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# References

## Aktuell


Marsden 2016

Clare D. Marsden et al., *Bottlenecks and selective sweeps during domestication have increased deleterious genetic variation in dogs.* PNAS **113** (2016), 152–156.

pnas113-00152-Supplement.xlsx

Clare D. Marsden, Diego Ortega-Del Vecchyo, Dennis P. O'Brien, Jeremy F. Taylor, Oscar Ramirez, Carles Vilà, Tomas Marques-Bonet, Robert D. Schnabel, Robert K. Wayne & Kirk E. Lohmueller

Population bottlenecks, inbreeding, and artificial selection can all, in principle, influence levels of deleterious genetic variation. However, the relative importance of each of these effects on genome-wide patterns of deleterious variation remains controversial. Domestic and wild canids offer a powerful system to address the role of these factors in influencing deleterious variation because their history is dominated by known bottlenecks and intense artificial selection. Here, we assess genome-wide patterns of deleterious variation in 90 whole-genome sequences from breed dogs, village dogs, and gray wolves. We find that the ratio of amino acid changing heterozygosity to silent heterozygosity is higher in dogs than in wolves and, on average, dogs have 2–3 % higher genetic load than gray wolves. Multiple lines of evidence indicate this pattern is driven by less efficient natural selection due to bottlenecks associated with domestication and breed formation, rather than recent inbreeding. Further, we find regions of the genome implicated in selective sweeps are enriched for amino acid changing variants and Mendelian disease genes. To our knowledge, these results provide the first quantitative estimates of the increased burden of deleterious variants directly associated with domestication and have important implications for selective breeding programs and the conservation of rare and endangered species. Specifically, they highlight the costs associated with selective breeding and question the practice favoring the breeding of individuals that best fit breed standards. Our results also suggest that maintaining a large population size, rather than just avoiding inbreeding, is a critical factor for preventing the accumulation of deleterious variants.

Keywords: deleterious mutations | domestication | bottleneck | selective sweep

Significance: Dogs have an integral role in human society, and recent evidence suggests they have a unique bond that elicits a beneficial hormonal response in both dogs and human handlers. Here, we show this relationship has a dark side. Small population size during domestication and strong artificial selection for breed-defining traits has unintentionally increased the numbers of deleterious genetic variants. Our findings question the overly typological practice of breeding individuals that best fit breed standards, a Victorian legacy. This practice does not allow selection to remove potentially deleterious variation associated with genes responsible for breed-specific traits.

Zona 2016

Donatella Zona et al., *Cold season emissions dominate the Arctic tundra methane budget.* PNAS **113** (2016), 40–45.

Donatella Zona, Beniamino Gioli, Róisín Commane, Jakob Lindaas, Steven C. Wofsy, Charles E. Miller, Steven J. Dinardo, Sigrid Dengel, Colm Sweeney, Anna Karion, Rachel Y.-W. Chang, John M. Henderson, Patrick C. Murphy, Jordan P. Goodrich, Virginie Moreaux, Anna Liljedahl, Jennifer D. Watts, John S. Kimball, David A. Lipson & Walter C. Oechel

Arctic terrestrial ecosystems are major global sources of methane (CH4); hence, it is important to understand the seasonal and climatic controls on CH4 emissions from these systems. Here, we report year-round CH4 emissions from Alaskan Arctic tundra eddy flux sites and regional fluxes derived from aircraft data. We find that emissions during the cold season (September to May) account for ≥50 % of the annual CH4 flux, with the highest emissions from noninundated upland tundra. A major fraction of cold season emissions occur during the "zero curtain" period, when subsurface soil temperatures are poised near 0 °C. The zero curtain may persist longer than the growing season, and CH4 emissions are enhanced when the duration is extended by a deep thawed layer as can occur with thick snow cover. Regional scale fluxes of CH4 derived from aircraft data demonstrate the large spatial extent of late season CH4 emissions. Scaled to the circumpolar Arctic, cold season fluxes from tundra total 12 ± 5 (95 % confidence interval) Tg CH4 y1, ≈25 % of global emissions from extratropical wetlands, or ≈6 % of total global wetland methane emissions. The dominance of late-season emissions, sensitivity to soil environmental conditions, and importance of dry tundra are not currently simulated in most global climate models. Because Arctic warming disproportionally impacts the cold season, our results suggest that higher cold-season CH4 emissions will result from observed and predicted increases in snow thickness, active layer depth, and soil temperature, representing important positive feedbacks on climate warming.

