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CHAPTER 1

A TRIBUTE TO THE CAREER OF NED K. JOHNSON: ENDURING STANDARDS THROUGH CHANGING TIMES

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Abstract.—Ned K. Johnson (1932–2003) served as Curator of Birds and Professor of Zoology at the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley, from 1961 to his death in 2003. His distinguished career in ornithology included major contributions on various topics (e.g., geographic variation, biogeography, speciation, systematics, integration of molt and migration) that resulted in his receiving the Brewster Medal from the American Ornithologists' Union in 1992. With eight peer-reviewed short publications in print by the time he finished his undergraduate degree at the University of Nevada, Johnson launched into his doctoral program at MVZ under Alden H. Miller. His dissertation monograph on western flycatchers (*Empidonax* spp.) provided a model of meticulous, detailed empirical analyses that represented the epitome of its genre and presaged a remarkable series of investigations on the biogeography, speciation, and geographic variation of birds. He kept pace with technological advances throughout his career, from sonograms to complex multivariate statistics to spectrophotometry and molecular genetics. Johnson's advocacy of the importance of specimen-based research has been a bulwark of strength for museum ornithologists. His contribution to MVZ of >7,200 data-rich vertebrate specimens adds an important dimension to his legacy. Johnson's consistent approach to research, namely an unimpeachable empirical foundation for addressing critical conceptual issues, continues to inspire students and colleagues to match his standards. *Received 23 January 2007, accepted 12 February 2007.*

Resumen.—Ned K. Johnson (1932–2003) fue curador de aves y profesor de zoología en el Museo de Zoología de Vertebrados (MVZ), Universidad de California, Berkeley, desde 1961 hasta su muerte en 2003. Su distinguida carrera como ornitólogo incluye importantes contribuciones en diversas áreas (variaciones geográficas, biogeografía, especiación, sistemática, relación entre muda y migración), siendo reconocido en 1992 con la medalla Brewster de la Unión de Ornitólogos Americanos. Johnson terminó sus estudios de pregrado en la universidad de Nevada con ocho publicaciones en revistas de reconocido prestigio. Inmediatamente después, comenzó el doctorado en el MVZ bajo la tutoría de Alden H. Miller. Su tesis sobre los papamoscas *Empidonax* presenta unos análisis empíricos minuciosos y detallados que constituyen un modelo en su género, presagiando una importante serie de investigaciones sobre biogeografía, especiación y variación geográfica en aves. Johnson siguió de cerca los avances tecnológicos durante su carrera, empleando desde sonogramas a estadística multivariante compleja, espectrofotometría o genética molecular. La importancia que Johnson imprimió a la investigación basada en especímenes de museo ha servido de plataforma para todos los ornitólogos que trabajan con colecciones de museo. Su contribución al MVZ, con más de 7,200 entradas de especies de vertebrados, confiere una importante dimensión a su legado. Su método de investigación, con una base empírica intachable a la hora de abordar cuestiones conceptuales críticas, continúa inspirando y sirve de ejemplo a estudiantes y colegas.

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NED K. JOHNSON served as Curator of Birds and Professor of Zoology at the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley, from 1961 to his death in 2003. During this period, he influenced North American ornithology to a remarkable degree through his rigorous approach to specimen-based research and his emphasis on the importance of amassing detailed, accurate empirical databases for generating new ideas (see Appendix 1, and Barrowclough and Zink 2004, Cicero 2004).

AN EARLY START

Johnson's research career began in high school. At the remarkably young age of 16, he published his first scientific paper in a prominent peer-reviewed journal. Reproduced here in its entirety (Fig. 1), this paper, brief as it is, nonetheless reveals some of the ingredients of his distinguished career. First, note that he already was collecting birds for the University of Nevada Museum in Reno. Second, it is clear that he already was attuned to bird behavior and its significance. Third, he had the precocial wherewithal not only to recognize the significance of his observation but also to publish it in one of the best ornithological journals, all this in 1949, from the relative isolation of western Nevada.

