

ARE AVIAN HEMATOCRITS INDICATIVE OF CONDITION? AMERICAN KESTRELS AS A MODEL

RUSSELL D. DAWSON, Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, SK S7N 5E2, Canada

GARY R. BORTOLOTTI, Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, SK S7N 5E2, Canada

Abstract: Diseased animals or those in poor condition are known to have reduced hematocrits. Many investigators have assumed that hematocrit levels thus reflect condition and disease status of an animal. This study tested these assumptions by examining the relation between hematocrits of American kestrels (*Falco sparverius*) during several stages of the breeding season, and condition, prey abundance, and blood parasite load. We also examined the potential effects of a number of intrinsic and extrinsic influences on hematocrit. Hematocrits did not differ between the sexes, or between the pre-laying and incubation periods. Among females, hematocrit did not vary with the date of sampling, breeding chronology, prey abundance, condition, age, or molt, although hematocrit increased with ambient temperature during incubation. Hematocrit of males was not related to breeding chronology, prey abundance, condition, age, or molt. During incubation, male hematocrit increased with the date of sampling and ambient temperature. Hematocrits of both sexes declined with the time of day that the sample was taken, and increased with the level of infection of the blood parasite *Haemoproteus*. The use of hematocrits to assess the health and condition of clinically normal kestrels is therefore questionable, and given the positive association with parasite loads, may even lead to erroneous conclusions.

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Hematology is frequently presumed to provide indicators useful in assessing the health and nutritional condition of animal populations (Cooper 1975, Hellgren et al. 1989, Averbeck 1992). Hematocrit, defined as the percentage of the total blood volume occupied by erythrocytes, represents oxygen-carrying capacity and therefore possibly can be used to evaluate the "health" of the oxygen transport system. Anemias, which are reflected by decreased hematocrit levels, can arise from decreased erythrocyte production when nutritionally stressed, erythrocyte destruction from hemolytic diseases or blood parasitism, dehydration, toxins, or from direct blood loss as a result of injury or blood-sucking parasites (LeResche et al. 1974, Hoffman et al. 1985, Vleck and Priedkalns 1985, Whitworth and Bennett 1992).

Despite the potential to use blood variables to assess condition, few studies of birds have confirmed the existence of an association between hematocrit and condition, and most merely have been descriptive. Perhaps because hematocrits are routinely assessed in clinical work (Stoskopf et al. 1983), many investigators have assumed that clinically normal birds in superior physical condition or free of disease will

have higher hematocrits than clinically normal birds in poorer condition (Cooper et al. 1986, Gavett and Wakeley 1986). The purpose of our study was to establish baseline levels of hematocrits of American kestrels, a small falcon, during the breeding season. We quantified physical condition, parasite load, and prey abundance, and attempted to relate variations in these variables to hematocrit levels. In addition, we investigated the "boundary" conditions (LeResche et al. 1974) of hematocrits; that is, we determined whether normal hematocrit values varied with the characteristics of the bird such as sex, season, age, reproductive status, time and temperature at sampling, and molt. All of these factors have the potential to influence blood variables to some extent (Ferrer 1990).

American kestrels are an ideal model to assess the relation between condition and hematocrit. Changes in mass over the course of the breeding season are different between males and females (this study, Iko 1991). The sex roles, and therefore behavior and activity, are different throughout the breeding season (Balgooyen 1976). In addition, condition potentially can affect mate choice (Bortolotti and Iko 1992) and reproduction (Wiebe and Bortolotti 1994) in this population of kestrels.

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STUDY AREA AND METHODS

We studied a wild population of American kestrels from April to July during 1994 and 1995 in the boreal forest of northcentral Saskatchewan, Canada, in the vicinity of Besnard Lake (55°N, 106°W). Since 1988, nest boxes have been available in a variety of habitats ranging from densely forested roadsides to nearly treeless clearcuts (Bortolotti 1994). Kestrels arrived on our study area in mid- to late April after migration, and began laying eggs in mid-May. Nest boxes were visited every 3 to 5 days during May and early June to determine laying date, and then again after laying was complete to capture adults.

Kestrels were trapped throughout the breeding season with bal-chatri traps (Berger and Mueller 1959), and in the nest box with traps or by hand. Birds were examined for molting remiges and rectrices, weighed to the nearest gram and 6 measures of size were taken: lengths (nearest mm) of the unflattened wing chord, tenth primary, outer rectrix, and central rectrix; and culmen length and width of the tarsus (nearest 0.1 mm). Mass of an animal is partly a function of its structural size, so to obtain an index of condition we scaled mass to body size for each bird. Multivariate measures of structural size are preferred over univariate measures (Rising and Summers 1989, Freeman and Jackson 1990), so we used the first component (PC1) of a principal components analysis (PCA) as an index of overall body size. The 6 linear measurements were used as input variables for the PCAs, and we performed separate analyses for females ($n = 454$) and males ($n = 336$; for details, see Bortolotti and Iko 1992).

