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HEMATOCRITS IN MONTANE SPARROWS IN RELATION TO REPRODUCTIVE SCHEDULE[1]

MARTIN L. MORTON
Department of Biology, Occidental College, Los Angeles, CA 90041-3392

Abstract. Hematocrits were measured in migratory Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) on their high altitude (3,000 m) breeding grounds during seven consecutive summers. Contrary to expectations, hematocrits were highest in newly arrived individuals then declined thereafter until the end of postnuptial molt. They then increased prior to autumnal migration. Hematocrits were higher in males than in females until onset of parental care but not thereafter. A large, rapid decrease in hematocrit was observed in females prior to ovulation and it remained low during oviposition. Hematocrits were at their lowest in both sexes during postnuptial molt.

These changes in relative quantity of erythrocytes may involve a variety of underlying causes. Among them are the metabolic demands associated with migration and thermoregulation, differential effects of sex steroids on erythropoiesis, osmotic effects on plasma volume when nutrient loads in plasma are high, such as during ovogenesis and perhaps molt, and transient changes in blood volume during molt.

Key words: Hematocrit; high altitude; Zonotrichia leucophrys*; erythropoiesis; migration; reproductive biology; oviposition; molt.*

INTRODUCTION

The hematocrit, or volumetric percentage of packed erythrocytes, is an easily obtained hematological value that has been used widely in studies of health and adaptation (Polo et al. 1992). Among migratory birds, for example, it has been reported and interpreted in relation to reproductive condition (Silverin 1981, Jones 1983, Keys et al. 1986), circulating hormone levels (Kern et al. 1972; Thapliyal et al. 1982, 1983; Wingfield et al. 1990), molt status (Chilgren and DeGraw 1977, DeGraw et al. 1979, DeGraw and Kern 1985), altitudinal shifts and associated metabolic demands (Carey and Morton 1976, Carpenter 1975, Weinstein et al. 1985, Clemens 1990), and stages of the annual cycle, especially migration (DeGraw et al. 1979, Hunter and Powers 1980, Wingfield and Farner 1980, Driver 1981, Gessaman et al. 1986, Swanson 1988).

Hypoxia is understood to be the fundamental erythropoietic stimulus in birds (Rosse and Waldmann 1966, Burton and Smith 1972, Weinstein et al. 1985, Sturkie 1986), although increased metabolic demands such as those imposed by migration (Carey and Morton 1976) or thermoregulation (Rehder et al. 1982, Swanson 1988), can apparently be a factor. As far as is known all such stimuli are mediated via a renally produced glycoprotein, erythropoietin, which then acts directly on bone marrow (Rosse and Waldmann 1966, Sturkie 1986). Days to weeks after translocation to high altitude or being held under hypobaric conditions birds exhibit an increase in hematocrit (Jaeger and McGrath 1974, Weathers and Snyder 1974, Clemens 1990) which cannot be attributed to dehydration or loss of plasma volume (Burton and Smith 1972, Weathers and Snyder 1974, Clemens 1990).

Of all the studies mentioned above, none has been conducted throughout the reproductive season on a migrant that summers and breeds in a high elevation montane environment. Herein I report on such a study not only to determine how hematocrit might vary in relation to clearly delineated stages of reproduction at high elevations, but also to test the hypothesis that an increase in hematocrit should be detectable in these migrants soon after they settle on their breeding areas.

MATERIALS AND METHODS

This study was conducted on a migratory passerine bird, the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*), near Tioga Pass in the central Sierra Nevada of California. The study site was a series of subalpine meadows covering an area of about 280 ha at an elevation of about 3,000 m. Members of this race of White-crowned Sparrow winter primarily in Mexico,

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presumably at low elevations, and summer and reproduce in montane settings of the western United States (Morton and Allan 1990). Data were gathered from the time the birds arrived on migration in May until they departed in September.

Individuals were lured into two- or four-cell live traps by the presence of seed and/or a conspecific held in one of the cells. Blood was taken from a wing vein into six heparinized capillary tubes per bird, stored on ice for 1–4 hr, then spun for 15 min at 1,900 rpm in a bench-top centrifuge (IEC). A test was conducted to see if spinning the blood for an additional 5 min decreased the hematocrit, but it did not. Hematocrits were read immediately after centrifugation using a microhematocrit capillary tube reader (Lancer). The value reported herein for each bird was the mean of the six tubes. The sampled birds were all adults, age one year or older, and subjects in a long-term study of their reproductive ecology and physiology. Each was banded, sexed, and often rather well known in terms of its reproductive history. Samples were collected only in the morning hours, 08:00–12:00, during seven summer reasons, 1985–1991.