By the time he was 21, Johnson had published seven additional short papers in *The Condor, Journal of Mammalogy,* and *Great Basin Naturalist* (Appendix 1) on birds and mammals of Nevada and had graduated with a B.S. from the University of Nevada, Reno (UNR). Instrumental to his early success was his mentor Ira LaRivers, a professor at UNR and an expert on the insects and fishes of Nevada. Although not an ornithologist, LaRivers encouraged Johnson to collect birds by adding him as a subpermittee on his collecting permit and taking him on numerous field trips throughout the state. Early on, Johnson realized the importance of scientific collecting for careful documentation of avian distribution and variation.

After two years in the U.S. Army in Germany, Johnson entered the doctoral program in the Department of Zoology, University of California, Berkeley, with Alden H. Miller at the MVZ as his advisor. At this time, after many decades of visionary leadership by Joseph Grinnell and Miller (Johnson 1995a), the MVZ was almost without rival as the world's leading university-based research museum, and the Grinnell-Miller tradition of specimen-based research was clearly what drew Johnson to the MVZ.

GEOGRAPHIC VARIATION AND SPECIATION

Johnson finished his Ph.D. in 1961, and publication of his dissertation soon followed (Johnson 1963a). Following decades of MVZ tradition, the dissertation was published in the *University of California Publications in Zoology* (UCPZ) series. This monograph was significant in many ways. Although Johnson's analyses included voluminous state-of-the-times morphometric analyses of exceptionally large series of specimens (3,253 in this case) that typified MVZ monographs in the UCPZ series, Johnson's was the first of the genre to include major analyses of vocalizations using sonograms. Johnson's monograph introduced quantitative analyses of the fine details of vocalizations as a major axis in the study of geographic variation. It thus contained a trademark of Johnson's career that carried through to his final years: adoption of the latest methods to address relevant questions. Also established in this monograph was Johnson's interest in "difficult" groups. Prior to his research, the *Empidonax* flycatchers of western North America were the least-understood group on the continent, with

Loggerhead Shrike Steals Shot Sparrow.—In early May, 1948, my brother and I were collecting birds at a small marsny pond in a grassy field about four and one-half miles southeast of Reno, Nevada. A Savannah Sparrow (*Passerculus sandwichensis*) flew up to a fence post about forty feet from where we stood. My brother snot the bird. The second it hit the ground, we ran to pick it up but were amazed to see a Loggerhead Shrike (*Lanius ludovicianus*) seize our bird and carry it away. The shrike carrieu tne sparrow with laborious strokes of its wings and flew to a spot in a large field of sagebrush about fifty yards away. Because the prey was comparatively heavy, the shrike flew low over the ground. It seems incredible but we could not locate either the shrike or the sparrow after searching the area for at least a half hour.—NED K. JOHNSON, *Reno, Nevada, February 13, 1949.*

FIG. 1. Ned K. Johnson's first publication, in *The Condor,* at age 16 (Johnson 1949; see Acknowledgments).

nagging questions of how many species really existed and how they differed from one another. Johnson discovered how they could be identified in all age, sex, and seasonal categories and how they differed ecologically and vocally. His measurement data are impressive in their detail (e.g., individual measurements of the six outermost primaries for each of three age categories for each sex of each species).

Johnson's interest in *Empidonax* flycatchers as models for the study of intraspecific geographic variation and of differences between closely related, extraordinarily similar species continued throughout his career. Although most studies of intraspecific variation gravitate toward species that show marked geographic variation, Johnson followed his UCPZ monograph with a study of a species of *Empidonax*, Hammond's Flycatcher (*E. hammondii*), that shows virtually no geographic variation despite a breeding distribution that extends from Alaska to the southwestern United States. Such an extensive latitudinal distribution typically guarantees at least some strong geographic variation in size-related morphology, but Johnson (1966:198) demonstrated that the species showed essentially no geographic variation in morphometrics or plumage:

> The analysis is based on 545 specimens of summer residents which were divided for treatment into 13 geographic populations, were segregated by sex and age, and were measured for the length of the tenth primary, tail length, bill length, bill depth, bill width, tarsus length, middle toe length, and body weight.... This species is remarkably uniform throughout its range....

Johnson pointed out the potential significance of this seemingly "negative" finding: "Reduction or absence of geographic variation...seems best attributed to strong genetic homeostasis" (Johnson 1966:199).

