## HISTORICAL PERSPECTIVES

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### CONDOR PHYSIOLOGY<sup>1</sup>

### William R. Dawson

#### Department of Biology and Museum of Zoology, The University of Michigan, Ann Arbor, MI 48109-1048

Walsberg's (1993) account of the history of The Condor traces the journal from its beginnings as a "A Bi-monthly Exponent of Californian Ornithology" through its days as "A Bi-monthly Magazine of Pacific Coast Ornithology" and as "A Magazine of Western Ornithology" to its present international position as "A Journal of Avian Biology." This change in geographic scope has been accompanied by a substantial increase in the subject areas covered and articles on avian physiology have become a prominent part of The Condor's offerings over the past 40 years, reflecting an increased emphasis on experimental approaches to avian biology (Walsberg 1993). In this fiftieth year of my membership in the Cooper Ornithological Society, I was pleased for both sentimental and scholarly reasons to have been asked to review this last circumstance in more detail. My first paper (a paleontological study) was published in The Condor. I have subsequently benefitted from having 19 physiological articles in which I was involved as an author or coauthor published in this journal. Of greater importance, I felt that the review would allow consideration of some matters important in understanding certain aspects of the development of North American studies of the physiology of wild birds.

Any consideration of physiological studies in The Condor requires a inventory of the contents of all 96 (and counting) complete volumes. Consequently, I created a bibliography of pertinent articles from which the present account has been constructed. This bibliography includes not only papers summarizing laboratory experiments, but also natural history observations with direct physiological implications and functionally oriented field studies. The latter two categories warrant some comment. Finley's (1909) description of the finding of a comatose hummingbird that later "opened his eyes with a start and flew away," and Hanna's (1917) report of finding White-throated Swifts (Aeronautes saxatilis) roosting in a "dazed or numb state" are examples of natural history observations that provide early records of apparent avian torpor. Other pertinent observations include several reports on the bird colonies at the Great Salt Lake, Utah, and other lakes in the Great Basin, which describe responses of adults and young to high air temperatures and strong insolation (e.g., Goodwin 1904, Behle 1935). Indeed, Behle's (1944) observations of adult and nestling American White Pelicans (Pelecanus erythrorhynchos) provide early documentation of the importance of gular fluttering for these birds in the heat. I also included in the bibliographic database observations on aspects of locomotor performance, including flight speed and range (e.g., Bassett 1921, Johnson and Morton 1976), depths and durations of dives by aquatic species (e.g., Clay 1911, Huin 1994), and sensory capabilities (e.g., Lequette et al. 1989). Functionally oriented field studies included in the database deal with such topics as determinate and indeterminate laying, the temporal relation of molt and reproduction, biophysical ecology, migratory physiology, ecological energetics, nutrition, seasonal changes in body composition, and so on. Some of these are considered further in a later portion of this account. I anticipated that the broad limits I used in deciding what constituted physiological relevance in papers would produce a lengthy bibliography. However, I was unprepared for the fact that it finally contained over 1,000 titles!

# PUBLICATION RATES FOR PHYSIOLOGICAL ARTICLES IN *THE CONDOR*

Walsberg's (1993) account provides a useful longitudinal analysis of the distribution by subject matter of feature articles appearing in *The Condor*. No articles containing a substantial physiological focus were found in the years sampled between 1899 and 1924 and less than 10% of the feature articles could be classed as such in those sampled between 1929 and 1949. Physiology occupied a more prominent position between 1954 and 1992, with 20% or more of the feature articles published in 1959, 1964, 1969, 1974, and 1984 having a substantial focus in this area. In fact, more than a third of the papers published in 1974 were so classified. However, Walsberg (1993) noted that the fractional representation of this area in *The Condor* has declined since the late 1970s.

