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Bergmann's Rule, Adaptation, and Thermoregulation in Arctic Animals: Conflicting Perspectives from Physiology, Evolutionary Biology, and Physical Anthropology After World War II

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Abstract. Bergmann's rule and Allen's rule played important roles in mid-twentieth century discussions of adaptation, variation, and geographical distribution. Although inherited from the nineteenth-century natural history tradition these rules gained significance during the consolidation of the modern synthesis as evolutionary theorists focused attention on populations as units of evolution. For systematists, the rules provided a compelling rationale for identifying geographical races or subspecies, a function that was also picked up by some physical anthropologists. More generally, the rules provided strong evidence for adaptation by natural selection. Supporters of the rules tacitly, or often explicitly, assumed that the clines described by the rules reflected adaptations for thermoregulation. This assumption was challenged by the physiologists Laurence Irving and Per Scholander based on their arctic research conducted after World War II. Their critique spurred a controversy played out in a series of articles in *Evolution*, in Ernst Mayr's *Animal Species and Evolution*, and in the writings of other prominent evolutionary biologists and physical anthropologists. Considering this episode highlights the complexity and ambiguity of important biological concepts such as adaptation, homeostasis, and self-regulation. It also demonstrates how different disciplinary orientations and styles of scientific research influenced evolutionary explanations, and the consequent difficulties of constructing a truly synthetic evolutionary biology in the decades immediately following World War II.

Keywords: Bergmann's rule, Allen's rule, Adaptation, Homeostasis, Thermoregulation, Carleton Coon, Laurence Irving, Ernst Mayr, Per Scholander

The problem involved [interpreting Bergmann's rule] is essentially a physiological one, but the comparative physiology of geographical races is in its infancy.

Theodosius Dobzhansky (1937, p. 171)

Evolutionists and physiologists meet in the concept of adaptation, and must listen to each other.

Per Scholander to Ernst Mayr (1955)[1]

Introduction

During the consolidation of modern evolutionary theory a set of biogeographical rules played a prominent role in wide-ranging discussions of adaptation, variation, and geographical distribution (Dobzhansky, 1937; Hesse et al., 1937; Goldschmidt, 1940; Mayr, 1942, 1963; Huxley, 1942; Rensch, 1960). Most notably, Bergmann's rule states that the size of individuals within a species tends to increase from warmer to colder climates. According to Allen's rule the lengths of limbs and other extremities tend to decrease from warmer to colder climates. These generalizations were inherited from the nineteenth-century natural history tradition and were based, in part, on widely accepted physiological ideas about how surface area and volume affected metabolism and thermoregulation in birds and mammals. Although the rules gained increased significance as evolutionists focused theoretical discussions on individual variation in populations during the mid-twentieth century, the causal basis of the biogeographical generalizations was challenged by comparative physiologists after World War II. The disagreement resulted in a controversy that remains incompletely resolved even today (McNab, 2012).

For systematists, the biogeographical rules provided a compelling rationale for identifying geographical races or subspecies (Mayr, 1942, Rensch, 1960). Physical anthropologists also applied the rules to human populations, and sometimes used them as a biological justification for elevating human races to the status of subspecies (Coon, 1962). Perhaps more importantly these geographical regularities provided powerful, albeit indirect, evidence for natural selection. Indeed, Ernst Mayr claimed that the geographical patterns described by the rules ''prove'' adaptation through natural selection (Mayr, 1942, p. 94). As such the rules played a critical role in the polytypic species concept that Mayr constructed after World War II. According to Mayr polytypic species were composed of numerous local populations that were in a constant adaptive tug-of-war between broad, species-specific homeostatic processes that maintained physiological constancy and minor ecotypic

[1] Letter from Scholander to Mayr, September 22, 1955 in Correspondence Box 4, Ernst Mayr Papers, Harvard University Archives.

variations that adapted individuals to local environmental conditions (Mayr, 1956, 1963 pp. 60–61, 1965). Bergmann's and Allen's rules exemplified the resulting geographic clines and their adaptive bases.[2]

Although Mayr sometimes treated the rules as empirical generalizations, he and other evolutionary biologists at least tacitly (and often explicitly) assumed that Bergmann's and Allen's rules reflected adaptations for thermoregulation based on volume and surface area. As an animal increases in size its heat-generating volume grows more rapidly than its heat-dissipating surface area. Thus, it seemed obvious that larger bodies would be advantageous in colder climates and smaller ones in warmer climates. This adaptive account was sharply criticized by the comparative physiologists Laurence Irving and Per Fredrik (Pete) Scholander based on their arctic research conducted after World War II. Irving (1959) dismissed attempts to use surface area to explain thermoregulation as "fictitious" and "absurd." The ensuing controversy played out in an exchange of articles in *Evolution* (Scholander, 1955, 1956; Mayr, 1956), in Mayr's later *Animal Species and Evolution* (1963), and in brief critical commentaries by other biologists and anthropologists (Irving, 1957, 1959; Newman, 1956; Rensch, 1960, Coon, 1962, Dobzhansky, 1970). This episode highlights both the complexity and ambiguity of important biological concepts such as adaptation, self-regulation, and homeostasis. These ideas were used both by comparative physiologists and evolutionary biologists, although not always with the same meaning or emphasis. Thus, this case also demonstrates how different disciplinary orientations and styles of scientific work influenced evolutionary explanations and the consequent challenges of establishing a truly synthetic evolutionary biology and an inclusive organismal biology in the decades immediately following World War II (Milam, 2010; Hagen, 2015).

The Irving–Scholander Partnership

Irving and Scholander left an enduring legacy in arctic biology and physiological ecology (Elsner, 2000; Dawson, 2007). Despite the fact that Scholander eventually settled in southern California with a professorship at Scripps Institution of Oceanography, his formative experiences as a young scientist involved several scientific expeditions to

[2] Although Mayr consistently argued that the rules were only valid at the subspecific level, other biologists (e.g. Hesse et al., 1937) used the rules to compare species within a genus or even higher level taxa (see also McNab, 2012).

Greenland and Spitzbergen during the early 1930s. His later exploits during World War II, including a daring, unauthorized parachute rescue of downed airmen on snow-covered Mount Pavlof made Scholander a legendary figure.[3] During the war Scholander and Irving conducted applied physiological research for the U.S. Army Air Forces in a variety of locations, including Alaska (Elsner, 2000). This arctic interlude and Scholander's enthusiastic encouragement spurred Irving's interest in physiological adaptations to cold environments. After the war Irving played a crucial role in establishing a small arctic research laboratory supported by the Office of Naval Research and housed in a Quonset hut at Point Barrow at the northern tip of the territory (Shelesnyak, 1948a, b; Irving, 1948; Britton, 1967; Reed, 1969). It was from this modest Arctic Research Laboratory that Scholander (Figure 1) led the team in writing a series of highly influential, and sometimes provocative, articles on temperature regulation in animals. Indeed, one recent commentator has suggested that these articles marked the beginning of modern physiological ecology (McNab, 2012, p. 26). By calling into question the physiological basis for Bergmann's and Allen's rules these articles also served as the flashpoint for a controversy with the evolutionary biologist Ernst Mayr and the physical anthropologist Carleton Coon who were strong proponents of these biogeographical rules. The issues raised in the controversy continue to challenge evolutionary biologists, ecologists, and comparative physiologists today.