In 1980, he published a second UCPZ monograph on *Empidonax* (Johnson 1980), this time focusing on the *difficilis–flavescens* group. In this monograph, Johnson added mulitvariate statistics and spectrophotometry to his repertoire of techniques; the spectrophotometry represented one of the first applications of this technique to analysis of geographic variation in bird coloration. As was typical of Johnson's papers, he included a theoretical section that presented a model for speciation mechanisms and diversification in the genus, with applications and implications far beyond *Empidonax* flycatchers. Unfortunately, both of Johnson's monographs on *Empidonax* are under-read and under-cited in bird biology. The following are samples of some of the significant findings from these two monographs.

> The important point to be stressed here is that each of the species *hammondii, oberholseri, wrightii, affinis*, and *minimus*...has a characteristic wing shape, which, although varying somewhat within each form, can be an extremely useful criterion for identification when interpreted in the light of variation with sex and age. (Johnson 1963a:94)

> [T]he habitat preference of each species is a characteristic trait which probably evolved far back during the geographic isolation and speciation of each form at the same time that morphologic and behavioral divergence was taking place. (Johnson 1963a:189)

> The advertising songs, distinctive in each of the three species, as proved by the physical analysis of tape recordings with a sonagraph, function chiefly in pair-bond establishment and maintenance; their role in territorial defense is relatively minor.... *oberholseri* and *wrightii* maintain territories both intra- and interspecifically by means of hostile displays and vocalizations. (Johnson 1963a:215)

> The broad continental pattern, of alternation between long-tailed with short-tailed groups of populations as one moves from the Channel Islands to the coast, through the interior, down through Mexico and into Central America, is again seen. (Johnson 1980:46)

> Purity of breast color reveals a beautifully clinal geographic variation. Three clear steps exist in this cline, a slight one between Coahuila and San Luis Potosí, a moderate one at the Isthmus of Tehuantepec, and a strong one between Nuclear Central America and Costa Rica. (Johnson 1980:56)

> The male position note provides an exceptionally clear example of geographic trends in a simple behavioral signal. Broad regions of uniformity in note structure are separated by relatively narrow belts where the character changes abruptly or where a mixture of note types is seen. (Johnson 1980:70)

> Whole complexes of features change more or less simultaneously over fairly narrow and

> well-defined zones. Between these zones are broad regions where character expression is comparatively uniform. (Johnson 1980:102)

With the advent of biochemical techniques to measure genetic variation, Johnson, in collaboration with then lab technician Jill Marten, was one of the leaders in applying them to the study of geographic variation. This was clearly an exciting time for Johnson; he could now explore the relationship between phenotypic and genotypic variation. Protein electrophoresis in the 1980s and DNA sequencing in the 1990s became standard techniques in Johnson's studies of geographic variation, allowing new perspectives on his studies of *Empidonax* (e.g., Johnson and Marten 1985, 1988, 1991; Johnson and Cicero 2002) as well as forming a framework for initiation of studies on sparrows (*Amphispiza* spp.; Johnson and Cicero 1991; Johnson and Marten 1992; Cicero and Johnson 2006, 2007) and vireos (*Vireo* spp.; Cicero and Johnson 1992, Johnson 1995b). Johnson, with his doctoral student Bob Zink and postdoctoral researcher George Barrowclough as collaborators, was at the forefront of the application of genetic techniques to studies of speciation patterns, not only in *Empidonax* (e.g., Zink and Johnson 1984) but also in sapsuckers (*Sphyrapicus* spp.; Johnson and Zink 1983) and vireos (e.g., Johnson and Zink 1985, Johnson et al. 1988). In addition, they also formulated early reviews and conceptual models of genetic diversification (Barrowclough et al. 1984, Barrowclough and Johnson 1988). Johnson later revisited these groups, using newer techniques (DNA sequencing) and his unequaled knowledge of these birds to map ecological and morphological characters onto the phylogeny to explore patterns of diversification (Cicero and Johnson 2002). The following are samples of the major conclusions of these analyses.