Using more inclusive criteria (see above) than Walsberg (1993), I analyzed the representation of physiological material (in both notes and feature articles) in each volume of *The Condor* through 1994. To lessen the impact of changing publication rates in other areas, this analysis (Table 1) deals with actual numbers of

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papers rather than their fractional representation in the journal. The rates for physiological material during five-year segments (mean annual number of papers and notes) lie between 0.6 and 2.0 items/year from 1898-1927. Somewhat higher rates, 2.0 and 3.8 items/year, are apparent for five-year segments between 1928 and 1952. A substantial increase in rates began in 1953 and by 1988–1992 more than 39 physiologically relevant items, on average, were being published annually. This result contrasts with the general picture Walsberg (1993) described using data on fractional representation of physiological material in samples at five-year intervals. Though, as he noted, this fractional representation reached its zenith in 1970s and has been declining since then, the absolute publication rates continued to increase through 1988-1992 and during 1993 and 1994 were near the mean rate of 34.6 items/year for the interval of 1983-1992 (Table 1). Differences in criteria employed to identify physiological articles and notes may account for some of the discrepancy between the absolute and fractional analyses. However, the trends in fractional representation of functional articles in The Condor appear to have been shaped more by changing rates of publication in other areas of avian biology than by any reduced rate in physiology and related areas.

### FACTORS IN THE INCREASED PROMINENCE OF PHYSIOLOGY IN THE CONDOR

The editorship. As Walsberg (1993) noted, the rise in prominence of physiological material in *The Condor* is probably an outgrowth of the increased emphasis on experimental approaches to avian biology that has developed in the last five decades. However, other factors also appear to have been involved. One surely concerns the editorship of the journal over this period. Alden H. Miller (Editor, 1939–1965) had a broad approach to ornithology exemplified by his research on an array of subjects ranging from paleobiology to physiology (Davis 1967). His publications in the latter area in *The Condor* (see below) must have provided encouragement for others to submit physiological contributions to the journal.

Following Miller's untimely death in 1965, the editorship of The Condor was assumed by James R. King (Editor, 1966-1968), who was in the early stage of a distinguished career of physiological research (see below). Though his tenure as editor was relatively brief due to departure on sabbatical leave, he had a major role in setting the future course of The Condor (Walsberg 1993). His abandonment of the regional focus of the journal and abolition of the policy of generally accepting material for publication only from members of the Cooper Ornithological Society (COS) launched The Condor on a course toward becoming an international journal. Walsberg (1993) cited a personal communication from James King stating that submissions by authors from outside North America began to increase soon after these actions and he, Walsberg, noted that fully 40% of the papers published in 1992 were written by scientists outside the United States. This broadening of access to The Condor was especially beneficial for physiology, owing to the important work in this field being conducted on wild birds in such

 TABLE 1. Publication rates for physiological papers appearing in *The Condor*.

Interval	Items/ year*	Interval	Items/ year*
1898-1902	0.8	1953-1957	7.0
1903-1907	0.6	1958-1962	11.4
1908-1912	0.8	1963-1967	12.6
1913-1917	0.8	1968-1972	18.0
1918-1922	1.8	1973-1977	25.0
1923–1927	2.0	1978-1982	18.6
1928-1932	3.6	1983-1987	29.8
1933-1937	3.8	1988-1992	39.4
1938-1942	3.8	1993	38
19431947	2.0	1994	35
1948-1952	3.8		

\* Numbers through 1992 represent mean annual rates for the respective five-year periods.

countries as Australia, Canada, Denmark, Finland, France, Germany, Norway, The Netherlands, Russia, Sweden, and South Africa. According to Walsberg (1993), King also appears to have initiated the system requiring that essentially all submissions to *The Condor* be subjected to external peer review. The quality control provided by this has undoubtedly been valuable in attracting submissions from leading authors in a variety of fields, including physiology.

The five editors of The Condor who, through 1994, have followed James R. King-Ralph Raitt (1969-1971), Francis S. L. Williamson (1972-1974), Peter Stettenheim (1975-1985), Martin L. Morton (1986-1990), and Glenn E. Walsberg (1991-1995)-have maintained the high editorial standards set by their predecessors and overseen the rise in international prominence of this journal in the past 25 years. Morton's term was additionally noteworthy for a substantial increase in volume size and the change in journal format. The designation of The Condor as "A Journal of Avian Biology" also occurred in his term. Perhaps the fact that three (King, Morton, Walsberg) of the six editors of The Condor since 1965 have had primary interests in the physiology of wild birds has provided an added attraction affecting the submission of physiological material to this journal.