Trained as a physician at the University of Oslo, Scholander quickly lost interest in his medical studies (Schmidt-Nielsen, 1987). He completed the medical degree without enthusiasm, but his intellectual focus had shifted to lichens. His fascination with these simple, symbiotic organisms attracted the attention of the Professor of Botany Bernt Lynge who arranged for Scholander to take part in three collecting expeditions to Greenland and Spitzbergen. Lichen systematics became a lifelong interest, although Scholander wrote his Ph.D. dissertation on

[3] Scholander's commanding officer specifically prohibited an air rescue attempt as too dangerous. Scholander, a medical officer, and a chaplain managed to convince a military pilot to fly them to the crash site. Although none of the men had ever used a parachute, they successfully jumped near the downed plane and aided the three surviving crew members until dog sleds arrived to evacuate them a few days later. Later accounts (Scholander, 1990, pp. 47–52; Schmidt-Nielsen, 1990) claimed that the three acted in direct defiance of the order, with Scholander telling his commander "Go to bloody Hell, this is my business." However, the letters of commendation after the event state that Scholander was unaware of the prohibition when he planned the rescue. In any case, the rescue mission was a gutsy and heroic act that probably saved the surviving crew members' lives; see news articles and letters of commendation in the Per Fredrik Scholander papers, Box 16, University of California at San Diego Archives.

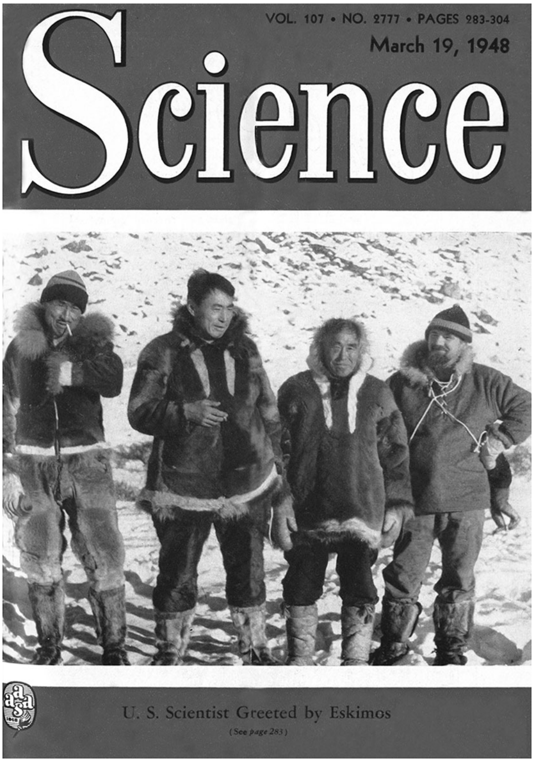

Figure 1. Per Scholander (far right) on the cover of an issue of *Science* that included articles about the newly established Arctic Research Laboratory. From *Science*, March 19, 1948, vol. 107, No. 2777. Reprinted with permission from AAAS

the vascular plants of Spitsbergen rather than lichens. Scholander would continue to make important contributions to botany. However, shortly after completing his Ph.D. in 1934, the direction of his research shifted once again, this time to the respiratory physiology of marine mammals. His early experiments conducted on small harbor seals submerged in a bathtub laid important foundations for the modern understanding of the diving reflex found in all mammals. The preliminary results of these experiments impressed the Nobel laureate August Krogh who invited Scholander to join his zoophysiology laboratory at the University of Copenhagen.

Through Krogh's influence, Scholander was awarded a Rockefeller fellowship to study in the United States, but with the outbreak of World War II the Institute decided to cancel all European awards

(Scholander, 1990, pp. 35–40).[4] Apparently Krogh caught wind of this decision and managed to get Scholander aboard a ship to the United States before the official notice of the cancellation arrived. Showing up in New York, Scholander presented the Rockefeller Foundation with a *fait accompli*. Unwilling to send him back to an uncertain wartime future in Denmark, the foundation decided to honor the fellowship. Following the original plan, Scholander moved to Swarthmore College to work with Irving, who was chair of the Biology Department and shared the Scandinavian physiologist's interest in diving mammals. Their joint research in this area was eventually cut short by military service, but the collaboration between 1939 and 1942 resulted in a series of important articles on the physiology of diving in harbor seals, dolphins, and manatees. Based on diving physiology, Scholander and Irving developed a more general model for understanding self-regulation and adaptation that combined comparative physiology, ecology, and evolution in a novel way. It later provided the intellectual foundation for their critique of the biogeographical rules of Bergmann and Allen.

The Diving Reflex as a Model of Adaptation and Self-regulation

The research on diving physiology provided the foundation for a strikingly new perspective on self-regulation that would later color the way Scholander and Irving interpreted adaptations to arctic environments. The adjustments made during diving involved integrated, systemic changes that maintained constancy in key physiological processes while allowing others to partially conform to environmental stresses. Although central nervous control was important, the body was compartmentalized and local tissues exhibited some autonomy throughout the dive and during recovery. According to Scholander, the highly developed adaptations to spending long periods underwater had evolved from more basic vertebrate responses to asphyxia that were widely distributed. Evolution had perfected these responses, but the self-regulatory mechanisms of diving physiology also reflected a fine line between adaptive responses and pathological derangements.

From their earlier studies Scholander and Irving knew that normal metabolism could not be maintained during prolonged dives (Irving, 1934; Elsner, 2015). Although diving mammals often had significantly

[4] See letters from Krogh to Irving concerning Scholander's fellowship dated May 31, 1939 and November 25, 1939 in Series 2, Box 3, Laurence Irving Collection, University of Alaska Archives.

more hemoglobin and larger volumes of blood than other animals of similar size, the amount of stored oxygen was far too small to support aerobic metabolism for the 20-min dives that seals sometimes made. The initial physiological response to diving was bradycardia. This reduction of heart rate was typical of all mammals and many other animals, but harbor seals exhibited an extreme cardiac response to submersion with heart rate almost immediately plummeting from more than 100 beats per minute to around 10. Blood pressure was maintained by largely shutting down peripheral circulation. This had profound physiological effects, particularly during long, active dives (what Scholander and Irving referred to as "struggling" dives). Oxygen used to maintain essential functioning of the heart and central nervous system was depleted in a slow, linear fashion that ultimately determined how long the animal could stay under water. Because muscle tissue was largely sequestered from the circulation the overall metabolic rate dropped, sometimes below the normal resting level. In prolonged, active dives this tendency was countered by increased muscular contraction needed for hunting prey or other energetic activities. In this case, muscle tissue quickly exhausted the limited oxygen stored in myoglobin and relied entirely on anaerobic energy production. In essence, the seal was experiencing localized asphyxia in the muscles, even though the brain was kept well-oxygenated.

Reduced metabolism also meant less heat production. As a result the body temperature except in core organs dropped, although this chilling effect was partly compensated by reduced peripheral blood flow. Nonetheless, the researchers characterized the compounding effects of reduced metabolism and body temperature as a "vicious circle" and after surfacing from long dives seals often exhibited prolonged shivering to restore body temperature (Scholander et al., 1942). After a dive lactic acid from the muscles literally "poured" into the blood stream. This "oxygen debt" was repaid by metabolizing the accumulated lactic acid, accomplished by increased respiration and peripheral circulation. The cooling effect of this increased flow of blood beneath the skin sometimes resulted in an actual drop in core body temperature during recovery from a prolonged dive.

