62, 42–45.
- Lombard, F. (2011). New opportunities for authenticity in a world of changing biology. In A. Yarden & G.S. Carvalho (Eds.), *Authenticity in Biology Education: Benefits and Challenges* (pp. 15–26). Braga, Portugal: Universidade do Minho. Centro de Investigação em Estudos da Criança (CIEC).
- Lu, H. & Sheng, H. (1986). Distribution and status of the Chinese tiger. In S. Miller & D. Everett (Eds.), *Cats of the World: Biology, Conservation and Management* (pp. 51–58). Washington, DC: National Wildlife Federation.
- Lynam, A., Traeholt, C., Martyr, D., Holden, J., Kawanishi, K., van Strien, N.J. & Novarino, W. (2013). *Tapirus indicus*. IUCN Red List of Threatened Species. Version 2013.2. Available online at <http://www.iucnredlist.org>.

- Nyhus, P. (2008). *Panthera tigris* ssp. *amoyensis*. IUCN 2013. IUCN Red List of Threatened Species. Version 2013.2. Available online at <http://www.iucnredlist.org>.
- Oliver, P.T.P. (1975). Population genetics simulated with playing cards. *Journal of Biological Education*, 9, 83–85.
- Ortiz, M.T., Taras, L. & Stavroulakis, A.M. (2000). The Hardy-Weinberg equilibrium: some helpful suggestions. *American Biology Teacher*, 62, 20–22.
- Oxford, G.S. (1993). Genetic drift in a visibly polymorphic spider, *Enoplognatha ovata*: antidote to the peppered moth. *Journal of Biological Education*, 27, 115–120.
- Perry, R. (1965). *The World of the Tiger* (p. 190). New York, NY: Atheneum.
- Prieur, D.J. & Collier, L.L. (1984). Maltese dilution of domestic cats: a generalized cutaneous albinism lacking ocular involvement. *Journal of Heredity*, 75, 41–44.
- Robischon, M. (2014). Hugh's book and Krogh's animals: biodiversity and textbook examples in teaching. *Advances in Physiology Education*, 38, 195–198.
- Staub, N.L. (2002). Teaching evolutionary mechanisms: genetic drift and M&M's. *BioScience*, 52, 373–377.
- Stauffer, R.C. (Ed.) (1975). *Charles Darwin's Natural Selection; being the second part of his big species book written from 1836 to 1858* (pp. 121, 122). Cambridge, UK: Cambridge University Press.
- Stern, C. (1943). The Hardy-Weinberg law. *Science*, 97, 137–138.
- Tilson, R., Defu, H., Muntifering, J. & Nyhus, P.J. (2004). Dramatic decline of wild South China tigers *Panthera tigris amoyensis*: field survey of priority tiger reserves. *Oryx*, 38, 40–47.
- van Grouw, H. (2014). Some black-and-white facts about the Faeroese white-speckled common raven *Corvus corax varius*. *Bulletin of the British Ornithologists' Club*, 134, 4–13.
- Winterer, J. (2001). A lab exercise explaining Hardy-Weinberg equilibrium and evolution effectively. *American Biology Teacher*, 63, 678–687.
- Wright, S. (1929). The evolution of dominance. *American Naturalist*, 63, 556–561.
- Young, H.J. & Young, T.P. (2003). A hands-on exercise to demonstrate evolution by natural selection & genetic drift. *American Biology Teacher*, 65, 444–448.

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