RESULTS

Hematocrit values changed markedly during the breeding season in both sexes of *Z. l. oriantha* (Fig. 1), being highest when they first arrived in May, then decreasing steadily until mid-August, then increasing thereafter until the birds departed on migration in September. The total seasonal change in mean values was about 18% in males and 16% in females (May to August). The seasonal pattern of change was similar in the sexes although in May and June hematocrits were substantially lower in females than in males (t-test, $P < 0.001$ for both months).

Because individuals within a given year were not in perfect reproductive synchrony and because there were large interannual variations in reproductive schedule, combining the data by common calendar date (Fig. 1) does not adequately inform as to possible functional linkages between the bird's hematocrit and its concurrent physiological and behavioral condition. Therefore, the data are also broken out according to a sequence of readily separable stages associated with reproduction and its aftermath, providing we knew this specific information about an individual (or its mate) at the time it was bled (Fig. 2). This analysis shows that hematocrits remained relatively high in females until the end of nest construction then dropped sharply until the clutch was completed. Hematocrits were again higher during the various stages of parental care, became low during postnuptial molt, and increased during the postmolt period when the birds were depositing fat just prior to autumnal migration. The pattern in males was similar to that of females except that their early season hematocrits did not decline until their mates began laying (Fig. 2).

When all the data shown in Figure 1 are lumped, they reveal that mean hematocrit ($\pm$SD) was 54.9 ($\pm$4.3, $n = 649$) in males and 53.2 ($\pm$4.4, $n = 550$) in females, a highly significant difference (t-test, $P < 0.001$). However, this difference was not consistent through the season, rather it was due to a large drop in female hematocrit that occurred during the early part of the nesting cycle (Fig. 1, 2). During the first nestling cycle of the season (to which these data are restricted) the female, unassisted by the male, builds her nest within about a two to four day period. The nest then sits empty, usually for an additional two to four days before she begins laying. Since modal clutch size is four and eggs are laid one per day, the period in question when hematocrits were very low, end of nest construction to end of laying, lasts about a week.

We can scrutinize this approximate period more closely by plotting hematocrits obtained on females whose exact schedule of laying was known (Fig. 3). In interpreting this figure, realize that eggs were laid one per day early in the morning, on days 10–13, a few hours before blood samples were taken. Ovulation, therefore, must have occurred on the mornings of days 9–12, assuming that ovulation precedes laying by ca. 24 hr (see Sturkie 1986). The lowest mean hematocrit occurred on the morning when the first egg was ovulated. It remained low during the subsequent days of ovulation and laying then increased somewhat thereafter. The only statistically significant one-day change in these data occurred between days 8 and 9 (t-test, $P < 0.01$).

Hematocrits were not obtained on *Z. l. oriantha* during migration because we have never known them to stop-over at Tioga Pass; all birds that we sampled were residents. A migratory conspecific, *Z. l. gambelii,* does stop-over during autumnal passage (Morton and Pereyra 1987) and we were able to obtain samples from them