Overall, the physiology presented by diving mammals was remarkably labile. Diving resulted in profound changes in metabolism, body temperature, and circulation. Self-regulation in this case was more than simple homeostatic control. It involved maintaining constancy in oxygen supplied to key tissues of the central nervous system, but also allowing other organs to conform to lack of oxygen in an orderly manner and to recover quickly after the stress ended. Body temperature was remarkably variable in diving mammals – an important idea that Scholander and Irving later elaborated when they studied thermoregulation in arctic animals. In the case of diving, fluctuating temperature was an important part of a response to lack of oxygen. Scholander came to identify bradycardia as a fundamental vertebrate response to impending asphyxiation (Scholander et al., 1942; Scholander, 1962, 1963; Elsner, 2015). It acted as a kind of "master switch" that reduced metabolism and body temperature in the face of impending oxygen deprivation.

This point was driven home by a rather unusual experiment Scholander and Irving conducted in Panama using three-toed sloths. Although diving was hardly a natural behavior for these arboreal animals, they were capable of remaining underwater for 20 min without apparent distress (Irving et al., 1941, 1942). During submersion heart rate and body temperature decreased just as it did in diving seals. Because the already low metabolism of these lethargic animals decreased even further they did not incur a large oxygen debt. At the end of the experiment the breathing rate of the sloths did not increase and little lactic acid was detected in the blood, in sharp contrast to the much more active diving mammals. Scholander and his students later found bradycardia followed by decreased metabolism in fish when they were removed from the water. In clinical medicine the response was found in fetuses during difficult deliveries and in pathological situations involving lack of oxygen. It was also part of the initiating sequence of events in hibernation. Evolution, it seemed to Scholander, had modified the "master switch" of bradycardia to regulate responses to a wide range of environmental stresses in different animals (Scholander, 1962, 1963). Diving physiology was simply an extreme elaboration of this general regulatory mechanism that allowed seals and other diving mammals to remain active underwater for extended periods.

"Self-regulation" in this case was more ambiguous than conventional physiological ideas of homeostatic control. Fluctuating body temperature during and after a dive was not necessarily adaptive in and of itself, but rather a consequence of decreased metabolism and changes in peripheral circulation. Characterizing this relationship between temperature, metabolism, and circulation as a potential "vicious circle," highlighted both the link between bradycardia and asphyxiation and the fine line between stability and pathological disorder. Fluctuating body temperature also blurred the distinction that comparative physiologists often made between animals that were environmental regulators and those that were conformers. Mammals were the quintessential temperature regulators, yet in the case of diving mammals body temperature was a labile characteristic that could vary significantly depending upon environmental conditions and behavior. The idea of "heterothermy" was sometimes applied to bats and other small mammals that occasionally abandoned temperature regulation in order to conserve energy. Scholander and Irving broadened this concept to include extremities and other body parts when they discussed thermoregulation in extreme environments. Temperature regulators did not necessarily regulate all parts of the body equally, and heterothermy could be both an adaptation for conserving energy and a mechanism for dissipating excess heat. Variable and fluctuating body temperatures among "warm-blooded" animals were so pervasive that the conventional idea of homeostasis was a misleading concept erroneously describing control systems that would be both "inoperable and unadaptable" in nature (Irving, 1959, p. 25).

The research on diving mammals was interrupted by the United States' entry into the war. Irving enlisted and was assigned to direct physiological research for the U.S. Army Air Forces (Elsner, 2000; Dawson, 2007). Scholander joined him in studying the effects of carbon monoxide given off by stoves in tents and helped develop protective clothing and survival equipment for use in cold environments.[5] A broader understanding of adaptations to cold climates continued to have great strategic significance during the Cold War (Farish, 2010, 2013), and Irving effectively combined the results of wartime research on human adaptation, earlier studies on diving mammals, and the political, economic, and strategic needs of a global superpower to argue for a permanent arctic laboratory for comparative physiological ecology. The hallmark of the "Scholander and Irving style" of physiological research was applying sophisticated laboratory procedures in remote and often hostile environments (Elsner, 2000), but also combining experimental biology with a deep understanding and appreciation for natural history (Dawson, 2007). Especially for Scholander (1978, 1990), the arctic laboratory also provided an idyllic vision of pure research done in isolated regions and free from the bureaucratic entanglements of academic science. In the postwar years both Irving and Scholander emphasized the peaceful uses of scientific research and the importance of international cooperation, but despite Scholander's later political misgivings the Office of Naval Research and other military agencies

[5] Although he did not become a naturalized citizen until 1945, Scholander was commissioned as a captain and promoted to major in the U.S. Army Air Forces during the war; see his curriculum vita in Box 1, Scholander Papers.

Figure 2. The physiology laboratory of the Arctic Research Laboratory at Point Barrow Alaska. Scholander is standing in the doorway (fourth from right) next to Irving (third from right). The original photo is in Box 43, Laurence Irving Collection, Archives of the University of Alaska Fairbanks. Reprinted with permission from the University of Alaska Fairbanks

provided the crucial support for establishing the Arctic Research Laboratory.[6] This remote laboratory (Figure 2) provided the base for a series of highly innovative experimental studies on adaptation to cold using a wide variety of organisms including mammals, birds, insects, aquatic invertebrates, mosses, and lichens (Scholander et al., 1950a, b, c, 1953).

Thermoregulation and Adaptations to Extreme Temperatures

Scholander's approach to research often started with seemingly casual observations that led to intriguing questions about self-regulation and adaptation. His ability to design simple, elegant experiments provided a way to test hypotheses, but he also had a penchant for using the results to make more sweeping generalizations that linked the initial observations to seemingly unrelated phenomena. Why, for example, did sled

[6] See the program and report of the ''Conference on Opportunities for Physiology in the Field under Natural Conditions,'' sponsored by the National Research Council and chaired by Irving, April 26, 1946 in Irving Papers, series 2, box 4. Scholander deplored the ''political and military chauvinism'' that opposed international cooperation in arctic research; see comments at the dedication of the Laurence Irving Building of Bioscience at the University of Alaska (undated), Box 9, Scholander Papers. The building opened in 1965.

dogs at the station sleep exposed on the frozen snow at −50 °C even when they were provided with shelter boxes? This curious canine behavior might be common knowledge to those living in the arctic, but it raised fundamental questions about animal energetics and thermoregulation. Through Irving's military connections Scholander was able to use army aircraft for expeditions to Panama and Cuba to conduct experiments and collect tropical specimens to compare with arctic animals. Thus what might have been a series of rather narrow studies on arctic adaptations in mammals, became a broader comparative study of the physiological ecology of a very wide range of animals – both warm and cold blooded, not to mention lichens and plants.