Western physiological research. Developments at three western universities in the years surrounding World War II also appear to have been influential in increasing the representation of physiological studies in The Condor. As a result of his doctoral work with Alden H. Miller at the University of California at Berkeley, Albert Wolfson published what I regard as the first major laboratory studies of avian physiology to appear in The Condor. These summarized his research on sexual cycles and regulation of spring migration in western Dark-eyed Juncos, Junco hyemalis (Wolfson 1940, 1942, 1945). Miller's interest in physiology also led to his publications in The Condor dealing with body temperatures for Common Poor-wills, Phalaenoptilus nuttallii (Miller 1950), photoperiodism in the sparrows Zonotrichia leucophrys, Z. atricapilla, and Z. capensis (Miller 1954, 1959), and with molt cycles in an equatorial population of the last species

(Miller 1961). These papers followed earlier reviews (Miller 1930, 1932) for *The Condor* of some classic works by William Rowan on avian photoperiodism and migration (for references see Miller [1930, 1932] entries in "Literature Cited"). The role of the University of California at Berkeley, particularly its Museum of Vertebrate Zoology (MVZ), in physiological studies of birds was increased by the appointment of Oliver P. Pearson to its staff in 1947. Primarily a mammalogist, he carried out several physiologically relevant studies of birds. One published in *The Condor* dealing with metabolism and torpor in hummingbirds (Pearson 1950) has received very wide notice and a popular account based on it was published in the *Scientific American* (Pearson 1953).

The contributions of graduates of Zoology and MVZ at Berkeley to the establishment of *The Condor* as a key outlet for work on physiology of wild birds also should be recognized. A quick count in the bibliographic database for the present account indicates approximately 60 papers authored or coauthored by these individuals. These concern such topics as growth, temperature regulation, torpor, energetics, respiratory anatomy, reproductive biology, molt, homing, incubation patches, and endocrinology. In addition to Albert Wolfson (see above), the following have published three or more physiologically relevant items in the journal: William H. Behle, John Davis, Harvey I. Fisher, Thomas R. Howell, David W. Johnston, Robert B. Payne, and Robert K. Selander.

The University of California at Los Angeles (UCLA) also has figured in the rise in prominence of physiology in The Condor. This followed George A. Bartholomew's (member COS, 1942) 1947 appointment to the faculty of the Department of Zoology at that institution. One part of the research program he established at UCLA dealt with avian physiology, with primary emphasis on temperature regulation and water balance. This led to his publication of 14 papers in The Condor between 1952 and 1971, the approximate years over which physiology was rising to prominence in the journal. Efforts in avian physiology at UCLA were enhanced by Thomas R. Howell (member of COS, 1947) and Robert C. Lasiewski's (member COS, 1962) joining the faculty of the Department of Zoology in 1951 and 1964, respectively. Howell and Bartholomew collaborated on several physiological studies, involving development of thermoregulation in tropical seabirds (e.g., Howell and Bartholomew 1961) and thermoregulation and torpor in several southern Californian birds, including the Common Poor-will, Phalaenoptilus nuttallii (e.g., Bartholomew et al. 1957, Bartholomew et al. 1962). During Lasiewski's six-year stay at UCLA, he established a productive program of research dealing with avian thermoregulation and respiration and contributed a dozen papers to The Condor (e.g., Lasiewski and Bartholomew 1966, Schmidt-Nielsen et al. 1969). Howell and Bartholomew have now retired, but UCLA continues to be an active center of research on avian physiology due to Kenneth A. Nagy's studies of water balance and energetics of free living birds (e.g., Obst and Nagy 1992, 1993). The importance of this institution in the rise of physiology to a prominent place in The Condor is indicated by the fact that the faculty mentioned above and over 30 persons (graduate students and postdoctoral scholars) associated at some time with their laboratories have contributed more than 100 physiological articles to the journal. Space limitations preclude a full listing of these persons, but the following are mentioned for having published as author or coauthor three or more physiologically relevant papers in *The Condor*. Marvin H. Bernstein, Tom J. Cade, William R. Dawson, Gilbert S. Grant, Jack W. Hudson, Richard E. MacMillen, F. Gary Stiles, Carol M. Vleck, Glenn E. Walsberg, Wesley W. Weathers, and Philip C. Withers.