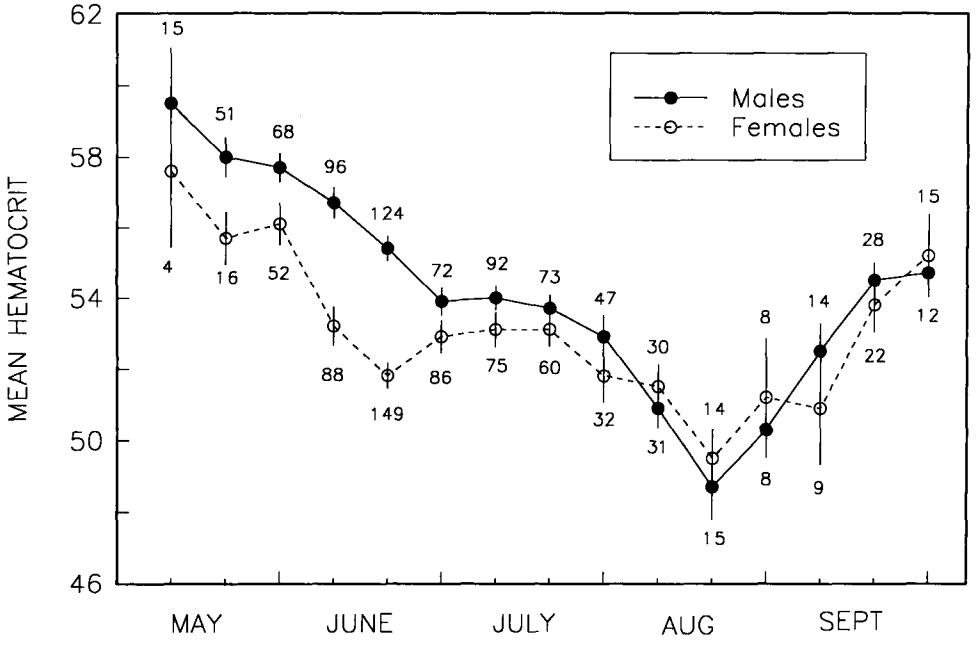

FIGURE 1. Seasonal changes in mean hematocrit of *Z. l. oriantha* at Tioga Pass. Bars indicate ±1 SE and numerals give sample sizes for each mean.

in late September. Their mean hematocrits (±SD) were 54.7 ± 2.3 (n = 10) in males and 55.1 ± 4.6 (n = 11) in females. These means were not different (t-test, $P > 0.9$).

DISCUSSION

The polycythemia that occurs upon initial exposure to hypoxia is undoubtedly a short-term homeostatic response and should not be viewed as adaptive for life at high altitude because it may eventually compromise both cardiac and pulmonary functions by inducing right ventricular hypertrophy and pulmonary arterial hypertension. In fact, birds that live for most or all of their lives in the high mountains do not have higher hematocrits or hemoglobin concentrations than those living at low elevations (Palomeque et al. 1980, Clemens 1990). It is interesting, therefore, that *Z. l. oriantha* arriving on vernal migration at Tioga Pass had the highest hematocrits we recorded during the season in both sexes and that, contrary to expectations, during the following three months of residency their hematocrits decreased considerably (Fig. 1).

Since hematocrit is only a measurement of relative volume, it can vary because of changes in either the cellular or acellular (plasma) compartment. In other words, the high hematocrits of newly arrived birds could be due to a relatively high rate of erythropoiesis and/or to dehydration. Migration flights of *Z. leucophrys* are nocturnal and cover about 50 to 300 km per night (Oakeson 1954, Cortopassi and Mewaldt 1965, DeWolfe et al. 1973, King and Mewaldt 1981). During their extended flights, respiratory water loss of migrants may exceed metabolic water production by about 30% (Hart and Berger 1972) although the ratio is highly sensitive to the ambient temperatures being encountered (Bartholomew 1972). Using the data provided by Hart and Berger (1972) and assuming that migration occurs only at night when it is coolest, I estimate that *Z. l. oriantha* would lose at the most 2 ml of body water, or about 8% of their body weight, during one overnight migration flight. Dehydrated birds can probably easily recover a loss of this magnitude within a few hours after exposure to a source of hypotonic drinking water (Smythe and Bartholomew 1966, Carey and Morton 1971). We defined newly arrived *Z. l. oriantha* as those captured for the first time on or before 20 May. Obviously most, if not all, of these individuals would have had many hours, if not days, to become rehydrated after arriving