The research intentionally challenged the traditional sharp distinctions between homeotherms that regulate body temperature and poikilotherms that conform to environmental temperatures. Noting that arctic fish and aquatic invertebrates were just as active as their tropical relatives, Scholander and Irving argued that poikilotherms used a variety of physiological and behavioral adaptations that constituted a "homeostatic tendency" allowing "cold-blooded" animals (and plants) to survive – and even thrive – in frigid temperatures (Scholander et al., 1953; Irving, 1959). Their studies also drew counterintuitive conclusions about the nature of thermal stresses encountered by tropical and arctic birds and mammals. In the topsy-turvy world that Scholander and Irving described some tropical mammals shivered to keep warm when environmental temperatures dipped a few degrees at night, while large arctic mammals risked overheating even at the coldest temperatures found on earth (Scholander et al., 1950b). Size was an important variable when comparing a range of large and small animals from various taxa, but Scholander claimed that the very modest clinal variation described by Bergmann's rule was swamped by more important physiological and behavioral factors.

For homeotherms, insulation was the important variable in temperature regulation. Within a broader or narrower range of environmental temperatures (the thermal neutral zone) birds and mammals can maintain body temperature without expending additional energy simply by increasing or decreasing insulation. In short term responses this means raising or lowering hair (or fluffing feathers), seasonally it may involve shedding or growing more insulation. Above an upper critical temperature energy must be expended to dissipate body heat through panting or sweating. Below a lower critical temperature increased metabolism and shivering are required to maintain body temperature. What was most striking from comparisons among animals from different climates or of different sizes was the range of temperatures over which thermal neutrality could be maintained. The thermal neutral zone was not simply shifted downward in arctic animals, it was broadened. Tropical birds and mammals appeared to exist near the upper temperature limit for life, and could maintain neutrality only over a small range of environmental temperatures. By contrast, many arctic mammals could maintain thermal neutrality over a very wide range of ambient temperatures.

Surprisingly, arctic mammals from foxes to caribou often had about the same amount of insulation. There was seemingly no reason why a 500 kg moose couldn't grow longer hair than a 5 kg arctic fox if staying warm was a major adaptive problem. Apparently, this wasn't the case except for the smallest birds and mammals which faced daunting physical constraints on thermoregulation. According to Scholander and Irving, small animals tend to lose heat disproportionately both because of size and inadequate insulation. To stay warm in even moderate conditions a mouse-sized mammal needed either an impossibly thick coat of fur or a very high rate of metabolic heat production.[7] In the harsh conditions of the arctic many small homeotherms avoided this conundrum through adaptive behavior. Lemmings and other small mammals protected themselves from winter cold by living under the snow or staying in underground burrows insulated with grass and caribou hair. By escaping from the intense cold, these small mammals utilized a form of ‘‘behavioral thermoregulation'' analogous to the shelter and clothing employed by humans (Scholander et al., 1950b). Most birds were unable to utilize this behavioral strategy, and either migrated to warmer climates during the winter or relied entirely on high metabolic rates to offset heat loss.

Finding that the amount of insulating fur was not significantly different in many arctic mammals larger than foxes or dogs suggested that heat loss was not the only thermoregulatory challenge facing larger homeotherms in cold climates – or perhaps even the most important. This was confirmed by comparing metabolic rates of animals at different environmental temperatures. In experimental tests on foxes and dogs at Barrow, ambient temperatures never got cold enough to determine the lower limits of the thermal neutral zone. Foxes tested in more sophisticated environmental chambers at the Naval Research Laboratory in Washington, D.C. finally began to shiver when the temperature drop-

[7] This point was highlighted by the physiologist Klieber's (1961, p. 11) estimate that if a mouse had the metabolic rate of a dog, it would require fur 20 cm thick to maintain body temperature even at moderate ambient temperatures found in temperate climates.

ped to about −70 °C, which approached the coldest temperatures naturally occurring on earth (Scholander et al., 1950a). Modestly increasing metabolism by 40% was adequate to maintain normal body temperature in the environmental chamber. Doubling the metabolic rate could theoretically allow the foxes to maintain body temperature even at −120 °C. If insulation were adequate to keep resting animals warm even in the intense cold of Alaskan winter nights, it seemed likely that overheating might be a serious adaptive challenge when these animals were active, especially in milder conditions.

Contrary to the implications of Bergmann's rule and Allen's rule, Scholander claimed that large arctic mammals didn't need to reduce the surface area of the body or extremities in order to prevent heat loss. Any mammal larger than a fox actually needed adaptations to dissipate body heat. Scholander and Irving pointed out that fur was usually unevenly distributed, and was often sparser on the belly and extremities. Far from needing to reduce the length of these extremities, as Allen's rule suggested, the physiologists claimed that poorly insulated legs and ears might actually serve as radiators to prevent overheating. Often these parts of the body were maintained in a heterothermic condition several degrees below core body temperature and other anatomical specializations appeared well-adapted for maintaining function at low temperatures. The fat found in legs of arctic mammals tended to have a significantly lower melting point than fat in the rest of the body. Peripheral nerve transmission in arctic mammals was unaffected by low temperatures, even though it was disrupted in the limbs of temperate animals exposed to the same temperature regime. Regulating peripheral blood flow was also an important thermoregulatory adaptation that could be used to either conserve or dissipate heat depending on environmental conditions.

Tropical mammals provided a sharp contrast with their arctic relatives. Because they generally had less insulating fur than comparably sized arctic mammals, the thermal neutral zone for tropical mammals was relatively narrow. Even dropping environmental temperatures a few degrees resulted in a sharp increase in metabolic heat production. In contrast to the sled dogs that could maintain body temperature while sleeping on frozen snow some tropical mammals faced hypothermia every night. Sloths, which have very low metabolic rates compared to other mammals, would actually start shivering at 27 °C despite furry insulation that was twice as thick as other tropical mammals of the same size. The long limbs used for arboreal locomotion, also resulted in loss of heat during cool tropical nights. As a thermoregulatory adaptation, the limbs had networks of veins surrounding arteries to allow countercurrent exchange of heat. Despite this adaptation, the temperature of the limbs often dropped several degrees during the night and sloths sometimes required an hour or more of activity to rewarm their limbs during the day. Interestingly this type of heterothermy in limbs was also found in some humans, although it remained unclear whether this was due to genetic adaptations or acclimatization. Disagreements about human adaptation (and adaptability) to cold environments became central to the broader debate over thermoregulation and biogeographical rules.

Biogeographical Rules and Human Adaptations to Cold Environments

Scholander (1955, 1956) was scathingly critical of evolutionary biologists and biogeographers who accepted Bergmann's and Allen's rules and who claimed that apparently insignificant changes in body size and limbs were adaptations for thermoregulation. If evolutionary biologists had taken physiology too lightly, Scholander was even more critical of physical anthropologists who applied biogeographical rules to human races. Scholander was stridently opposed to the ideas of "climatic engineering" in human evolution that Carleton Coon used to explain supposed racial differences. In particular, Scholander (1955, 1956) argued that there was no evidence for a reduction in length of extremities or overall body size of Alaskan Natives compared to other ethnic groups. Scholander was deeply interested in the question of thermoregulation in humans, but he considered the success of indigenous arctic people in adapting to cold climates to be primarily cultural rather than biological:

> In the Eskimo the main adaptation lies not in physiology, but in an age-long experience and technical skill in ducking the cold. They conquered the arctic not by submitting to it but by surrounding themselves successfully with a little piece of the same tropical microclimate upon which we also depend (Scholander 1955, p. 23).