A 27-gauge needle was used to lance the brachial vein of each bird and blood was collected in a heparinized micro-capillary tube. A blood smear was made, air dried, and fixed immediately in 100% ethanol. Slides were sent to the International Reference Centre for Avian Haematozoa at Memorial University, St. John's, Newfoundland, Canada, where they were examined for the prevalence and intensity of hematozoa by G. F. Bennett. Hematozoa were quantified by counting the number of parasites in 100 microscope fields under oil with 100× objective and 12× ocular lenses. To compensate for variation in blood thickness that is common in smears, the 100 fields were chosen in a line from one end of the slide to the other. Although 5 genera of blood parasites occur in kestrels on our study area (R. D. Dawson and G. R. Bortolotti, unpubl. data), we restricted our analyses to birds parasitized with *Haemoproteus* species, which were the most common parasites.

Blood remaining in the micro-hematocrit tube was stored in a cooler until it was centrifuged for 5 minutes in an International Micro-capillary Centrifuge (Model MB, Int. Equipment Co., Needham Heights, Mass.) some hours later. We determined hematocrit directly on a micro-hematocrit reader.

We obtained blood samples from adult kestrels during all phases of the breeding season: pre-laying, egg laying, incubation, soon after eggs hatched, and just before the young left the nest. To reduce disturbance to birds during laying, we did not sample actively at this time; therefore, we restricted most of our analyses to the pre-laying and incubation periods where our sample sizes were large. Both of these periods were analyzed separately because of changes in the birds' behavior and physiology. We also examined hematocrits and condition of females caught during 1995 when their offspring were about to fledge.

We assessed the relative abundance of food on territories by censusing the main prey of kestrels, small mammals (Bortolotti et al. 1991, Iko 1991). During early July 1994, trap lines consisting of 10 stations spaced 30 m apart and situated parallel to, and 10 m from a road, were set on most territories. At each station 2 Museum Special snap traps (Woodstream Co., Lititz, Pa.) were baited with peanut butter. Each line operated for 3 days. The same protocol was used in July 1995, except that some lines had only 5 stations spaced 60 m apart. We examined

Table 1. Correlation coefficients and *P*-values for correlations between hematocrit and Julian date of sampling, number of days before or after egg laying commenced ("breeding chronology") that the sample was taken on, time of sampling, ambient temperature at sampling, prey abundance as measured by an index of small mammal numbers, and condition (see STUDY AREA and METHODS for calculation) of American kestrels during pre-laying and incubation in northern Saskatchewan. Correlation coefficients are Pearson's for all variables except prey abundance which are Spearman's.

Variable	Sex	Pre-laying			Incubation		
		<i>r</i>	<i>P</i>	<i>n</i>	<i>r</i>	<i>P</i>	<i>n</i>
Sampling date	F	-0.09	0.33	111	0.01	0.87	193
	M	-0.15	0.19	82	0.21	0.01	146
Breeding chronology	F	-0.20	0.13	62	0.04	0.56	187
	M	0.02	0.91	40	0.09	0.28	141
Time of sampling	F	-0.17	0.07	111	-0.25	0.0004	193
	M	-0.27	0.02	82	-0.27	0.0008	146
Temp at sampling	F	-0.05	0.61	111	0.18	0.01	193
	M	0.06	0.58	82	0.27	0.001	146
Prey abundance	F				-0.01	0.88	118
	M				-0.03	0.81	92
Physical condition	F	-0.03	0.77	106	0.01	0.91	181
	M	0.08	0.50	80	0.12	0.16	140

the effect of prey abundance on hematocrit for incubating birds only. During pre-laying, both sexes can be fairly transient and often switch between one or more territories before egg laying begins (Bortolotti and Iko 1992). By testing for prey-abundance effects only during incubation, we were more confident that birds had been present on territories for a sufficient length of time for potential food-mediated alterations of hematocrit to become apparent.

Minimum age was known for birds banded in previous years and that returned to the study area. We attempted to classify other kestrels as either in their second year (SY) of life, or older (after-second year: ASY), based on plumage characteristics and feather fault bars (Smallwood 1989). Because this method is not always applicable (G. R. Bortolotti, unpubl. data), we restricted our analyses of age effects to individuals classified reliably as SY or known from banding to be SY or ASY.