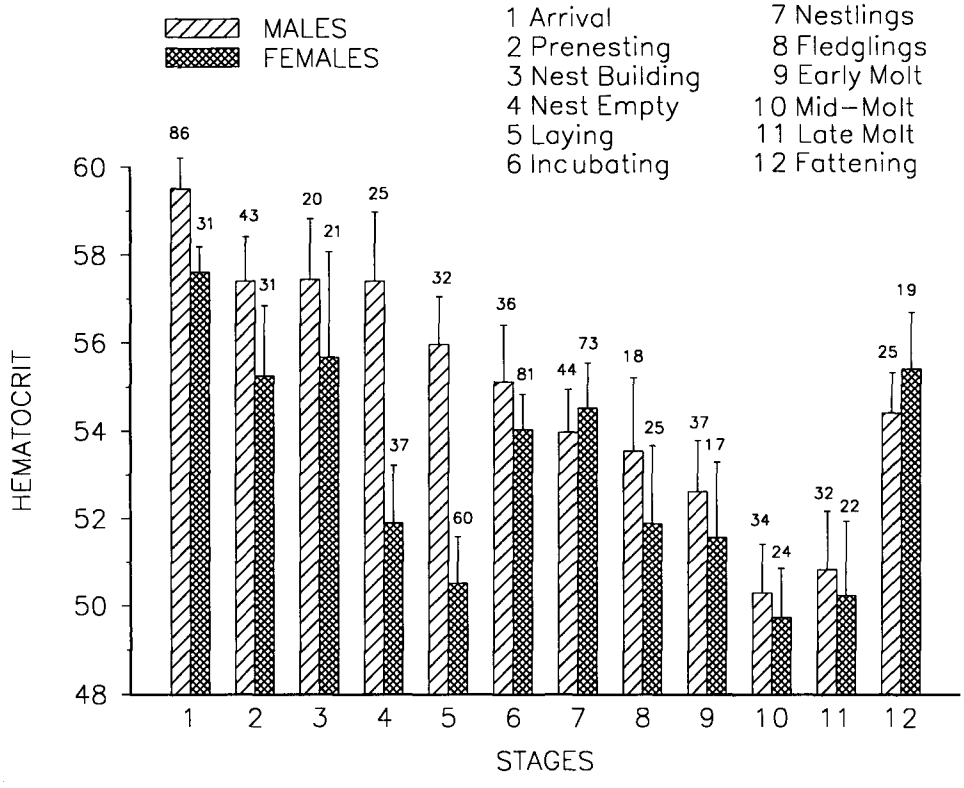

FIGURE 2. Mean hematocrits of *Z. l. oriantha* at Tioga Pass during various functionally separable stages of the summer season. Stage 1: birds sampled at the time of first capture for the season if it occurred on or before 20 May. Stage 2: birds sampled after arrival but before nest-building activities had begun by them or their mate. Stage 3: the female of a pair was engaged in nest construction. Stage 4: nest built but sitting empty. Stage 5: female of a pair engaged in laying. Stage 6: female incubating a full clutch. Stage 7: hatchlings present in the nest. Stage 8: dependent fledglings present. Stage 9: postnuptial molt in progress but not beyond shedding of primary 3. Stage 10: molt now includes primaries 4–6. Stage 11: molt now includes primaries 7–9. Stage 12: postnuptial molt completed, premigratory fattening in progress. Bars above the means show 1 SE and numerals give sample sizes.

at the study area and before being trapped and sampled by us, so loss of volume in the plasma compartment should probably be ruled out as a factor contributing to their high hematocrits. Although free-running water for drinking was sometimes scarce on the study area in May because of persistent winter conditions, *Z. l. oriantha* will also satisfy their thirst by eating snow.

Small passerines are known for their high metabolic rates even while at rest (Lasiewski and Dawson 1967), so an improved capacity for oxygen uptake and transport at the time of migration would seem to be desirable, although they may already be somewhat preadapted for strenuous activity because their hematocrits and hemoglobin concentrations are relatively high even in the nonmigratory state (Carey and Morton 1976, Palomeque et al. 1980). The data in Figure 1 clearly indicate, however, that during vernal migration in *Z. l. oriantha* there was increased stimulation of erythropoiesis. Supportive information can also be found in other studies. For example, Wingfield and Farner (1980) found that wintering *Z. l. gambelii* had lower mean hematocrits (51.7) than those in vernal migration (56.6) and our data show *Z. l. gambelii* with mean hematocrits of 54.9 during autumnal passage at Tioga Pass in September. This did not differ from hematocrits of *Z. l. oriantha* concurrently completing their metabolic preparations for autumnal migration (Fig. 2). Interestingly, Oakeson (1953) discovered that spleen weights decreased substantially during vernal migration in male *Z. l. gambelii* but not in females. No effect could be discerned in her autumnal data on the same birds. This could be due to fundamental differ-

