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Editor's Choice: Honoring Joel Asaph Allen

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Joel Asaph Allen (19 July 1838 to 29 August 1921; Fig. 1) was a formative figure in the early years of the American Society of Mammalogists (ASM). Prior to the constitution of the Society, Allen had been appointed by Hartley H. T. Jackson as a member of the Committee on the Organization of the Mammal Society (Hoffmeister 1969). By all accounts a retiring individual, he was elected to honorary membership in the Society at the first meeting of the ASM (Washington, DC, 3–4 April 1919—Hoffmeister 1969). Honorary Membership is "the highest honor that the Society bestows" (Genoways and Freeman 2001).

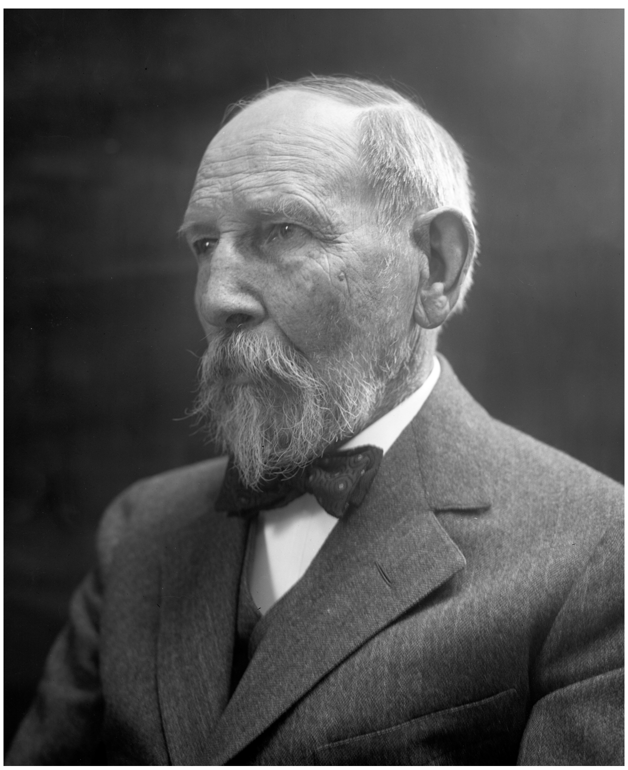

Fig. 1.—Joel Asaph Allen, in an undated photograph taken while he was working at the American Museum of Natural History. Image number 38088, American Museum of Natural History; courtesy G. Raml, AMNH Library Special Collections.

Allen had begun his duties as the first curator of birds and mammals at the American Museum of Natural History (AMNH) on 1 May 1885 (Allen 1916). "The collection of mammals then consisted of about 1000 mounted skins and 300 mounted skeletons, all on exhibition in the exhibition halls" (Allen 1916:33). From his position at the AMNH, and as a result of his general body of work, Allen became one of the most prominent mammalogists (and ornithologists) of the late 19th and early 20th centuries (Storer 1969): his obituary in the New York Times (30 August 1921, p. 11) noted, "An unusually prolific author in his special field, Dr. Allen's writing [sic] number more than 1000."

The fourth annual meeting of the Society was held at the AMNH 16–18 May 1922, the year after Allen's passing. At that meeting, the North American Mammal Hall was dedicated to the memory of Allen by the president of the AMNH, Henry Fairfield Osborn (Genoways and Freeman 2001). Also at that meeting, the Board of Directors of the ASM established a fund in his name, to "be used for the publication of certain numbers of the Journal of Mammalogy to be dedicated to the memory of Doctor Allen" (Genoways et al. 2020). As a measure of the esteem in which Allen was held by his friends and colleagues, 275 individuals and organizations contributed $7,770.98 to the J. A. Allen Memorial Fund (Hoffmeister 1969). Updating the figures provided in Genoways et al. (2020), that is approximately $120,485 as of this writing. As a result of the fund and fundraising, "To continue to honor Dr. J. A. Allen, the lead article in each issue of the Journal is dedicated to his memory" (Genoways et al. 2020:3).