A third center of western physiological research also began in 1947 when Donald S. Farner (member COS, 1947) joined the faculty of the Department of Zoolegy at Washington State University in Pullman, WA, where he established the Laboratory of Zoophysiology. He and some of his students were to play particularly important roles in increasing the prominence of physiology in The Condor. James R. King (member of COS, 1953), one of these students, returned to Washington State University in 1960, after three years as a faculty member at the University of Utah. His efforts maintained the prominence of Washington State in functional studies of wild birds following Farner's leaving in 1965 to accept the Chairship of the Department of Zoology at the University of Washington. L. Richard Mewaldt (member of COS, 1947) and Martin L. Morton (member of COS, 1959), two other Farner students, also have figured importantly in the affairs of the Cooper Ornithological Society and The Condor, particularly after their assumption of faculty appointments at San Jose State College (later, State University) and Occidental College, respectively. I return to a further consideration of the research of the Washington State/ Washington group later in this discussion.

Following his departure for the University of Washington, Farner continued to coauthor articles in The Condor, dealing primarily with photoperiodism in White-crowned and Rufous-collared Sparrows, Zonotrichia capensis (Lewis and Farner 1973, Lewis et al. 1974) and field endocrinology or migratory physiology in the former (e.g., Wingfield and Farner 1976, Moore et al. 1982). His last paper in the journal, an endocrinological study (Schwabl and Farner 1989), appeared after his death in 1987. In the meantime, King maintained a productive research program at Washington State University, adding biophysical ecology and ecological energetics to the major themes of his research. In the decade before his death in 1991, he worked extensively on amino acid metabolism and molt in Gambel White-crowned Sparrows, collaborating with his former graduate student Mary E. Murphy (e.g., Murphy and King 1984), who had returned to Washington State in 1987 to accept a faculty position and who continues an active program of avian nutritional ecology there. Altogether through 1994, Farner, Mewaldt, King, and Morton had published in The Condor as author or coauthor over 50 physiologically relevant papers. Publications in this journal by 16 of the persons associated at some time with the King or Farner (Washington State and Washington) laboratories as graduate students or postdoctoral scholars increases this figure to more than 80. Among these persons, it is appropriate to mention Robert A. Lewis, Michael D. Kern, Ellen D. Ketterson, Mary E. Murphy, D. Randy Webb, Glenn

E. Walsberg (also included above with the UCLA group), and John C. Wingfield for having as an author or coauthor contributed three or more physiologically relevant papers to *The Condor*. It is also important to note a further contribution by the Washington connection to the journal through the fact that three of the last six editors have participated in physiological research at Washington State University as either graduate student (King and Morton), faculty member (King), or postdoctoral scholar (Walsberg).

#### THE SCOPE OF PHYSIOLOGY IN THE CONDOR

Introduction. Physiologically relevant material appearing in *The Condor* covers a broad spectrum. Rather than being concerned just with analysis of particular physiological processes, many of the studies appear oriented toward elucidation of the biology of various birds through analysis of their functional capacities and energetic relationships. It is certainly beyond the scope of this account to provide a comprehensive review of the physiologically relevant material appearing in *The Condor* over the past 96 years. However, it seems useful to indicate the scope of this work by commenting briefly on some of the prominent themes.