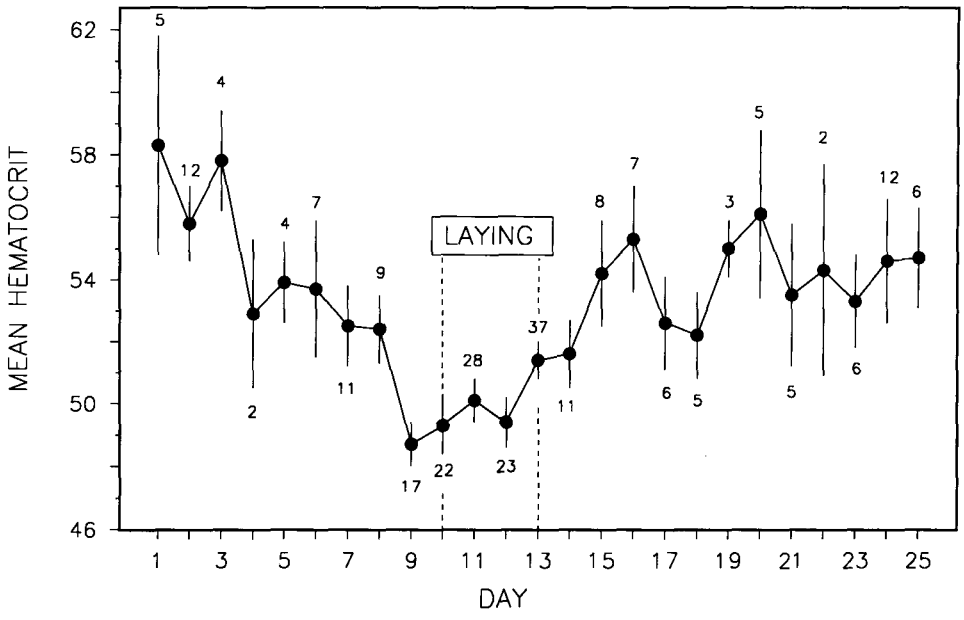

FIGURE 3. Mean hematocrit in female *Z. l. oriantha* in relation to time of laying a four-egg clutch, the first egg being laid on day 10 of the 25 days shown. Bars indicate ±1 SE and numerals give sample sizes for each mean.

ences in the metabolic demands associated with vernal and autumnal migrations, certainly the latter is more leisurely in *Z. l. gambelii* (Morton and Pereyra 1987) than the former (King and Mewaldt 1981). In summary, it seems likely that the high hematocrits observed in *Z. l. oriantha* upon their arrival at breeding areas were due to increased synthesis of erythrocytes induced by the metabolic requirements associated with vernal migration. In males, at least, an additional aliquot of erythrocytes may have been supplied to the circulation by splenic emptying. The altitude at which *Z. l. oriantha* conduct migration flights might be a contributing factor in this response as well because the hypoxic drive associated with heavy exercise could be magnified if they were flying at especially high altitudes. This does seem unlikely because more than 99% of passerine migration is thought to occur below 3,000 m (Welty 1975), even though portions of flights can occur as high as 6,000 m when birds are trying to avoid headwinds (Williams et al. 1977).

Hematocrits were significantly higher in *Z. l. oriantha* males than in females from time of arrival until clutches had been completed and females had begun incubating, but not thereafter (Fig. 2). This may be due at least in part to differences in sex steroids. Androgens are known to stimulate erythrocyte synthesis and estrogens to inhibit it (Domm and Taber 1946, Dukes and Goldwasser 1961, Mirand and Gordon 1966, Kern et al. 1972, Nirmalan and Robinson 1972) and plasma testosterone titers were high in males from the time they arrived at Tioga Pass until their mates had begun laying (Morton et al. 1990). We have not yet completed our studies of female steroids in *Z. l. oriantha,* but estrogen levels are known to be increasing or high in migratory conspecific females (*Z. l. gambelii* and *Z. l. pugetensis* from arrival at breeding areas until at least onset of the ovulatory sequence (Wingfield and Farner 1978a, 1978b). So either estrogens are not fully inhibiting erythropoiesis in migrants preparing for reproduction or their effect is being partially swamped by concurrent stimuli emanating from the rigors of migration and possibly of territory and mate acquisition. There may also be some underlying endogenous component to seasonal changes in hematocrit in photoperiodic species such as the *Zonotrichia* because ovariectomy prior to the winter solstice, but not after it, prevented an increase in hematocrit in captive photostimulated female *Z. l. gambelii* (Wingfield et al. 1990).

A sudden, large decrease in hematocrit occurred in *Z. l. oriantha* females preparing to lay (Figs. 2, 3). The response clearly was not initiated

until nest building had ceased (Fig. 2). Silverin (1981) and Jones (1983) also found that hematocrit decreased rapidly in laying wild birds. In the latter study, some day-to-day changes were reported and the first decrease in hematocrit was evident in Red-billed Queleas (*Quelea quelea*) on the day that the first egg of the clutch was ovulated. There was a large drop in *Z. l. oriantha* females on that day as well (Fig. 3, day 9), but the hematocrit had already been declining for several days previous (Fig. 3). Because the females in his study were in poor physical condition, Jones suspected that the demands of egg formation imposed a severe nutritional stress that caused hemopoiesis to be suppressed. That, coupled with a presumed rapid turnover rate of erythrocytes, led to the depressed hematocrits. Female *Z. l. oriantha* in the present study, however, always carried at least some visible subcutaneous fat and appeared to be in excellent condition.