Keywords: permafrost | aircraft | fall | winter | warming

Significance: Arctic ecosystems are major global sources of methane. We report that emissions during the cold season (September to May) contribute ≥50 % of annual sources of methane from Alaskan tundra, based on fluxes obtained from eddy covariance sites and from regional fluxes calculated from aircraft data. The largest emissions were observed at the driest site (<5 % inundation). Emissions of methane in the cold season are linked to the extended "zero curtain" period, where soil temperatures are poised near 0 °C, indicating that total emissions are very sensitive to soil climate and related factors, such as snow depth. The dominance of late season emissions, sensitivity to soil conditions, and importance of dry tundra are not currently simulated in most global climate models.

## Anthropologie

### Hawkes 2016

Kristen Hawkes, *Genomic evidence for the evolution of human post-menopausal longevity*. PNAS **113** (2016), 17–18.

However, in the grandmother hypothesis an ancestral shift away from the independent mothering of the great apes occurred when drying and more seasonal environments reduced the availability of foods that just-weaned juveniles could handle. Then the few older females still surviving as their fertility declined could increase their fitness in a novel way; and those novel benefits at older ages resulted in selection for increased somatic maintenance and repair. In simulations of Peter Kim's two-sex agent-based model of the grandmothering scenario even very weak grandmothering drives populations from an ancestral ape-like equilibrium to a human-like one. At the ancestral equilibrium fewer than 1 % of the adult females are past their fertility, but their helpful grandmothering drives populations to a

new equilibrium with about 40 % of the adult females past their fertility, very like the age structures of modern hunter-gatherers.

## Hein 2016

Grit Hein, Jan B. Engelmann, Marius C. Vollberg & Philippe N. Tobler, *How learning shapes the empathic brain*. PNAS **113** (2016), 80–85.

Deficits in empathy enhance conflicts and human suffering. Thus, it is crucial to understand how empathy can be learned and how learning experiences shape empathy-related processes in the human brain. As a model of empathy deficits, we used the well-established suppression of empathy-related brain responses for the suffering of out-groups and tested whether and how out-group empathy is boosted by a learning intervention. During this intervention, participants received costly help equally often from an out-group member (experimental group) or an in-group member (control group). We show that receiving help from an out-group member elicits a classical learning signal (prediction error) in the anterior insular cortex. This signal in turn predicts a subsequent increase of empathy for a different out-group member (generalization). The enhancement of empathy-related insula responses by the neural prediction error signal was mediated by an establishment of positive emotions toward the out-group member. Finally, we show that surprisingly few positive learning experiences are sufficient to increase empathy. Our results specify the neural and psychological mechanisms through which learning interacts with empathy, and thus provide a neurobiological account for the plasticity of empathic reactions.

Keywords: empathy | in-group | learning | prediction error | fMRI

Significance: Deficits in empathy for out-group members are pervasive, with negative societal impact. It is therefore important to ascertain whether empathy toward out-groups can be learned and how learning experiences change empathy-related brain responses. We used a learning intervention during which participants experienced help from a member of their own social group or of a generally depreciated out-group. Our results show that the intervention successfully increased empathy-related brain responses toward the out-group. These changes in out-group empathy were triggered by the learning signal (prediction error) elicited during the first two positive out-group experiences. Together, our results show that classical learning signals update empathic brain responses and that surprisingly few positive experiences with an out-group member are sufficient to increase out-group empathy.

## Schwarz 2016

Flavio Schwarz, Stevan A. Springer, Tasha K. Altheide, Nissi M. Varki, Pascal Gagneux & Ajit Varki, *Human-specific derived alleles of CD33 and other genes protect against postreproductive cognitive decline*. PNAS **113** (2016), 74–79.

pnas113-00074-Supplement1.pdf

The individuals of most vertebrate species die when they can no longer reproduce. Humans are a rare exception, having evolved a prolonged postreproductive lifespan. Elders contribute to cooperative offspring care, assist in foraging, and communicate important ecological and cultural knowledge, increasing the survival of younger individuals. Age-related deterioration of cognitive capacity in humans compromises these benefits and also burdens the group with socially costly members. We investigated the contribution of the immunoregulatory receptor CD33 to a uniquely human postreproductive disease, Alzheimer's dementia. Surprisingly,

even though selection at advanced age is expected to be weak, a CD33 allele protective against Alzheimer's disease is derived and unique to humans and favors a functional molecular state of CD33 resembling that of the chimpanzee. Thus, derived alleles may be compensatory and restore interactions altered as a consequence of human-specific brain evolution. We found several other examples of derived alleles at other human loci that protect against age-related cognitive deterioration arising from neurodegenerative disease or cerebrovascular insufficiency. Selection by inclusive fitness may be strong enough to favor alleles protecting specifically against cognitive decline in postreproductive humans. Such selection would operate by maximizing the contributions of postreproductive individuals to the fitness of younger kin.