Energetics. More than 10% of the entries in the bibliography assembled for this account deal in some way or other with avian energetics, for there is a persistent interest among students of avian biology in the energetic costs of various processes and behaviors and in the total energy expenditures of the animals in the field. The Condor has been the outlet for several papers providing allometric equations based on empirical data, which deal with avian standard metabolism and daily energy expenditures. These have indicated differences in metabolic level among representatives of various orders (Lasiewski and Dawson 1967, Zar 1968) illustrated the greater impact of cold on existence costs for small as compared with large birds (Kendeigh 1970, Pimm 1976), and suggested a correlation of metabolic rate with climate or latitude in falconiforms and in hatchlings of various shorebirds and aquatic species (Wasser 1986, Klaassen and Drent 1991).

The journal has also presented articles on the energy costs of certain processes, based on respirometry, determinations of metabolizable energy intake, measurements of egg or parental body composition, or estimates of heat exchange. For example, egg production can involve an energy expenditure of up to 280% of basal metabolic rate in Ruddy Ducks, Oxyura jamaicensis (Alisauskas and Ankney 1994). Additionally, incubation, in at least some species, involves more than merely recycling heat that would have been produced by the incubating parent. These costs are estimated to represent increments equivalent to 40% and 20% of basal metabolic rate in incubating Wandering Albatross, Diomedea exulans (Brown and Adams 1984) and the Zebra Finch, Poephila guttata (El-Wailly 1966, Vleck 1981). The incubation period entails daily energy expenditures of nearly 6.5 × basal metabolic rate for female Orange-breasted Sunbirds, Nectarinia violacea (Williams 1993), a level more than twice that recorded for non-incubating females of other species and one that approached the sunbirds' maximal working capacity (Williams 1993). Beyond its impact on amino

acid metabolism (see, for example, Murphy and King 1984), molt also has an energetic cost, which is estimated in Japanese Quail (*Coturnix coturnix japonica*) to be 14% over maintenance requirements (Thompson and Boag 1976).

Analyses of body composition and material balance have figured prominently in various energetics studies appearing in The Condor. The extent of mid-winter maximal fat reserves in the Golden-crowned Kinglet, Regulus satrapa (Blem and Pagels 1984) are sufficiently limited as to suggest that this bird must resort to nocturnal hypothermia during cold winter nights. Fat content of Pacific Golden Plovers (Pluvialis dominica) on Wake Island before spring migration averages 26.5 g. well in excess of the estimated 18 g required to fuel the 4,000 km flight to the Aleutian Islands (Johnston and McFarlane 1967). Fat content of adult Bristlethighed Curlews (Numenius tahitiensis) averages 42% of body mass at the start of the spring migration from Laysan Island, providing fuel for the 4,000 km or more overwater flight to western Alaska (Marks and Redmond 1994). Bromley and Jarvis (1993), through body composition analysis of Dusky Canada Geese (Branta canadensis occidentalis) collected in Oregon and Alaska before and after spring migration, found this movement to be unexpectedly costly, reducing lipid reserves by 52%. This reduction was considered sufficient to influence the subsequent energy dynamic of reproduction. Migratory activity is affected by extent of energy reserves in North American thrushes following spring passage across the Gulf of Mexico, with lean migrants foraging more during the day and displaying less nocturnal activity than fatter ones (Yong and Moore 1993).

Determinations of daily energy expenditures or field metabolic rates (FMR) by birds in nature occupy an important interface between ecology and physiology and these have appeared with increasing frequency in The Condor in recent years. The use of the doubly labeled water technique has greatly facilitated such determinations in nestlings as well as adults (see, for example, Gabrielsen et al. 1987, Powers and Conley 1994). More detailed energy budgets have been obtained by combining time-activity budgets and microclimatic measurements for birds in the field, e.g., the Red Knot, Calidris canutus (Wiersma and Piersma 1994), with metabolic measurements in the laboratory. In certain instances the reliability of estimates of daily energy expenditures obtained from time-activity budgets has been assessed by comparing them with FMR determined with the doubly labeled water method (e.g., Weathers and Sullivan 1991).