On *Empidonax*:

> The pattern resulting from evolution within the genus *Empidonax* resembles more of a "bush" than a dichotomous sequence of cladogenic events.... We conclude, therefore, that external morphological similarity among species is due to developmental canalization of an *Empidonax* phenotype, rather than to an extremely recent origin of most species. (Zink and Johnson 1984: 213–214)

> Occupancy of temperate habitats by certain genera in this group is coincident with their evolution of migratory behavior and with independent diversification in foraging modes that reduces potential competition in sympatry. (Cicero and Johnson 2002:289)

> A major result of this study is the strong congruence between mtDNA sequences and other characters (allozymes, morphology, behavior).... (Cicero and Johnson 2002:297)

On sapsuckers:

> Therefore, the finding of genic divergence and phenotypic similarity (mosaic evolution) suggest that *varius* and *nuchalis* have simply retained the ancestral plumage condition, while evolution has proceeded at the genic level, probably in a more-or-less uniform, time-dependent manner. (Johnson and Zink 1983:880)

> Our mtDNA data firmly establish the conclusions presented by Johnson and Zink (1983) concerning evolutionary relationships among North American sapsuckers. In particular, the nearly perfect association between genetic distances estimated by allozymes and mtDNA sequences provides incontrovertible evidence that *ruber* and *nuchalis* shared a very recent common ancestor.... (Cicero and Johnson 1995:560)

On vireos:

> We speculate that "*chivi*" arose from wintering individuals of *V. olivaceus* that failed to return to North America. (Johnson and Zink 1985:433)

> Molecular phylogenetic evidence suggests that migration and seasonal habitat shifts evolved multiple times in the radiation of vireos. (Cicero and Johnson 1998:1367)

In investigating the mechanics of the speciation process, Johnson assembled an impressive data set on mate preferences in the contact zone between *Sphyrapicus ruber* and *S. nuchalis* (Johnson and Johnson 1985). This study, which is the primary data set supporting the ranking of the component taxa as separate biological species (Red-breasted and Red-naped sapsuckers; American Ornithologists' Union [AOU] 1998), consisted of 145 mated pairs in which both members were collected so that phenotype and genotype could be assessed. Assessments of mate preference and extent of hybridization led to the following conclusions:

> [A]lthough parental phenotypes predominate in the hybrid zone, F_1 hybrids seem to enjoy equivalent viability, and their occurrence is in proportion to the frequency of interspecific matings.... F_2 hybrids, however, do seem to be at a disadvantage. (Johnson and Johnson 1985:11)

> It is well established that *daggetti* arrives on the sympatric nesting areas ahead of *nuchalis*.... We speculate that the reddest males of *daggetti* dominate the less-red males, win the best territories quickly, and are the earliest to gain mates.... Some of these paler male *daggetti* possess territories before any *nuchalis* males. A small percentage of female *nuchalis* choose established male *daggetti* as mates because of the superstimulus value of the extensive red. (Johnson and Johnson 1985:13)

As a follow-up to the morphological study of *E. hammondii*, Johnson and Marten (1991) used allozymes to compare levels of genetic variation with the striking morphological homogeneity observed across the broad latitudinal breeding distribution of this species. At the time of this study, "genetic analyses of breeding samples of birds across most of their range [were] especially rare" (Johnson and Marten 1991:232). The genetic data paralleled those for morphology, with minimal population structuring, low levels of variability, and high estimates of gene flow. In interpreting these findings, Johnson and Marten (1991:236–237) concluded that

> The essentially homogeneous genetic structure of the species across its broad modern range agrees with a scenario of moderately rapid expansion into newly available habitat from a previously confined distribution.... [T]he ancestral stock could have moved into the Pacific Northwest region during the early Holocene from a Boreal refuge of forest or woodland located anywhere south of Cordilleran ice.... The absence of geographic variation in morphology could also be a consequence of reduced genetic variability, a suggestion that assumes that low genetic variability at enzyme-coding loci reflects reduced variability at loci controlling the expression of the external phenotype.... [I]f the postglacial distribution is as recent as implied above, it is plausible to suggest that insufficient time has elapsed for the evolution of observable phenotypic variation.

This early connection between glaciation and genetic and morphological patterns in birds continues to shape current thinking about processes of speciation and biogeography (e.g., Johnson and Cicero 2004, Lovette 2005).

Johnson's studies of geographic variation and speciation were based on strong and outspoken support for a Biological Species Concept that allows for limited hybridization (see Johnson et al. 1999, Winker et al. 2007), and he believed that "essential genetic independence resulting from reproductive isolation...is responsible for the evolution of avian biodiversity" (Johnson et al. 1999:1470). He also believed that speciation can occur relatively rapidly and that genetic divergence alone is insufficient to determine species status (Johnson and Cicero 2004). By applying a variety of field- and museum-based approaches to understanding species limits in birds (e.g., morphology, genetics, vocalizations, distribution, ecology), he produced definitive papers that often took years to complete but encompass the suite of traits important for reproductive isolation.