Estrogen inhibits erythropoiesis in mice (Mirand and Gordon 1966) but aside from this possible effect on hematocrit there are profound, rapid increases in the protein, lipid, and calcium content of the plasma of female birds at the time of vitellogenesis and egg laying (Lush 1963, Schjeide et al. 1963, McIndoe 1971, Christie and Moore 1972, DeGraw et al 1979, Sturkie 1986) which can be expected to change the osmotic properties of their plasma. As the osmolality of plasma increases its volume should also increase resulting in dilution of the circulating cellular components and a reduction of the hematocrit. This sort of mechanism has been invoked to explain hematocrit changes observed during yolk utilization by neonates (Atwal et al. 1964) during vitellogenesis (DeGraw et al. 1979), and immediately following administration of exogenous estrogen (Kern et al. 1972) and I view it to be the most likely mechanism involved in the rapid day-to-day changes in hematocrit observed in ovipositing *Z. l. oriantha*. It seems worth noting that the plasma water compartment at the time of oviposition could also be affected by the neurohypophysial hormone arginine vasotocin (AVT). Ordinarily AVT acts as an antidiuretic in birds but its release is substantially increased at the time of oviposition when it, along with mesotocin, also acts to stimulate uterine motility (Sturkie 1986). Thus excess AVT might help preserve plasma volume more than usual during the egg laying period and be a contributing factor to the hematocrits observed.

Beyond the period of reproduction in *Z. l. oriantha,* hematocrit varied most during the time of postnuptial molt when it decreased significantly in both sexes (Fig. 2). In females the decrease appeared to begin at an earlier stage, that is, during the time they were feeding fledglings (Fig. 2). This is deceptive, however, because many males curtailed parental care as they entered molt whereas females did not (Morton and Morton 1990, Morton 1992). In other words, the stages of feeding fledglings and early molt often overlapped in females.

A marked decline in hematocrit has also been noted in ducks (Driver 1981) and in sparrows (Chilgren and DeGraw 1977, DeGraw et al. 1979, DeGraw and Kern 1985) during periods of heavy molt. There appears to be agreement that blood volume increases during plumage renewal and that this is due principally to expansion of the plasma volume; thus the hematocrit declines even though total number of circulating erythrocytes does not (Chilgren and DeGraw 1977).

Two final points are worth making about the foregoing data on *Z. l. oriantha*. First, more studies of blood volumes, such as those cited above for the molting period, as well as hemoglobin concentrations and erythrocyte volumes are needed during the periods of migration and nesting. Second, representative hematocrit values cannot be reliably reported for a sex or a species from only a brief sampling period. Hematocrit values are likely to be highly variable in seasonal breeders and will be found to be related to physiological and behavioral phases of the annual cycle, especially in migrants.

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LITERATURE CITED

ATWAL, O. S., L. Z. MCFARLAND, AND W. O. WILSON. 1964. Hematology of *Coturnix* from birth to maturity. Poult. Sci. 43:1392–1401.

BARTHOLOMEW, G. A. 1972. The water economy of seed-eating birds that survive without drinking. Proc. XV Int. Ornithol. Congr., p. 237–254.

BURTON, R. R., AND A. H. SMITH. 1972. The effect of chronic erythrocytic polycythemia and high al-

titude upon plasma and blood volumes. Proc. Soc. Exp. Biol. Med. 140:920–923.

CAREY, C., AND M. L. MORTON. 1971. A comparison of salt and water regulation in California Quail (*Lophortyx californicus*) and Gambel's Quail (*Lophortyx gambelii*). Comp. Biochem. Physiol. 39A: 75–101.

CAREY, C., AND M. L. MORTON. 1976. Aspects of circulatory physiology of montane and lowland birds. Comp. Biochem. Physiol. 54A:61–74.

CARPENTER, F. L. 1975. Bird hematocrits: effects of high altitude and strength of flight. Comp. Biochem. Physiol. 50A:415–417.

CHILGREN, J. D., AND W. A. DEGRAW. 1977. Some blood characteristics of White-crowned Sparrows during molt. Auk 94:169–171.

CHRISTIE, W. W., AND J. H. MOORE. 1972. The lipid components of the plasma, liver, and ovarian follicles in the domestic chicken (*Gallus gallus*). Comp. Biochem. Physiol. 41B:287–295.

CLEMENS, D. T. 1990. Interspecific variation and effects of altitude on blood properties of Rosy Finches (*Leucosticte arctoa*) and House Finches (*Carpodacus mexicanus*). Physiol. Zool. 63:288–307.