Keywords: CD33 | Siglec | postreproductive lifespan | Alzheimer's disease | cognitive capacity

Significance: Most vertebrates die soon after they stop reproducing, but humans are an exception. Postreproductive humans care for offspring, assist in foraging, and communicate ecological and cultural knowledge, increasing the survival of younger individuals. Loss of cognitive capacity disrupts these benefits and burdens the group with the care of older members. We studied how the immunoregulatory receptor CD33 contributes to Alzheimer's disease, a human-specific postreproductive condition. Surprisingly, a protective CD33 allele is derived and unique to humans, despite weak direct selection on older individuals. We identified several genes with derived alleles that protect against neurodegenerative disease and cerebrovascular insufficiency in old age. Selection by inclusive fitness may be strong enough to favor alleles that protect against cognitive decline in postreproductive humans.

## Datierung

Boaretto 2005

Elisabetta Boaretto, A. J. Timothy Jull, Ayelet Gilboa & Ilan Sharon, *Dating the Iron Age I/II Transition in Israel, First Intercomparison Results*. Radiocarbon **47** (2005), 39–55.

Nearly a decade ago, a different chronology than the conventional absolute chronology for the early Iron Age in Israel was suggested. The new, lower chronology "transfers" Iron Age I and Iron Age IIA contexts in Israel, traditionally dated to the 11th and 10th centuries BCE, to the 10th and 9th centuries, respectively. Thus, it places the Iron I|IIA transition at about 920–900 BCE. This alternative chronology carries important implications for Israelite history, historiography, and Bible research, as well as for the chronologies of other regions around the Mediterranean. Relevant radiocarbon data sets published to date, which were measured at different sites by different laboratories, were claimed to be incompatible. Therefore, the question of agreement between laboratories and dating methods needs to be addressed at the outset of any study attempting to resolve such a tight chronological dilemma. This paper addresses results pertaining to this issue as part of a comprehensive attempt to date the early Iron Age in Israel based on many sites, employing different measuring techniques in 2 laboratories. The intercomparison results demonstrate that: a) the agreement between the 2 laboratories is well within the standard in the 14C community and that no bias can be detected in either laboratory; and b) calculating the Iron I|IIa transition in 3 different ways (twice independently by the measurements obtained at the 2 labs and then by combining the dates of both) indicates that the lower chronology is the preferable one.

Finkelstein 2010

Israel Finkelstein & Eli Piasetzky, *Radiocarbon dating the Iron Age in the Levant, A Bayesian model for six ceramic phases and six transitions*. Antiquity **84** (2010), 374–385.

Antiquity084-0374-Supplement.pdf

The Bayesian model presented in this article is the first attempt to produce a chronological framework for the Iron Age in the Levant, using radiocarbon dating alone. The model derives from 339 determinations on 142 samples taken from 38 strata at 18 sites. The framework proposes six ceramic phases and six transitions which cover c. 400 years, between the late twelfth and mid eighth centuries BC. It furnishes us with a new scientific backbone for the history of Iron Age Levant.

Keywords: Levant | Iron Age | radiocarbon dating | chronology debate | Bayesianmodel | biblical | history

Mazar 2008

Amihai Mazar & Christopher Bronk Ramsey, *$^{14}C$ Dates and the Iron Age Chronology of Israel, A Response*. Radiocarbon **50** (2008), 159–180.

Boaretto et al. (2005) published 68 radiocarbon dates relating to 30 samples from 10 Iron Age sites in Israel as part of their Early Iron Age Dating Project. Though the main goal of their paper was an interlaboratory comparison, they also presented results of Bayesian models, calculating the transition from Iron Age I to Iron Age II in Israel to be about 900 BCE instead of the conventional date of about 1000 BCE. Since this date has great importance for all of Eastern Mediterranean archaeology, in this paper we examine the results in light of the dates published in the above-mentioned article. Our paper was revised in light of new data and interpretations published by Sharon et al. (2007).

Following a survey of the contexts and specific results at each site, we present several Bayesian models. Model C2 suggests the date range of 961–942 BCE (68 % probability) for the transition from Iron Age I to Iron Age II, while Model C3 indicates a somewhat later date of 948–919 BCE (compare the date 992–961 BCE calculated at Tel Rehov for the same transition). In our Model D, we calculated this transition date at Megiddo as taking place between 967–943 BCE. Finally, we calculated the range of dates of major destruction levels marking the end of the Iron Age I, with the following results: Megiddo VIA: 1010– 943 BCE; Yoqne'am XVII: 1045–997 BCE; Tell Qasile X: 1039–979 BCE; Tel Hadar: 1043–979 BCE (all in the 68.2 % probability range). Figure 4 indicates that the transition between Iron I and II probably occurred between these above-mentioned destruction events and the dates achieved in our Models C2 or C3, namely during the first half of the 10th century BCE.