In sum, Johnson's approach to the study of geographic variation and speciation was to (1) accumulate large samples of target species from key areas through extensive field work, with a focus on breeding material for migratory species and fresh fall-plumaged material for resident species, (2) study the specimens in meticulous detail using traditional techniques as well as the latest technology, (3) analyze those empirical data using advanced analytical techniques, and (4) synthesize the results and evaluate their generality and theoretical significance. The outcome of this system then was used to plan the next season's field work, and this "annual cycle" was repeated unfailingly until a few months before Johnson's death. The patience and zeal with which Johnson pursued these studies is a hallmark of his work.

Molt–Migration–Life History

Stimulated by the marked differences among superficially similar species of *Empidonax*, Johnson was a leader in the study of integrating molt and migration into the comparison of life-history patterns among closely related species. These studies, done relatively early in his career, included a comparison of molt cycles in *Empidonax* (Johnson 1963b) and analyses of molt or migratory patterns in *E. hammondii* (Johnson 1963a, 1965, 1970), *E. oberholseri* and *E. wrightii* (Johnson 1963a), *E. difficilis* (Johnson 1973, 1974a), and *E. flavescens* (Johnson 1974a). At the time of his death, Johnson also was comparing tail molt patterns among tyrannid flycatchers (unpublished). As with his morphological data, specimens were divided by sex and age classes in addition to geography. Johnson (1963b:879) found that the

> most obvious relationship between molt and migration in *Empidonax* is that molts occurring after migration tend to be protracted. In other words, an early molt on the breeding grounds is correlated with a leisurely, prolonged southward migration, and an early and rapid fall migration is associated with a subsequent protracted molt.

Other important findings were that populations of *E. hammondii* differed geographically and seasonally in their migration patterns, and that juvenile mortality was high during fall migration (Johnson 1970:182–185):

> In the spring migration of this species, an early rapid migration in coastal regions contrasts with a protracted movement northward through the interior.... An opposite pattern is shown by the fall movement, in which there is a leisurely migration through coastal areas compared to an early and comparatively rapid passage southward from the interior.... Differences in age composition between autumn and winter samples point to a comparatively high mortality of immatures in the late fall and early winter.

Both for individual *Empidonax* species and for the genus as a whole, Johnson concluded that such differences in molt and migration patterns are adaptive: "In my opinion, these differences between coastal and interior migrants [of *E. hammondii*] are adaptive..." (Johnson 1970:182) and "the degree of interspecific variation in timing is so great as to suggest that the exact position in the annual cycle of these molts is chiefly a reflection of adaptation at the species level" (Johnson 1963b:883).

Pigmentation and Coloration

Johnson was fascinated with pigmentation and the evolution of color differences in birds and published several significant papers on this topic that probably have not received the attention they deserve. Although he routinely used color spectrophotometry to study patterns of color variation within and among populations (e.g., Johnson 1980, Johnson et al. 1998), he wanted to go beyond that technique to understand the pigmentary basis for such variation. Thus, he collaborated with Alan Brush to apply pigment chemistry in addition to colorimetry in studies of tanagers (*Chlorospingus* spp.; Johnson and Brush 1972) and warblers (*Vermivora* spp.; Brush and Johnson 1976). The study of the tanagers involved *C. pileatus* and *C. "zeledoni,"* which at the time were considered separate taxa that exhibited local sympatry on two high mountains in central Costa Rica. Using these methods, Johnson and Brush (1972) elegantly corroborated prior suggestions that the two taxa actually represent different color phases of the same species. By extracting pigment from the breast plumage of a single specimen (MVZ 162203), they transformed it from the "gray-green morph" to the "yellow-green morph." In a major finding, they proposed

> that on Volcanes Irazú and Turrialba genotypes responsible for increased grayness (= reduced yellowness), operating through decreased concentration of lutein pigmentation, owe their survival and maintenance to the long history of vulcanism that has characterized the central highlands. (Johnson and Brush (1972:260)

Johnson also integrated his interest in color and plumage pigmentation with his interest in molt, natural history, and the annual cycle. In a study of the Green Jay (*Cyanocorax yncas longirostris*) in seasonally dry deciduous woodland in the mid-Marañon Valley of Peru (Johnson and Jones 1993), he divided specimens by collection date as well as age and analyzed them for spectral reflectance, molt, and feather wear. Unlike other subspecies that occupy more humid habitats and are dorsally green year-round, individuals in this population gradually fade from bright yellow-green to greenish-blue or blue dorsally. This study showed that "autoxidation and accompanying bleaching from exposure to sunlight [as opposed to feather wear] are implicated in this striking color change" (Johnson and Jones 1993:389).