The foregoing narrative of Allen is relatively well known to members of the ASM. But what Allen best is remembered for outside the Society is Allen's Rule, generally summarized as the phenomenon whereby animals (generally circumscribed to homeotherms, but extended to some poikilotherms—Alho et al. 2011) will have shorter limbs and appendages (e.g., pinnae) under regimes of cold weather, and correspondingly longer limbs and appendages under warmer conditions. The adaptive explanation ascribed to this generalized observation is that shorter appendages are advantageous in heat conservation in homeotherms (Mayr 1963). Allen (1877:112) wrote that "Geographical variation, as exhibited by the mammals and birds of North America, may be summarized under the following heads: namely, (1) variation in general size, (2) in the size of peripheral parts, and (3) in color." Later in that same work, he noted that, "As a general rule, certain parts of the organism vary more than does general size, there being a marked tendency to enlargement of peripheral parts under high temperature, or toward the tropics, hence southward in North America. […] In mammals it is manifested occasionally in the size of the ears and feet" (Allen 1877:116). Most recently, Alhajeri et al. (2020) suggested that it was in fact adaptation to cold, rather than warm temperatures, that drove this pattern. Notwithstanding, Allen's Rule, while at times controversial, appears to generally be applicable among most endotherms (Alhajeri et al. 2020). Interestingly, although the prototypical example of the phenomenon, jackrabbits (*Lepus*) and other leporid lagomorphs may run counter to the generalized trend (Stevenson 1986).

Lost in the sea of "Allen's Rule" is that for much of that paper, Allen in fact focused on body size, what we now call Bergmann's Rule (Stobo-Wilson et al. 2020; Westover and Smith 2020), rather than size of appendages, with his principal thesis being that the environment, rather than natural selection, was the causative agent of speciation: "The modifying influence of conditions resulting from geographic or climatic causes […] has been considered by many writers as explanatory of much of the diversity existing […] among animals" (Allen 1877:108). It is therefore fitting to have as the lead article in this issue of the Journal, dedicated to the memory of Dr. J. A. Allen, an article dealing precisely with the sorts of issues that would have appealed to Allen. On pages 13 – 27 of this issue, Wen and colleagues examine body mass and niche characteristics of tropical montane small mammals to explain patterns of abundance along an elevational gradient.

Historically, elevational range has not been examined in as much detail as its latitudinal correlate (summaries by MacArthur 1972; Stevens 1992). Despite the apparent neglect, Brown et al. (1996:605) called the elevational gradient in range sizes (along with other ecogeographic gradients) "One of the most interesting patterns of variation in range sizes." Stevens (1992) called the generalized pattern of increasing range sizes with increasing elevation across higher taxonomic groups "Rapoport's Rule," after the observation of the same phenomenon across subspecies within individual species (Rapoport 1982). Brown (2014), following up on Allen et al. (2002), implicated kinetics (the temperature dependence of ecological and evolutionary rates) as the underlying mechanistic cause: "These results establish a thermodynamic basis for the regulation of species diversity and the organization of ecological communities" (Allen et al. 2002:1545). The problem faced by Wen et al. (2021) was the combination of topographic heterogeneity (Badgley et al. 2017), climatic heterogeneity (Rahbek et al. 2019), and the complexity of elevational gradients located near the tropics (Janzen 1967; Heaney 2001; Ghalambor et al. 2006), along with the potential association between niche breadth and range size (Brown 1995; Kambach et al. 2019).

While McCain (2006) masterfully examined and synthesized these phenomena for Costa Rican rodents at a local scale between 750 and 1,840 m, Wen et al. extended the experimental system beyond the tropics, and to a broader taxonomic and geographic scale. Their most divergent sites (Sejila and Wolong) are over 750 km from each other, and the total elevation sampled ranged from 1,470 m (2,500 – 3,970 m; Baima Snow) to 2,800 m (1,200 – 4,000 m; Gongga). A remarkable 94,800 trap nights were expended in securing 3,463 specimens of 46 species in three orders of mammals: Eulipotyphla, Lagomorpha, and Rodentia. Body mass and abundance were not significantly associated, as previously demonstrated on Costa Rican rodents (McCain 2006). Niche position, reflective of the differences between the realized versus fundamental niche ("how typical the environmental conditions in which a species occurs are of the full set of conditions under consideration"), was related to mean abundance and elevational range size: species inhabiting areas more distant from conditions central to their niche were less abundant and had smaller elevational ranges. Similarly, niche breadth positively affected mean abundance and elevational range size, as proposed by Brown (1984) and reviewed by Gaston et al. (1997).

Wen et al. (2021) used data and an analytical approach that enabled them to proffer support for the resource availability and niche breadth hypotheses along elevational gradients. Support for the resource availability hypothesis is important in light of the suggestion by Gaston et al. (1997) that it was untestable. The niche concept (Hutchinson 1957) and its tight linkage with individual and species abundances (MacArthur 1957) remain central to understanding distributional patterns at local to global scales, and, as Wen et al. (2021) have shown, a research agenda focused on niche breadth shows promise in illuminating mechanisms whereby geographic distributions and species richness may be shaped (Heino and Tolonen 2018). Much work remains to be done in this area, as a recent review by Carscadden et al. (2020) showed: a research endeavor worthy of Joel Asaph Allen, to who's memory the lead article by Wen and colleagues is dedicated.

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