CORTOPASSI, A. J., AND L. R. MEWALDT. 1965. The circumannual distribution of White-crowned Sparrows, Bird-Banding 36:141–169.

DEGRAW, W. A., AND M. D. KERN. 1985. Changes in the blood and plasma volume of Harris' Sparrows during postnuptial molt. Comp. Biochem. Physiol. 81A:889–893.

DEGRAW, W. A., M. D. KERN, AND J. R. KING. 1979. Seasonal changes in the blood composition of captive and free-living White-crowned Sparrows. J. Comp. Physiol. 129:151–162.

DEWOLFE, B. B., G. C. WEST, AND L. J. PEYTON. 1973. The spring migration of Gambel's Sparrows through southern Yukon territory. Condor 75:43–59.

DOMM, L. V., AND E. TABER. 1946. Endocrine factors controlling erythrocyte concentration in the blood of the domestic fowl. Physiol. Zool. 19:258–281.

DRIVER, E. A. 1981. Hematological and blood chemical values of Mallard, *Anas p. platyrhynchos*, drakes before, during and after remige moult. J. Wildl. Dis. 17:413–421.

DUKES, P. P., AND E. GOLDWASSER. 1961. Inhibition of erythropoiesis by estrogens. Endocrinology 69: 21–29.

GESSAMAN, J. A., J. A. JOHNSON, AND S. W. HOFFMAN. 1986. Hematocrits and erythrocyte numbers for Cooper's and Sharp-shinned Hawks. Condor 88: 95–96.

HART, J. S., AND M. BERGER. 1972. Energetics, water economy and temperature regulation during flight. Proc. 15th Int. Ornitol. Congr., p. 189–199.

HUNTER, S. R., AND L. R. POWERS. 1980. Raptor hematocrit values. Condor 82:226–227.

JAEGER, J. J., AND J. J. MCGRATH. 1974. Hematologic and biochemical effects of simulated high altitude on the Japanese Quail. J. Appl. Physiol. 37:357–361.

JONES, P. J. 1983. Hematocrit values of breeding Red-billed Queleas (*Quelea quelea*) (Aves: Ploceidae) relation to body condition and thymus activity. J. Zool. Lond. 201:217–222.

KERN, M. D., W. A. DEGRAW, AND J. R. KING. 1972. Effects of gonadal hormones on the blood composition of White-crowned Sparrows. Gen. Comp. Endocrinol. 18:43–53.

KEYS, G. C., R. C. FLEISCHER, AND S. I. ROTHSTEIN. 1986. Relationships between elevation, reproduction and the hematocrit level of Brown-headed Cowbirds. Comp. Biochem. Physiol. 83A:765–769.

KING, J. R., AND L. R. MEWALDT. 1981. The average rate of travel by migrating White-crowned Sparrows, *Zonotrichia leucophrys gambelii*, in spring. N. Am. Bird Bander 6:98–100.

LASIEWSKI, R. C., AND W. R. DAWSON. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. Condor 69: 13–23.

LUSH, J. E. 1963. The relationship of egg-laying to changes in the plasma proteins of the domestic fowl. Br. Poult. Sci. 4:255–260.

MCINDOE, W. M. 1971. Yolk synthesis, p. 1209–1223. *In* D. J. Bell and B. M. Freeman [eds.], Physiology and biochemistry of the domestic fowl. Academic Press, London and New York.

MIRAND, E. A., AND S. A. GORDON. 1966. Mechanism of estrogen action in erythropoiesis. Endocrinology 78:325–332.

MORTON, G. A., AND M. L. MORTON. 1990. Dynamics of postnuptial molt in free-living Mountain White-crowned Sparrows. Condor 92:813–828.

MORTON, M. L. 1992. Control of postnuptial molt in the Mountain White-crowned Sparrow: a perspective from field data. Ornis Scand. 23:322–327.

MORTON, M. L., AND N. ALLAN. 1990. Effects of snowpack and age on reproductive schedules and testosterone levels in male White-crowned Sparrows in a montane environment, p. 239–249. *In* M. Wada, S. Ishii and C. G. Scanes [eds.], Endocrinology of birds: molecular to behavioral. Japan Sci. Soc. Press, Springer Verlag, Tokyo.

MORTON, M. L., AND M. E. PEREYRA. 1987. Autumn migration of Gambel's White-crowned Sparrow through Tioga Pass, California. J. Field Ornithol. 58:6–21.

MORTON, M. L., L. E. PETERSON, D. M. BURNS, AND N. ALLAN. 1990. Seasonal and age-related changes in plasma testosterone levels in Mountain White-crowned Sparrows. Condor 92:166–173.