More recently, Johnson dove into the study of pigmentary properties of feathers. As a mentor for undergraduates, he worked with a student examining the basis for color variation in the "red" crown plumage of woodpeckers (Picidae;

Hopenstand and Johnson 2001). In another paper (Johnson 2001), he presented a theory for the evolutionary origin of feathers:

> I propose that the "aerodynamic features" of modern feathers, including a distinctive combination of flatness, light weight, resilience, and smooth-contour, initially evolved in a context unrelated to flight. Instead, flatness and lightness evolved in response to selection favoring maximally effective shape for the exhibition of pigments and structural colors.... The physical characteristics and individual mobility of feathers, serving to expose pigments and iridescece during display, were preadaptive for the eventual use of feathers in flight and thermoregulation. (Johnson 2001:91)

Biogeography and Natural Range Expansions

Johnson's voluminous contributions to the documentation of breeding distributions of insular montane avifaunas in the western United States naturally provoked his interest in the patterns and their underlying processes. Aware that distributions can change with lightning speed compared with geological time, he focused primarily on ecological processes that might govern the patterns. One of his major contributions to the field (Johnson 1975), conducted when studies of island biogeography were "cutting edge," showed that almost all of the pattern on montane islands could be explained not by distance and area effects, much less historical biogeography, but by the simplest of ecological variables, namely habitat availability:

> Total area and area of forest-woodland, variables of significance in other, similar studies, here predict only from 28 to 45% of the variation in total species number. In contrast, an index of habitat diversity explains 91% of the variation in total bird species. (Johnson 1975:561)

In another important contribution, Johnson (1978) showed that avifaunal distributions, contact zones, and areas of active speciation in the western Intermountain Region are coincident with physiographic, climatic, and floristic discontinuities.

Although Johnson was interested primarily in continental biogeography, especially in the Great Basin, he also published two important papers on the California Channel Islands (Johnson 1972, Lynch and Johnson 1974). In the first, he reviewed the composition of the avifauna on different islands and considered evidence explaining the distribution and differentiation (or lack thereof) of island populations. The second paper involved a literature survey of minimum avifaunal turnover rates (immigration vs. extinction) on islands, including those reported by Diamond (1969) for the Channel Islands. Diamond (1969) reviewed early distributional records summarized by Howell (1917), compared those with his own records, and concluded that although the total number of resident bird species on each island has remained fairly constant over time, the species composition of the avifauna has changed markedly on most islands, which suggests high turnover (17–62%). In a bold critique, Lynch and Johnson (1974) faulted Diamond for not publishing the majority of records and species' identities on which his rates were based, thus making his figures "impossible to interpret properly" (Lynch and Johnson 1974:375). They also noted that

> the great majority of extinctions reported by Diamond to have occurred on the California Channel Islands are attributable either to human interference or to faulty interpretation of faunal data (pseudoturnover). While a few "natural" extinctions may have occurred, we can find only a single reasonably well-documented example out of 41 specified extinctions. (Lynch and Johnson 1974:378)

Therefore, on the basis of their literature survey, they concluded that minimum avifaunal turnover rates on islands have been seriously overestimated, especially in regard to natural processes.