Warm clothing and shelter, not natural selection of morphological characteristics, allowed humans to thrive in the arctic. Humans might vary in their physiological responses to cold, but according to Scholander these responses were more a matter of adaptability, acclimatization, and cultural innovation than hereditary adaptations molded by climate. These points were echoed by Irving (1959) who wrote:

> In the case of the Eskimos they have suited their physiological adaptability to arctic cold by an ingenious and highly developed

> material and social culture which has secured their racial existence during ten centuries which have seen the disappearance of most of the societies and many of the populations living in milder lands.

There was no shortage of studies to base competing claims about the validity of biogeographical rules in humans. World War II and the Korean War focused considerable attention on human performance and survival in cold conditions, and brought together insights from physical anthropology, physiology, and the nascent ''science of clothing'' (Newburgh, 1949). Many of these studies investigated differences between populations and were conducted within a context that assumed the biological basis for human races that Coon and others supported (Farish, 2013). Nonetheless, the extent to which adaptations reflected racial characteristics or were the product of physiological acclimatization remained an open question. The antipathy that Scholander and Irving held for Coon's views was motivated not only by a disdain for biogeographical rules, but also by their deep admiration for native Alaskan culture and their fears that native folk knowledge of the arctic that had proved so adaptive was rapidly disappearing as a result of the spread of modern western technologies and culture (Irving, 1959, 1965).[8]

During the late 1950s and early 1960s Scholander and Irving became deeply involved in comparative studies of human responses to cold temperatures.[9] Ironically, Coon joined Scholander and a group of other

[8] Irving treated the Alaskan Natives who he worked with at the Arctic Research Laboratory as colleagues and experts on local natural history and life in the arctic (Brewster, 1997; Dawson, 2007). Success in the arctic depended upon cultural traditions, experience, and adaptability rather than innate physiological characteristics found in different populations (Irving, 1959; Irving et al., 1960). Indicative of this attitude was Irving's early plan for research on humans which was based on the assumption that the physiology of cold tolerance was based on acclimatization, adjustment, and diet, rather than genetic differences among humans (Irving, 1948). Irving's attitude toward native peoples is in marked contrast to the ''fascination with race'' that Farish (2013) describes as underlying physiological research on Alaskan Natives conducted by scientists at the nearby Arctic Aeromedical Laboratory at Ladd Air Force Base in Fairbanks. The scientists described by Farish looked for racial differences even in the face of contrary data. The opposite tendency was sometimes evident in the research on human thermoregulation conducted by Irving and Scholander.

[9] The perceived strategic importance of studies of adaptation and acclimatization to cold is evidenced by the fact that the international expeditions that Scholander organized were supported by the Rockefeller Foundation, Office of Naval Research, United States Air Force, Royal Canadian Air Force, and several Australian Universities and government agencies. Correspondence concerning the planning of these expeditions can be found in the Scholander Papers, Boxes 7 and 8.

physiologists on an expedition to Tierra del Fuego. His interpretation of the results of experiments done on the Alacaluf and other ethnic groups was diametrically opposed to Scholander's skeptical attitude toward hereditary adaptations to cold. These studies highlighted the difficulty of separating the effects of genetics, acclimatization, and cultural adaptability. This difficulty complicated the application of Bergmann's and Allen's rules to humans, and formed an important part of the controversy between Irving and Scholander on one side and Mayr and Coon on the other.

The native Fuegians' remarkable ability to tolerate extreme cold was made famous by Charles Darwin's vivid descriptions in the *Voyage of the Beagle*. When the physiologists visited in the late 1950s some of the tribes remained sufficiently remote that Coon considered them to be an "unmixed" race (Coon, 1962, pp. 60–68).[10] The physiologists found that the Alacaluf's ability to swim in near freezing water and survive largely unclothed was an extreme elaboration of a physiological response shared by all humans – they produced heat by increasing metabolism. This adaptation was also found to be true of Alaskan Natives – and was at least latent in urban Europeans. Scholander managed to convince a group of Norwegian college students to sleep unclothed in near freezing conditions. The experience was intensely unpleasant at first, but within a matter of days the students were able to sleep comfortably through the night by significantly increasing metabolic heat production (Scholander et al., 1958a; Hammel, 1964).[11]

In another study, Scholander and his colleagues discovered a strikingly different adaptation among Australian Aborigines of the Pitjandjara tribe who slept comfortably without clothing in freezing temperatures with only small fires for heat (Scholander et al., 1958b).[12] When the physiologists tried to match this feat they spent an uncomfortable, sleepless night. Careful measurements of oxygen consumption

[10] For a quite different account of indigenous people living in cold climates, see Irving (1965, 1972, Chap. 12). Irving was critical of Darwin's observations of Fuegians, which he considered exaggerated.

[11] The research on human thermoregulation is also described by Scholander (1978, 1990, Chaps. 17 and 18). Extensive correspondence related to planning the expedition is in Box 8, Scholander papers.

[12] See correspondence between Scholander and Australian biologists, including Cedric Stanton Hicks about the expedition, Box 7, Scholander Papers. Hicks' earlier research during the 1930s on thermoregulation in Australian Aborigines is described in Anderson (2003, pp. 211–214). Anderson provides a detailed study of shifting views on genetics, environment, and race in Australian anthropology and medical research prior to World War II.

showed that the Aborigines' metabolism remained at the resting rate throughout the night. However, the temperature of their limbs dropped to about 10°C while they slept. In the morning the Aborigines quickly rewarmed their arms and legs by stomping around the camp. This heterothermy, so reminiscent of the adaptations found in many of the arctic animals that Scholander and Irving studied, seemed to be a unique characteristic found in no other human population – at least that was Coon's conclusion when he later summarized the physiological research in his book *The Origin of Human Races*.

Although he was merely an observer not directly involved in the physiological research and not an author on any of the resulting articles, Coon had a deep interest in using the data to support his claim that human races are biologically real and sufficiently different to be considered subspecies. Bergmann's and Allen's rules were a critical part of Coon's argument (Coon, 1962, pp. 60–68). Racial differences in stature, facial structure, size of feet and other extremities might only be statistical, but they were significant and from Coon's perspective they had an obvious adaptive basis for thermoregulation. Repeating the claim that these differences were based on the effects of surface area and volume on heat loss, Coon claimed that natural selection had molded some races to face the challenges of frigid climates and others desert heat. Noting that Scholander had criticized this explanation, Coon placed himself squarely in the camp of Ernst Mayr and other "taxonomists and physical anthropologists" who defended the biogeographical rules (Coon, 1962, p. 60). Denying that cultural and technological innovations outweighed subspecific differences in human adaptation to climate, Coon believed that the results of physiological studies of thermoregulation held an important key to understanding human evolution:

> Once man's inventive genius had made it possible for him to live in extreme environments previously barred to him, a new burden was placed on his physiology because he could not, with his incipient skills, overcome all climatic obstacles. We must expect to see the results of genetic responses, through natural selection, to differences in environment, and we must know how to interpret them, for the patterns they take will tell us much about the early history of our genus and species (Coon 1962, p. 40).

According to Coon, the different adaptations to cold found in Fuegians (and other groups) on one hand, and Australian Aborigines on the other reflected ancient genetic, physiological, and anatomical differences between human subspecies. The physiologists who actually conducted the research took a more skeptical attitude toward the racial implications of the studies. When interviewed by a reporter, Scholander's protégé Robert Elsner cautioned against drawing conclusions about a genetic basis for racial differences in thermoregulation, stating "We don't know that there might not be some kind of psychological or social conditioning factor here" (Pastorius, 1958).[13] Ted Hammel, the University of Pennsylvania physiologist who organized the expedition to Tierra del Fuego, was willing to consider Coon's claims, but he remarked that any evolutionary conclusions based on the physiological research were speculations (Hammel, 1964).