Temperature regulation, nocturnal hypothermia, and hibernation. More than 15% of the physiologically relevant material published in *The Condor* to date concerns avian thermal relations. A partial list of topics includes the nest microenvironment (e.g., Calder 1974), regulation of nest mound temperature by megapodes (Seymour and Bradford 1992); development of temperature regulation in young birds (e.g., Farner and Serventy 1959, Ricklefs and Hainsworth 1968), heat conservation through communal roosting (Walsberg 1990), the effects of flocking and orientation into the wind on heat loss (Wiersma and Piersma 1994), relation of absorption of thermal radiation to skin or plumage color (Heppner 1970, Ohmart 1973), metabolic response to temperature of birds under standard conditions (e.g., Goldstein 1974, Withers and Williams 1990), thermogenic mechanisms (e.g., Olson et al. 1988, Brigham and Trayhurn 1994), seasonal adjustments of metabolism and/or insulation (e.g., Rising and Hudson 1974, Swanson 1991), vascular arrangements affecting heat exchange (e.g., Midtgård 1985), mechanisms of and capacities for evaporative cooling (e.g., Bartholomew et al. 1968, Withers and Williams 1990). Species studied range in size from the Calliope Hummingbird, *Stellula calliope* (Calder 1971), to the Ostrich, *Struthio camelus* (Schmidt-Nielsen et al. 1969). The study of the Ostrich provided an early indication of the unidirectional pattern of air flow through the lungs and air sac system.

Following the classic articles by Jaeger (1948, 1949) and Pearson (1950), natural hypothermia and torpidity in birds have represented a major theme in *The Condor*, where approximately two dozen accounts dealing with a variety of species have been published (e.g., Bartholomew et al. 1957, Bucher and Worthington 1982, Hiebert 1991, Williams 1993). These comprise a significant fraction of knowledge about this topic in birds. Nocturnal torpor or, in the case of the Poor-will, hibernation, allows these animals to husband their energy reserves. For the Rufous Hummingbird (*Selasphorus rufus*), it also facilitates premigratory fattening (Carpenter and Hixon 1988).

Water and electrolyte balance. Studies of facets of avian water balance are also well represented in *The Condor*, with the approaches used ranging from observations of the transport of water by adult sandgrouse to their young (Cade and Maclean 1967) and use of desert water sources by various birds (Smyth and Coulombe 1971, Fisher et al. 1972) to quantification of water losses and gains by various routes (Moldenhauer and Wiens 1970) and modelling of the water economy of granivorous birds (MacMillen 1990). In recent years, information on water turnover in birds has been provided by following isotope dilution through injection of birds with isotopically or doubly isotopically labeled water (e.g., Carmi-Winkler et al. 1987, Weathers and Stiles 1989).

Due to the extensive attention devoted to thermoregulation, there is a substantial representation of studies on evaporative water loss (e.g., Lasiewski and Bartholomew 1966, Lasiewski et al. 1970), some of which estimate cutaneous losses of water (e.g., Marder et al. 1986, Withers and Williams 1990). The Condor was the site of the first major attempt to define an overall relation between total evaporation and body mass in birds (Crawford and Lasiewski 1968). Electrolyte and water metabolism are tightly linked. The initial publications on former in The Condor were anecdotal observations on consumption of salt by cardueline finches (e.g., Kelly 1921, Aldrich 1939). Subsequently, laboratory studies involving assessment of the capacities of certain species for using saline waters as fluid sources were reported (e.g., Poulson and Bartholomew 1962, Basham and Mewaldt 1987). Only a few articles concerning the structural and functional characteristics of avian kidneys have appeared in The Condor. Johnson and Mugaas (1970) compared the renal medullary organization of seven taxa which differ in kidney efficiency. Medullary lobules were found to be two to three

times more abundant per unit of renal cortex in birds with more effective abilities for excretory water conservation.

Salt glands provide an means of excreting ions, principally sodium and chloride, with a minimal loss of water in many species of birds. Their function in falconiform birds was examined by Cade and Greenwald (1966) in *The Condor*. Reports on these glands in several other species have also appeared in this journal (Carpenter and Stafford 1970, Ohmart 1973, Hughes 1984). Hughes (1970) in a study of 51 species of nonpasserine birds with functional salt glands showed that the presence of such glands is associated with an increased renal mass.