Johnson's interest in biogeography and his intensive field work through the decades in the western United States put him in a unique position to detect and document avifaunal range changes (Johnson 1974b, 1994, 1995c; Johnson and Garrett 1974, Johnson and Cicero 1985). The changes in which he was interested did not involve obvious responses to modification of the landscape by humans; rather, he focused on regions and habitats with minimal direct human influence, such as coniferous forests on remote mountain ranges. The significance of this type of range change is clearly much greater, as Johnson (1994) noted years in advance of widespread attention to global climate change:

> These range adjustments are not responses to anthropogenic influences. Instead, climatic change in the new regions of occupancy apparently has provided regimes of increased summer moisture and higher mean summer temperature typical of pre-expansion distributions. (Johnson 1994:27)

His interest in these phenomena culminated in a landmark symposium volume on avifaunal change in western North America, co-edited with J. R. Jehl (Jehl and Johnson 1994). In keeping with his interest in applying new methods to ongoing problems, Johnson would have been excited to see the application of climatic and ecological niche modeling in detailing natural range changes in birds (e.g., Barred Owl [*Strix varia*]; Monahan and Hijmans 2007).

Reviews

Johnson published what we suspect is an exceptional number of book, symposium, and monograph reviews. He was the unquestioned authority on birds of the Great Basin and geographic variation of birds in western North America, as well as being highly respected for his general knowledge of bird biology. Thus, editors turned to Johnson for many important reviews, such as of the *Birds of North America* series and the *Handbook of the Birds of the World*. Johnson's reviews were not only fair but also always insightful. Our personal favorite is one of his earliest, of Lester Short's research on flickers (Johnson 1969). In this review, he proposed a novel, alternative hypothesis for the phenotypic patterns found by Short, one that represented the equivalent of a null hypothesis for genetic variation:

> The philosophy underlying Short's entire discussion is that traces in one population, A, of characters expressed in another population, B, and presumably evolved when A and B were not in contact, means that genes from population A are infiltrating population B because of secondary contact.... However appealing this explanation may be for certain situations of hybridization in birds, for the North American flickers I feel that Short's interpretation is incorrect.... The likely explanation of most of the occurrence of red nuchal traces, then, in *most* of the populations of *cafer* in western North America away from the hybrid zones, is that these traces have their genetic basis deep in the stock that gave rise to all flickers and their relatives.... (Johnson 1969: 227–228)

This talent for original ideas was also a trademark of Johnson's in public seminars and meetings. Whether the topic was close to his research or remarkably distant, Johnson routinely posed insightful questions to speakers that revealed how closely he followed their presentations.

Specimen Contributions

Johnson's specimen catalog contained entries up to number 7,212. These were primarily birds, with some mammals, reptiles, and amphibians, most of which are deposited at the MVZ; some of his earlier material is deposited in the Museum of Biology, University of Nevada, Reno. This number of specimens is probably higher than those collected by his peers in academic ornithology and represents a lasting contribution and legacy. The beautiful quality of his specimens, the geographic importance of the specimens collected, and the quantity and quality of data on their labels, overshadows in value the sheer volume of specimens. With at least 10–12 data fields per label, Johnson directly contributed roughly 72,120–86,544 "data cells" to vertebrate biology, which would certainly rank him among the most important contributors ever among tenure-track ornithologists. Further, this does not take into account the many thousands of research specimens contributed by his students and associates.

Many ornithologists who conduct specimen-based research directly contribute little to these resources, the quality and volume of which are often the rate-limiting step in such research. Johnson was the antithesis of this approach. Not only was his field work collection-oriented, but he also believed philosophically that direct involvement generated original insights and better research. Johnson respected colleagues with a similar philosophy and disdained those whose specimen contributions were minuscule, particularly if they were employed as curators of research collections.

Professional Service

Johnson strongly believed in service to professional societies and to the University of

California, Berkeley, where he worked for 42 years. Although outwardly cynical about anything having to do with authority and bureaucracy, he felt that it was his duty to serve in positions of influence. Thus, he was President of both the Cooper Ornithological Society (1981–1983) and the AOU (1996–1998), and was involved in many other professional organizations, including the International Ornithological Committee. His 69 committee-years of service to the AOU, including 36 years on the Committee on Classification and Nomenclature, led to his winning the Marion Jenkinson Service Award from the AOU in 2001. At UC Berkeley, Johnson helped to define the undergraduate curriculum in biology and fought for the importance of field-based organismal courses in a growing era of molecular and cell biology. In addition to serving as a mentor or advisor for countless undergraduate students, Johnson also sponsored 3 Master's and 15 Ph.D students (Appendix 2). Arguably his greatest professional legacy was the enthusiasm for natural history that he instilled in students at all levels—students who, years later, still remember Johnson's infectious passion while teaching Ornithology and the wildly popular class on Natural History of the Vertebrates.