Irving (1960) challenged the idea that heterothermy was a unique hereditary adaptation of Australian Aborigines in a somewhat flippant article in *Nature* that he hoped would "arouse response."[14] Irving had become the leading authority on heterothermy in arctic animals and he shared Scholander's disdain for racial distinctions. In the brief, two-page note Irving reported the results of cold tolerance tests done on a young airman who had been stationed for 2 years in the arctic and two students at the University of Alaska. As members of the Fount of Venta religious cult which had recently moved from California to Alaska, the students wore only light robes and went barefoot even during the Alaskan winter. Clothed as they were, the students were able to stand comfortably or even sit and read for 90 min at freezing temperatures in a controlled cold room. Thermocouples attached to their toes and fingers recorded oscillations in skin temperature dropping to as low as 9°C during the experiment. The students were able to rather precisely distinguish between the warming and cooling phases of these cycles. They reported little discomfort and retained feeling in their digits. Even after an hour of inactivity, they experienced only mild shivering. At the end of the experiment, they reported no pain as their toes and fingers rewarmed.

The reaction of the airman was strikingly different, even though he was apparently highly motivated to duplicate the students' performance. Dressed in his military fatigues, he began violently shivering

[13] A copy of this news article is in Box 17, Scholander Papers.

[14] Though hardly a definitive study, Irving wanted to make his point in a striking and provocative way: see the letter from Irving to Scholander, May 27, 1959, in the Irving Papers, Series 2, Box 12. Irving originally planned the note to appear in *Science*, and the nine-month hiatus between his letter and the eventual publication in *Nature* suggests that the original submission was unsuccessful. Irving later placed this experiment within the broader context of heterothermy in human and arctic animals in a longer review article (Irving, 1962, pp. 133–174).

almost immediately. Although the skin temperature of his fingers and toes did not get as cold as the students, he reported extreme pain. After about 40 min, Irving concluded that the airman's ''fortitude was not contributing further to physiology'' and he terminated the experiment. In contrast to the students, the airman reported discomfort as his fingers and toes warmed.

In his conclusion Irving emphasized the ''latent adaptability'' of humans. By deliberately exposing themselves to cold conditions during the 2 years that they had belonged to the Fount of Venta the students had developed some of the same physiological responses found in indigenous groups which had inhabited cold climates for millennia. Not only were they able to tolerate cold with little discomfort, but they had developed a heightened awareness of changes in body temperature. Rather than experiencing a generalized pain or numbness, they had developed the ability to distinguish very subtle changes in skin temperature. Irving pointed out that this same awareness was used by Alaskan Natives who rarely suffered frostbite because they knew when to protect exposed skin or seek shelter. He also suggested that the students had probably not reached the limits of adaptability and that cult members who habitually worked outdoors might be even more tolerant of cold than those who spent their days in the classroom. Presumably these physiological changes were possible for any human given proper motivation and practice.

Scholander's and Irving's attacks on biogeographical rules, especially as applied to humans, put evolutionary biologists and anthropologists on the defensive. The quandary faced by physical anthropologists is highlighted in the response of Marshall Newman. Newman's left-leaning politics, particularly on issues of racial equality, were considered sufficiently subversive that both the FBI and Navy Intelligence kept him under surveillance during the early 1950s (Price, 2004, pp. 177–184). His willingness to defend racial minorities also antagonized some of his colleagues at the Smithsonian Institution.[15] Although skeptical of the sweeping claims about the biological basis of human races, Newman had written a generally favorable book review of Carleton Coon's earlier book, *Races* (Newman, 1950). He applauded Coon's attempts to infuse physical anthropology with the latest evolutionary theory

[15] According to Price (2004) the FBI concluded that Newman was not a communist but his ''poor judgement'' might lead him to be duped into subversive activities. Newman's supervisor at the Smithsonian Institution criticized his ''championing the underdog'' particularly in racial matters. This caused particular concern when Newman sought permission to act as an expert witness for the NAACP in the case of a couple accused of violating Virginia's miscegenation statute.

developed by population geneticists, paleontologists, and systematists during the modern synthesis. Newman had also staked much of his professional reputation on the application of Bergmann's and Allen's rules to human populations (Newman, 1953). Although acknowledging that Scholander's criticism of the thermoregulatory basis for the rules warranted serious consideration, he hoped that further study would vindicate the biogeographical rules (Newman, 1956). *Homo sapiens* provided an ideal ''test species'' for studying geographic variation because humans thrived in virtually every terrestrial habitat on earth (Newman, 1953, p. 313). Despite some contrary results, Newman believed that the weight of the evidence supported Bergmann's and Allen's rules as applied to humans. The major problem in interpreting these results was disentangling the effects of heredity, development, nutrition, and acclimatization to climatic extremes. Although he acknowledged Scholander's claim that clothing, shelter, and other cultural innovations were the primary reasons for human success in the arctic, Newman held out hope that combining morphology and physiology would lead to ''more and better controlled studies on native peoples'' (Newman, 1956, p. 105).

Newman's (1956) article was part of an exchange in the pages of *Evolution* stemming from a highly critical article by Scholander (1955) attacking the thermoregulatory explanation for Bergmann's and Allen's rules. According to Scholander, the rules had become ''dogma'' among biogeographers, evolutionary biologists, and anthropologists.[16] This dogma was undermined both by the fact that Bergmann's rule sometimes applied to ''cold blooded'' poikilotherms, but also by the detailed physiological research conducted on birds and mammals by Scholander and his colleagues. Scholander had not mentioned Ernst Mayr in his article, but the attack on these widely accepted biogeographical rules in the journal that Mayr had helped establish struck a raw nerve. In his earlier writings, Mayr had placed great weight on Bergmann's rule both as a useful taxonomic tool for classifying subspecies and as proof of adaptation through natural selection (Mayr, 1942, p. 94). Thus, when Scholander sent Mayr a reprint of his article, the evolutionary biologist replied courteously, but he was emphatic in dismissing Scholander's claims. According to Mayr, Scholander misunderstood the subtlety with

[16] Scholander specifically cited Coon, Huxley, Goldschmidt, and Rensch as supporters of this idea, but thermoregulation based on surface area to volume ratios was also discussed as the likely physiological explanation for Bergmann's and Allen's rules by other prominent biologists (Hesse et al., 1937, pp. 462, 466, Dobzhansky, 1937, p. 171). This idea was implicit in Mayr's *Systematics and the Origin of Species* (1942, pp. 91–94) and explicit in his response to Scholander (Mayr, 1956).

which natural selection could shape adaptations, writing "I am very much tempted to point this out in a note to *Evolution*. No doubt you realize that if one challenges a widely accepted conclusion one exposes oneself to questioning."[17]

Three weeks later Mayr sent Scholander a draft of his note asking for comments. Scholander's response was uncompromising in its challenge to the evolutionary validity of the biogeographical rules. Remarking sarcastically on the misuse of Bergmann's and Allen's rules, Scholander wrote Mayr:

> Evolutionists must beware of physiological interpretations involving factors so subtle that they can neither be measured nor even discussed in physiologically relevant terms. Evolutionists and physiologists meet in the concept of adaptation, and must listen to each other. The trouble with the rules is that they are statistically weak, they cannot be appraised thermally, and their interpretation as the result of temperature adaptation is conspicuously contradicted on the species level.