This study emphasizes the sensitivity of Bayesian models to outliers, and for reducing or adding dates from the models. This sensitivity should be taken into account when using Bayesian models for interpreting radiometric dates in relation to subtle chronological questions in historical periods.

Sharon 2007

Ilan Sharon, Ayelet Gilboa, A. J. Timothy Jull & Elisabetta Boaretto, *Report on the First Stage of the Iron Age Dating Project in Israel, Supporting a Low Chronology*. Radiocarbon **49** (2007), 1–46.

The traditional chronology of ancient Israel in the 11th–9th centuries BCE was constructed mainly by correlating archaeological phenomena with biblical narratives and with Bible-derived chronology. The chronology of Cyprus and Greece,

and hence of points further west, are in turn based on that of the Levant. Thus, a newly proposed chronology, about 75–100 yr lower than the conventional one, bears crucial implications not only for biblical history and historiography but also for cultural processes around the Mediterranean. A comprehensive radiocarbon program was initiated to try and resolve this dilemma. It involves several hundreds of measurements from 21 sites in Israel. Creating the extensive databases necessary for the resolution of tight chronological problems typical of historical periods involves issues of quality control, statistical treatment, modeling, and robustness analysis. The results of the first phase of the dating program favor the new, lower chronology.

## Klima

Kopec 2016

Ben G. Kopec, Xiahong Feng, Fred A. Michel & Eric S. Posmentier, *Influence of sea ice on Arctic precipitation*. PNAS **113** (2016), 46–51.

Global climate is influenced by the Arctic hydrologic cycle, which is, in part, regulated by sea ice through its control on evaporation and precipitation. However, the quantitative link between precipitation and sea ice extent is poorly constrained. Here we present observational evidence for the response of precipitation to sea ice reduction and assess the sensitivity of the response. Changes in the proportion of moisture sourced from the Arctic with sea ice change in the Canadian Arctic and Greenland Sea regions over the past two decades are inferred from annually averaged deuterium excess (d-excess) measurements from six sites. Other influences on the Arctic hydrologic cycle, such as the strength of meridional transport, are assessed using the North Atlantic Oscillation index. We find that the independent, direct effect of sea ice on the increase of the percentage of Arctic sourced moisture (or Arctic moisture proportion, AMP) is $18.2 \pm 4.6\,\%$ and $10.8 \pm 3.6\,\%$/100,000 km2 sea ice lost for each region, respectively, corresponding to increases of $10.9 \pm 2.8\,\%$ and $2.7 \pm 1.1\,\%$/1 °C of warming in the vapor source regions. The moisture source changes likely result in increases of precipitation and changes in energy balance, creating significant uncertainty for climate predictions.

Keywords: water cycle | precipitation | sea ice | climate change | deuterium excess

Significance: There has been a growing consensus that a decrease in sea ice would cause an increase in Arctic precipitation because of the potential for increased local evaporation. We quantify the effect of sea ice on the percentage of moisture sourced from the Arctic, using measurements of the isotopic composition of precipitation at six sites across the Arctic. These moisture proportion changes are important in that they indicate systematic adjustment and/or reorganization of the global hydrological cycle with climate change and provide validation for climate models. We explore how much these changes may increase Arctic precipitation and its impact on the energy balance.

## Kupfer

Bouzek 1989

Jan Bouzek, Drahomír Koutecký & Klaus Simon, *Tin and Prehistoric Mining in the Erzgebirge (ore mountains), Some new evidence*. Oxford Journal of Archaeology **8** (1989), 203–212.

A number of settlements and other traces of occupation have been identified in the mountainous areas near to tin and copper deposits in the Erzgebirge, and some of them excavated. The newly collected evidence seems to suggest that many small sources of metals, both tin and copper, were exploited, the former metal by washing from the river and creek beds. Though these sources were more modest than the British and Spanish tin supply, they seem to have served the Bohemian and Saxon Bronze Age cultures well.

TAYLOR 1983

John W. Taylor, *Erzgebirge Tin, A closer look.* Oxford Journal of Archaeology **2** (1983), 295–298.

The publication of Muhly's Copper and Tin in 1973 was an important contribution to the study of the metal trade in antiquity. However, in his section on Central and Eastern European tin ore deposits, he ruled out the possibility, on geological grounds, that the Erzgebirge might be a source of tin ore in the Bronze Age. This paper is not in agreement with this conclusion, and attempts to reinstate the Erzgebirge as a viable source of tin in antiquity.