Functional studies of clutch size, eggs and embryos. Stimulated by Lack's (1967) paper on possible limiting effects of food on clutch size of precocial birds, the types of nutrients that may be limiting and the timing of such limitation in waterfowl have received considerable attention in The Condor in recent years (e.g., Drobney 1982, Afton and Ankney 1991, Esler and Grand 1994). Controversy surrounding this topic led Editor Walsberg to invite several workers in the field to contribute essays stating their views. In one of these essays, Drobney (1991) noted that general agreement appears to exist that females that feed little during egg synthesis are limited by their endogenous nutrient reserves. The situation is less clear for species, including most temperate-nesting species of waterfowl, in which both endogenous and dietary nutrients are used to satisfy reproductive requirements. Ankney et al.'s (1991) essay summarized evidence for clutch size limitation by nutrients in waterfowl and for lipids rather than protein being the key substrates. Drobney (1991) noted that neither an hypothesis based on lipid limitation of clutch size nor one involving protein limitation provides a universally acceptable explanation of such limitation in all temperate-nesting waterfowl, perhaps because of interspecific differences in food availability and feeding ecology. Arnold and Rohwer's (1991) essay enunciated nine general points (e.g., variation in nutrient reserves greatly exceed variation in clutch size, variance in nutrient reserves remains high in post-laving birds), which they believe cast doubts on the nutrient-limitation hypothesis as a general explanation of clutch-size limitation in waterfowl. They concluded that the primary selective factor affecting clutch size in temperate waterfowl has been the amount of time required to complete a clutch, which they suggested most of these birds minimize by using nutrient reserves to maintain high rates of egg production (one egg/day) despite day to day shortfalls in the availability of dietary nutrients. Arnold and Rohwer (1991) noted that even if nutrient reserves do not determine clutch size per se, they may affect reproductive success via tradeoffs involving the role of such reserves in determining a female's ability to incubate successfully.

The gas conductance properties of avian eggshells became an important area of research in the 1970s through the work of the late Hermann Rahn and associates. The paper by Rahn and Ar (1974) summarizing the relation between water loss and incubation time in eggs is a particularly important contribution resulting from this work. Another indication of *The Condor's* involvement with such studies is provided by Carey et al. (1990), who have documented a compromise in eggshell properties for birds nesting at high altitudes. This involves restriction of water vapor conductance somewhat, but not to a level commensurate with the reduction of barometric pressure from sea level, thereby permitting maintenance of adequate oxygen tensions for the embryo.

The Condor has also published physiological studies on the metabolism and thermoregulatory capacities of embryos. The metabolic rate of the growing embryo of the Ostrich reaches a peak about six days before hatching, which is followed by a decline of about 25% that is thought to be associated with a decreasing growth rate (Hovt et al. 1978). Metabolic rate of embryonic White Terns (Gvgis alba) reaches a plateau just before external pipping, and then increases three-fold thereafter as the animal traverses internal pipping, establishment of a pip hole, and hatching (Pettit et al. 1981). Metabolic rate also increases during pipping in Sooty Terns (Sterna fuscata), but these semi-precocial birds only become endothermic following emergence from the egg (Mathiu et al. 1994). Increased incubation by parents in response to calling by American White Pelican embryos in pipped eggs undergoing cooling apparently provides a mechanism for behavioral thermoregulation in these altricial young (Evans 1988).