Scientific Standards

In the tradition of his MVZ predecessors, Grinnell and Miller, Johnson was a strong advocate of accuracy and rigor in all aspects of data gathering. With missionary zeal, he inspired his students and colleagues to strive for the highest standards of authenticity and repeatability, and always insisted on meticulous detail in data collection—from the label on a specimen, which he considered sacrosanct, to the analysis and interpretation of data. Johnson was noted for his candor in both the spoken and the written word, and often spoke up for what he believed was true, regardless of the consequences. To that end, he published an influential paper on standards for scientific specimens (Johnson et al. 1984) and also took to task (Lynch and Johnson 1974; Johnson 1994; Cicero and Johnson 1996, 2006) those whose empirical database was of poor quality. A quotation from Lynch and Johnson (1974) captures this philosophy:

> Indeed, a respected colleague has offered a friendly admonition to the effect that our standards for acceptable faunal data are so stringent that, if generally adopted, they would prevent a lot of good research from being done. We are compelled to reply that we are unaware of any examples of good research in the area of faunal analysis which do *not* involve attention to detail and a realization of the inherent limitations of observational data (Lynch and Johnson 1974:383).

We like to imagine that as Ned died, he still dreamed of collecting sparrows in the Great Basin, while a rival shrike, with silvery sagebrush-matching sheen comparable to his own, races him for the specimen.

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Appendix 2. Master's (3) and Ph.D (15) students sponsored or cosponsored (*) by Ned K. Johnson, excluding students sponsored at the time of his death in 2003.

1965	George T. Ferrell, MA	Variation in blood group frequencies in populations of Song Sparrows of the San Francisco Bay Region
1965	Mercedes Foster, MA	Pterylography, molt, and age determination of the Orange-crowned Warbler.
1969	Robert B. Hamilton, Ph.D	Comparative behavior of the American Avocet (*Recurvirostra americana*) and the Black-winged Stilt (*Himantopus h. mexicanus*)
1972	Luis F. Baptista, Ph.D	Demes, disperson and song dialects of sedentary populations of the White-crowned Sparrow (*Zonotrichia leucophyrys nuttalli*)
1973	Richard E. Johnson, Ph.D*	Biosystematics of the avian genus *Leucosticte*
1974	James F. Lynch, Ph.D*	Ontogenetic and geographic variation in the morphology and ecology of the black salamander (*Aneides flavipunctatus*)
1977	Carolyn S. Connors, MA	Foraging ecology of Black Turnstones and Surfbirds on their wintering grounds at Bodega Bay, California
1978	Stephen F. Bailey, Ph.D	Foraging strategies of frugivorous birds in relation to the availability of berries, with special reference to central California
1983	Robert M. Zink, Ph.D	Patterns and evolutionary significance of geographic variation in the schistacea group of the Fox Sparrow (*Passerella iliaca*) (Oregon, Nevada, California)
1990	Jeffrey G. Groth, Ph.D	Cryptic species of nomadic birds in the Red Crossbill (*Loxia curvirostra*) complex of North America
1992	Douglas A. Bell, Ph.D	Hybridization and sympatry in the Western Gull/Glaucous-winged Gull complex
1992	Scott V. Edwards, Ph.D*	Gene flow and mitochondrial DNA evolution in social babblers (Aves: *Pomatostomus*)
1993	Carla Cicero, Ph.D*	Sibling species of titmice in the *Parus inornatus* complex (Aves: Paridae)
1993	Julia I. Smith, Ph.D	Environmental influence on the ontogeny, allometry, and behavior of the Song Sparrow (*Melospiza melodia*)
1996	Kevin J. Burns, Ph.D	Molecular phylogenetics of tanagers and the evolution of sexual dimorphism in plumage

APPENDIX 2. Continued.

2001	Thomas A. Stidham, Ph.D*	The origin and ecological diversification of modern birds: Evidence from the extinct wading ducks, Presbyornithidae (Neornithes: Anseriformes)
2002	Alison L. Chubb, Ph.D	Molecular evolution and phylogenetic utility of the ZENK gene in birds
2002	Jason A. Mobley, Ph.D	Molecular phylogenetics and the evolution of nest building in kingbirds and their allies (Aves: Tyrannidae)