NIRMALAN, G. P., AND G. A. ROBINSON. 1972. Hematology of Japanese Quail treated with exogenous stilbestrol dipropionate and testosterone propionate. Poult. Sci. 51:920–925.

OAKESON, B. B. 1953. Cyclic changes in liver and spleen weights in migratory White-crowned Sparrows. Condor 55:3–16.

OAKESON, B. B. 1954. The Gambel's Sparrow at Mountain Village, Alaska. Auk 71:351–365.

PALOMEQUE, J., L. PALACIOS, AND J. PLANAS. 1980. Comparative respiratory functions of blood in some passeriform birds. Comp. Biochem. Physiol. 66A: 619–624.

POLO, F. J., J. F. CELDRAN, V. I. PEINADO, G. VISCOR, AND J. PALOMEQUE. 1992. Hematological values for four species of birds of prey. Condor 94:1007–1013.

REHDER, N. B., D. M. BIRD, AND P. C. LAGUE. 1982. Variations in blood packed cell volume of captive

American Kestrels. Comp. Biochem. Physiol. 72A: 105–109.

ROSSE, W. F., AND T. A. WALDMANN. 1966. Factors controlling erythropoiesis in birds. Blood 27:654–661.

SCHJEIDE, O. A., M. WILKENS, R. MCCANDLES, R. MUNN, M. PETERSON, AND G. CARLSEN. 1963. Liver synthesis, plasma transport and structural alterations accompanying passage of yolk protein. Am. Zool. 3:167–184.

SILVERIN, B. 1981. Reproductive effort, as expressed in body and organ weights in the Pied Flycatcher. Ornis Scand. 12:133–139.

SMYTH, M. AND G. A. BARTHOLOMEW. 1966. The water economy of the Black-throated Sparrow and the Rock Wren. Condor 68:447–458.

STURKIE, P. D. 1986. Avian physiology. Springer-Verlag, New York.

SWANSON, D. L. 1988. Seasonal variation of vascular oxygen transport in the Dark-eyed Junco. Am. Zool. 28:129A.

THAPLIYAL, J. P., P. LAL, A. K. PATI, AND B.B.PD. GUPTA. 1983. Thyroid and gonad in the oxidative metabolism, erythropoiesis, and light response of the migratory Red-headed Bunting, *Emberiza bruniceps*. Gen. Comp. Endocrinol. 51:444–453.

THAPLIYAL, J. P., A. K. PATI, V. K. SINGH, AND P. LAL. 1982. Thyroid, gonad, and photoperiod in the hemopoiesis of the migratory Red-headed Bunting, *Emberiza bruniceps*. Gen. Comp. Endocrinol. 46:327–332.

WEATHERS, W. W., AND G. K. SNYDER. 1974. Functional acclimation of Japanese Quail to simulated high-altitude. J. Comp. Physiol. 93:127–137.

WEINSTEIN, Y., M. H. BERNSTEIN, P. E. BICKLER, D. V. GONZALES, F. C. SAMANIEGO, AND M. A. ESCOBEDO. 1985. Blood respiratory properties in pigeons at high altitudes: effects of acclimation. Am. J. Physiol. 249:R765–R775.

WELTY, J. C. 1975. The life of birds. 2nd ed. W. B. Saunders, Philadelphia, London, Toronto.

WILLIAMS, T. C., J. M. WILLIAMS, L. C. IRELAND, AND J. M. TEAL. 1977. Autumnal bird migration over the western North Atlantic Ocean. Am. Birds 31: 251–267.

WINGFIELD, J. C., AND D. S. FARNER. 1978a. The endocrinology of a natural breeding population of the White-crowned Sparrow (*Zonotrichia leucophrys pugetensis*). Physiol. Zool. 51:188–205.

WINGFIELD, J. C., AND D. S. FARNER. 1978b. The annual cycle of plasma irLH and steroid hormones in feral populations of the White-crowned Sparrow, *Zonotrichia leucophrys gambelii*. Bio. Reprod. 19:1046–1056.

WINGFIELD, J. C., AND D. S. FARNER. 1980. Control of seasonal reproduction in temperate-zone birds. Prog. Reprod. Biol. 5:62–101.

WINGFIELD, J. C., H. SCHWABL, AND P. W. MATTOCKS, JR. 1990. Endocrine mechanisms of migration, p. 232–256. *In* E. Gwinner [ed.], Bird migration. Springer-Verlag, Berlin.