Annual cycles. Nearly 20% of the functionally oriented articles from The Condor that I included in the database on which these comments are based concern molt, the relation of molt and reproduction, premigratory fattening, or migration. The fraction would be increased substantially had I included items dealing with winter adjustments and those confined to definition of breeding schedules of various species. Clearly, understanding the annual cycles of birds and their control has been a central theme of functionally oriented research in The Condor. Work that had its start at Washington State University with Farner, King, Mewaldt, and Morton has been prominent in developing this theme and it seems appropriate here in the limited space available to focus on the contributions of these workers and their associates. As noted above, much of their work has involved the White-crowned Sparrow and the resultant publications have contributed substantially to this species' attaining distinction in The Condor as the most prominent taxon for physiological studies, having been a primary subject in more than 50 papers published there. Abundant, widely distributed, tractable, readily maintained in captivity, strongly photoperiodic, and containing both migratory and non-migratory forms, the White-crowned Sparrow is an ideal subject for studies of the annual cycle and its control in birds at middle and high latitudes. The compressed timing of reproduction, molt, and autumnal migratory preparation in populations breeding in the brief productive periods of the arctic and subarctic (DeWolfe 1967) or in montane situations in the west (Morton and Welton 1973) adds further interest to such studies. The major contribution of Farner, King, Mewaldt, Morton, and their associates to The Condor has been to provide both field and laboratory studies of such topics as gonadal cycles, molt, fattening (winter and, where relevant, premigratory), nestling growth, and the interrelations and control of these processes in the White-crowned Sparrows. Zonotrichia leucophrys gambelii has been the subject of a substantial portion of these efforts (e.g., Farner and Mewaldt 1955, King et al. 1966, Morton et al. 1969, Moore et al. 1982). Zonotrichia l. pugetensis, and the non-migratory Z. l. nuttalli have both received study (e.g., Mewaldt et al. 1968; Mewaldt and King 1977; Lewis 1975a, 1975b) and Z. l. oriantha has been the subject of a long term investigation of physiology and population biology on its breeding grounds in the Sierra Nevada by Morton and associates (e.g., Morton et al. 1972, 1990; Morton 1992). Differences in timing and extent of prenuptial molt, reproductive and migratory schedules, in fattening patterns and, apparently, in photosensitivity exist among the various populations of White-crowned Sparrows (see, for example, King et al. 1966, Morton and Welton 1973, Lewis 1975b, Mewaldt and King 1977), and differences in timing of gonadal development and timing and extent of prenuptial molt and of nocturnal and diurnal locomotor activity persisted between northern and southern sparrows (Z. l. pugetensis and Z. l. nuttalli, respectively) maintained in neighboring outdoor aviaries (Mewaldt et al. 1968). Study of the White-crowned Sparrow has paid rich dividends for the understanding of the functional basis of the annual cycle of birds at middle and high latitudes and it has contributed to the development of avian field endocrinology (e.g., Wingfield and Farner 1976) and to avian nutritional ecology (e.g. Murphy and King 1984). All these studies in The Condor and those by these authors appearing elsewhere represent an impressive contribution not only to understanding the functional characteristics of the annual cycle of the White-crowned Sparrow, but also to comparative biology generally.

# THE PLACE OF PHYSIOLOGY IN *THE CONDOR*

Over the more than 96 years of The Condor, the contents of the journal have shifted from anecdotal natural history observations, description of field trips, and lists of species seen or collected at various localities to a coverage of all the facets of modern avian biology. ranging from community ecology to molecular systematics. The rise in prominence of physiology in the journal in the past 50 years has been an important component of this diversification. Contributions dealing with functional topics appear to have been well received, judging by the fact that three of them (Dawson and Evans, 1960, Rahn and Ar 1974, Nottebohm 1984) have been included among the 17 (through 1994) winners of the H. R. Painton Award. The winners also include two studies dealing, respectively, with the compression of breeding, parental care, molt, and fattening of the Red-backed Sandpiper (Calidris alpinus) into the brief arctic summer (Holmes 1966) and with the migration biology of the Mountain White-crowned Sparrow (Morton 1992), topics with sufficient physiological relevance to justify inclusion of the awardwinning studies in the bibliographic database for this account. Incentives for publishing physiological material in The Condor must include the quality of the editing and production characterizing this journal, as well as the opportunity to reach a broad audience concerned with avian biology. However, the paramount incentive is probably that cited "with some trepidation" by Walsberg (1993)—"... in 1991 (the most recent year for which data are available) *The Condor* was either the first- or second-most frequently cited ornithological journal in the world, depending on the manner in which the citations are counted." As the centennial of the journal approaches, we find it providing a worldwide audience for an international group of investigators in the physiology of wild birds.

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