Scholander suggested organizing a joint seminar to air their differences in public. Although this meeting apparently never occurred, Mayr's note and a detailed rebuttal from Scholander were published in *Evolution* the following year, along with commentaries by Newman and Irving (Mayr, 1956; Scholander, 1956; Newman, 1956; Irving, 1957).

Adaptation might have been common ground for physiologists and evolutionary biologists, but finding an accommodation proved vexingly difficult when examining the biogeographical rules. Mayr based his support for the ecological rules on an expansive understanding of homeostasis that was broadly based on both physiology and genetics (Mayr, 1956, 1963 pp. 61, 295, 361; 1965).[18] On the organismal level, homeostasis implied "species specific" adaptations for self-regulation that were shared by all members of the species. For Mayr, homeostasis was an inherently conservative or centripetal force that maintained physiological constancy in organisms and held populations and species together. Countering these conservative homeostatic mechanisms was

[17] The correspondence between the two scientists includes letters from Mayr to Scholander, August 24, 1955 and September 14, 1955; Scholander to Mayr, September 22, 1955, Correspondence Boxes 4 and 17, Mayr Papers.

[18] Provine (2004) describes the influence of I. Michael Lerner and Theodosius Dobzhansky on Mayr's ideas about genetic homeostasis at the population level. However, Mayr's interest in a physiological explanation for Bergmann's rule in terms of thermoregulation suggests that his interests in homeostasis were very broad and provided a promising basis for unifying organismal and population biology.

the ecotypic variation that allowed individuals in local populations to adapt to particular environmental challenges. Whatever the physiological details underlying the biogeographical rules, they were part of this complex homeostatic mechanism that allowed for local adaptation while at the same time providing unity to the species, as a whole. There was a constant give-and-take between small-scale adaptation to local circumstances and maintaining the "historical heritage of the species as a whole" that had been shaped by natural selection and defined the broader limits of tolerance for the species (Mayr, 1956). Bergmann's rule was a prime example of how this compromise was maintained by natural selection in many species of birds and mammals.

In contrast to Mayr's emphasis on constancy and the conservative nature of homeostasis, Scholander's perspective on self-regulation highlighted a more flexible balance characterized by physiological lability and behavioral adaptability. Whether in the case of diving mammals or arctic homeotherms, organisms regulated some internal processes while allowing others to conform to environmental stresses. In both the diving reflex and heterothermy, evolution had enhanced basic, widely distributed physiological processes to adapt certain species to extreme conditions. But organisms could also acclimatize to new conditions or use behavior adaptively to meet environmental challenges. This was particularly true of humans who had successfully adapted to life in nearly all terrestrial habitats.

Mayr never directly responded to Scholander's criticism of applying Bergmann's rule to human races. He completely avoided the issue in his short note in *Evolution*. In *Animal Species and Evolution* he walked a fine line on human races and the adaptive significance of racial characteristics. On one hand, Mayr strongly argued that from the perspective of evolutionary theory humans were no different than other animal species (Mayr, 1963, pp. 644–648). Therefore, there was no reason why the adaptive ecotypic variation found in other species should not also be found among human populations. Indeed, he cited the work of anthropologists, including Coon, as evidence that much of the variation among human populations was indeed adaptive and that some features such as body build and limb length exemplified Bergmann's and Allen's rules (Mayr, 1963, pp. 323, 645). At the same time, he cautioned that this ecotypic variation was likely disappearing both as a result of continual gene flow among human populations and because of technological innovations that protected humans from climatic extremes (Mayr, 1963 pp. 657–658).

Like other leading evolutionary biologists such as Theodosius Dobzhansky and George Gaylord Simpson, Mayr was sharply critical of how early anthropologists had misunderstood evolution and had drawn odious racist conclusions based on typological concepts of species and subspecies. Yet there were significant differences in how the evolutionary biologists reacted to Carleton Coon's claim that human races are biologically real and constituted distinct subspecies. Despite Coon's use of modern systematics, population genetics, and paleontology to support his claims, Dobzhansky dismissed his evolutionary conclusions about race and vigorously attacked them (Jackson, 2001; Caspari, 2003; Farber, 2011, pp. 70–72; 2015; Collopy, 2015). Mayr also denied that *Homo sapiens* could be divided into subspecies and he was skeptical about attempts to define human races, all of which were more or less arbitrary.[19] Nonetheless, Mayr admired Coon's work, accepted his claims about the adaptive significance of human characteristics particularly in relation to climatic extremes, and used these claims to support the validity of Bergmann's and Allen's rules. Coon, therefore, served as a useful ally not only for bringing the modern synthesis to physical anthropology, but more specifically for challenging Scholander's critique of biogeographical rules as applied to humans.[20] Mayr avoided wading deeply into contentious issues of human race by selectively referring his readers to studies by Coon, Newman, and other anthropologists who supported Bergmann's rule without committing himself to any broader social implications of racial concepts.

Laws, Rules, and Contrasting Styles of Scientific Work

It might be tempting to view the heated exchange between Scholander and Mayr as a tempest in a teapot pitting two outsize personalities who refused to consider alternative perspectives on adaptation. Scholander's habit of challenging authority whether military commanders, university administrators, or leading scientists from other disciplines was a le-

[19] Mayr (1963, pp. 643–644, 647) claimed that the idea of pure races was "sheer nonsense" and he emphasized that humans formed a single biological unit and that the differentiation among human populations was less than that of many other polytypic species. These cautious and critical statements notwithstanding, Mayr (1962) had written a long and rather glowing review of Coon's *The Origin of Human Races*.

[20] Coon thanked Mayr for sending a reprint of his response to Scholander in *Evolution* and urged him to send a copy to Ted Hammel, the University of Pennsylvania physiologist who worked with Scholander on human thermoregulation; letter from Coon to Mayr, January 27, 1958, Correspondence Box 5, Mayr Papers.

gendary part of his larger-than-life persona. Scholander's (1956) tongue-in-cheek thank you to the editor of *Evolution* for allowing him to ''enter the lion's den and confront morphologically oriented evolutionists'' reflected an irreverence that endeared him to his friends but often irritated his opponents. From Mayr's perspective Scholander's critical article in *Evolution* amounted to an attack on his own significant contributions to the modern synthesis, specifically his idea of polytypic species and the role of natural selection in shaping adaptation in the subtle ways exemplified by the biogeographical rules. Yet, despite their wrangling both men seemed to acknowledge that the concept of adaptation was common ground where physiologists and evolutionary biologists should meet. Somewhat buried in the more confrontational parts of their articles was a broader agreement that climatic adaptations were complex and could not be reduced to a single variable.

Mayr did not deny the importance of insulation and he emphasized that adaptations were almost always compromises among competing selective pressures. Nonetheless he remained committed to the traditional explanation of the biogeographical rules based upon the relationship between surface area and volume (Mayr, 1956, 1963 p. 321). Bigger bodies (and shorter extremities) maximized heat producing volume while minimizing the body's surface area through which metabolic heat was lost. This seemed to be an obvious advantage in colder climates, and Mayr's (1956, 1963, pp. 361, 318–319, 645) arguments for biogeographical rules drew equally upon natural selection and physiological homeostasis. This relationship between surface area and volume had been mainstream physiological thinking about self-regulation for over a century. The relationship between surface area, volume, and metabolism was sometimes referred to Rubner's Surface Law after Max Rubner, the German physiologist who claimed that metabolism scaled to the 2/3 power of body weight (i.e. the ratio of surface area to volume). Although it was never entirely repudiated, Rubner's claim was subjected to searching criticism after World War II, and on both methodological and theoretical grounds many physiologists rejected it as a way of understanding metabolic rates. In this regard, Scholander's experimental studies were pioneering works and his critique of Bergmann's rule reflected new ways of thinking that were gaining ground among a younger generation of physiological ecologists (McNab, 2012).

Scholander didn't completely dismiss surface area and he emphasized the importance of size, at least in comparisons of adaptive challenges facing small versus large mammals. However, he denied that the modest clines in body size and length of appendages among populations of the same species could make a difference in thermoregulation. Scholander's reasoning rested on physiology, but also reflected a deep suspicion of the morphological basis for the biogeographical rules. The surface area of animals was notoriously difficult to measure accurately, and this problem was compounded when researchers relied upon study skins from museum collections. More fundamentally, both Bergmann's "rule" and Rubner's "law" struck Scholander as mere rules of thumb that had numerous exceptions. Indeed, Mayr sometimes (but inconsistently) argued that the biogeographical rules were nothing more than empirical generalizations that were valid if they held more than 50% of the time. He was willing to accept the exceptions as an inevitable result of organic complexity and evolutionary compromises among conflicting selection pressures, but from Scholander's perspective this amounted to sloppy science. For his part, Scholander based his understanding of thermoregulation on the seemingly firmer theoretical foundation provided by Newton's Law of Cooling. Yet, he, too, realized that organisms were not simply idealized heat-radiating bodies, but also active and adaptable agents that relied upon both physiology and behavior to regulate their internal environments in the face of external stresses. When sleeping in freezing conditions, sled dogs curled up to minimize exposure of limbs, ears, noses and other poorly insulated body parts. When running these same poorly insulated structures acted as efficient radiators to prevent overheating. Although he denied that small morphological differences along geographic clines contributed to this thermoregulatory mechanism, Scholander's explanation was broadly evolutionary. As in the case of the diving reflex, the thermoregulatory adaptations found in arctic mammals were evolutionary elaborations of more basic physiological processes common to all birds and mammals. Nonetheless, when Mayr accused Scholander of applying "all or none solutions" to understanding adaptation, he emphasized that the physiologist's evolutionary approach was not deeply informed by the population-thinking that was so important in evolutionary biology after World War II (Mayr, 1956, 1963 p. 321).

Though not as influential as in the past, Bergmann's rule continues to generate interest among some physiological ecologists and evolutionary biologists (McNab, 2012, pp. 93–100). The issues debated by Scholander and Mayr remain only partially resolved. Bergmann's rule applies to many species of birds and mammals, although the significance of the trends is heavily influenced both by the group studied and the methods used by different researchers. Scholander's attack on the thermoregulatory basis of the biogeographical rules has been widely influential and largely substantiated. Whatever the causal relationship between climate and body size, thermoregulation based on surface area and volume does not appear to be the most important factor. Correlations with productivity of ecosystems, protection against starvation, and the size of available prey have all been suggested as possible alternative explanations for why the average body size often increases in colder climates. Teasing apart the relationship between natural selection and adaptation as it relates to Bergmann's rule remains an open question.

At the time, however, the controversy over Bergmann's rule occurred when Mayr was formalizing a sharp philosophical distinction between proximate and ultimate causation (Mayr, 1961). According to Mayr biology (and biologists) could be divided into ''two largely separate fields'' on the basis of focusing on either functional or evolutionary explanations. While emphasizing that the two forms of explanation were complementary, Mayr argued that confusing the two often led to fruitless controversy and misunderstanding. Although this distinction might have seemed useful for criticizing Scholander and disentangling the disagreements involved in the controversy over Bergmann's rule, Mayr didn't employ it either in his article in *Evolution* or in *Animal Species and Evolution*.[21] The neat and tidy example of bird migration that Mayr used to illustrate the differences between proximate and ultimate causation in his 1961 article highlighted clear-cut explanatory categories, but he, himself, blurred the distinctions when he discussed Bergmann's rule. Indeed, during the late 1950s and early 1960s Mayr was deeply interested in homeostasis both as a functional concept applied to the physiology of individual organisms and as an evolutionary mechanism for stabilizing populations. Particularly in *Animal Species and Evolution* he moved freely from one sense to the other, sometimes mixing functional and evolutionary metaphors (Mayr, 1963, pp. 60–61, 295, 361). In this context, the neat distinction between proximate and ultimate causation became less compelling and might not have seemed

[21] A number of historians have emphasized that Mayr used the proximate-ultimate distinction primarily as a defense of organismal biology against the perceived threats of an aggressive molecular biology (Beatty, 1994; Dietrich, 1998; Hagen, 1999; Milam, 2010). To the extent that this defensive strategy motivated Mayr, the distinction might have seemed less apt for criticizing another organismal biologist. A slightly different interpretation has been put forward by philosophers and biologists who argue that Mayr's emphasis on the dichotomy between proximate and ultimate causation, but also the complementarity, acted as a conservative strategy to stabilize the dominant paradigm in post-World War II evolutionary biology (Laland et al., 2011). Nonetheless, Mayr apparently didn't find this argument useful for stabilizing traditional interpretations of Bergmann's rule against Scholander's critique.

to provide a useful vantage point for attacking Scholander's ideas which also mixed functional and evolutionary causation. Scholander provided broad evolutionary explanations for adaptation and self-regulation, even though he did not couch his discussion in terms of populations, genetic variation, and natural selection emphasized by biologists associated with the modern synthesis.

That this extended argument began in the pages of *Evolution* is Illustrative of a broader problem of inclusion facing evolutionary biology after World War II (Hagen, 2015). As the founding editor of the journal, Mayr had made a concerted, though not always successful, effort to attract contributions from a wide range of biological disciplines (Cain, 1994, Smocovitis, 1994). Networking and community-building were important parts of Mayr's organizational and administrative plan for evolutionary biology. His desire to build a unified evolutionary biology was also evident in his prefatory remarks in *Animal Species and Evolution*, if not always in the body of the book. Yet, his confrontational attitude toward Scholander's ideas on thermoregulation displayed an unwillingness to seriously consider important and influential evolutionary perspectives that seemed to clash with his commitment to the biogeographical rules. Ironically, this intransigence seemed at odds with Mayr's deep interest in self-regulation and drawing parallels between homeostasis at the organismal and population levels. Scholander was equally confrontational, and although he claimed a deep admiration for the modern synthesis, population-thinking seemed alien to the physiological ecology that he and Irving were pioneering – despite the fact that their younger followers would later effortlessly bridge the gap. Scholander relished his skirmish with "morphologically oriented" evolutionary biologists, but he recognized that *Evolution* was foreign turf during the mid-1950s.

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