Ambient temperatures were recorded at hourly intervals throughout both years by a weather station located on the study area.

We analyzed data for each sex separately because kestrels are sexually dimorphic with respect to size (Bird 1988) and behavior. Males undertake nearly all of the hunting duties for the pair from weeks before egg laying to about 10 days after eggs hatch (Balgooyen 1976). In addition, physiological processes within each sex obviously differ during reproduction. Finally, PC1 scores were calculated for each sex separately, so condition indices were not directly comparable.

We used correlation analyses to test for associations between hematocrit and date, time and ambient temperature when samples were taken, physical condition, prey abundance, and parasite load. We feel that prey abundance, measured as the number of small mammals per 100 trap nights, is considered better as an index rather than an estimate. We therefore used Spearman's rank correlation coefficient to examine the relation between prey abundance and hematocrit (Sokal and Rohlf 1981). Similarly, nonparametric techniques were used to examine the relation between hematocrit and parasitism by *Haemoproteus*, because intensities of infection should be considered indices (G. F. Bennett, pers. commun.).

We also compared hematocrits of birds with and without molt, different intensities of molt, and between different age classes. Where significant correlations were detected between hematocrit and other variables (Table 1), we entered these latter variables as covariates in an analysis of covariance (ANCOVA). However, as sample sizes in ANCOVAs were often smaller than in the original correlations, and the original relations were not strong, these variables did not always contribute significantly to the ANCOVA model. We therefore removed nonsignificant covariates from the models and repeated the analyses again. In some cases, no variables that correlated with hematocrit contributed significantly to the ANCOVA model, in which case we tested for differences between groups using *t*-tests. All statistical analyses were performed with the SAS statistical package

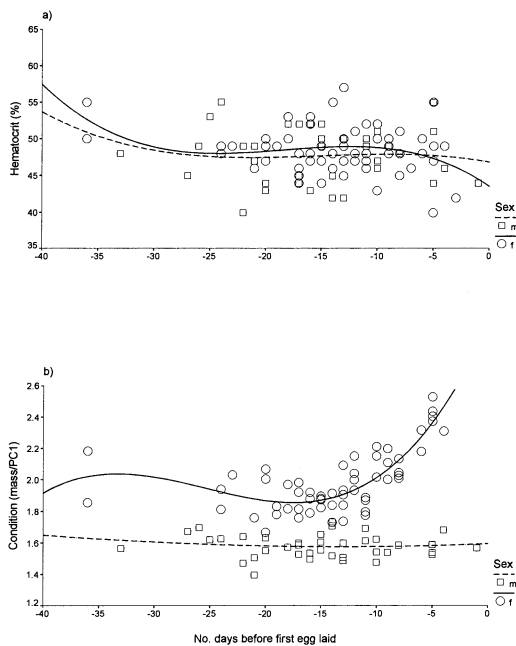


Fig. 1. Changes in (a) hematocrit level and (b) condition with the number of days preceding egg laying for American kestrels in northcentral Saskatchewan, Canada, during 1994 and 1995. Lines were fitted to illustrate trends with a cubic regression function. Condition was calculated by dividing mass by the first component (PC1) of a principal components analysis.

(SAS Inst. Inc. 1990) and results were considered significant at the 0.05 level.

RESULTS

Mean hematocrit for females was $48.8\% \pm 0.35$ (SE) (range = 38–58%, $n = 111$) during pre-laying and $49.0\% \pm 0.29$ (range = 38–61%, $n = 193$) during incubation. Male hematocrit averaged $47.9\% \pm 0.39$ (range = 40–55%, $n = 82$) and $48.5\% \pm 0.34$ (range = 37–59%, $n = 146$) during pre-laying and incubation. Using analysis of variance (ANOVA), we could not detect any differences in hematocrit that could be attributed to year ($F = 0.69$, 1 df, $P = 0.41$), sex ($F = 1.49$, 1 df, $P = 0.22$), or season (pre-laying and incubation: $F = 0.98$, 1 df, $P = 0.32$). As no year differences were detected, nor were there significant interactions between year and season ($P > 0.23$ in all cases), we pooled data from both years in subsequent analyses to increase statistical power.

We could not detect any differences in condition between years for either sex with analysis of variance (females: $F = 0.01$, 1 df, $P = 0.91$; males: $F = 3.00$, 1 df, $P = 0.08$), but both sexes were in better condition during incubation than

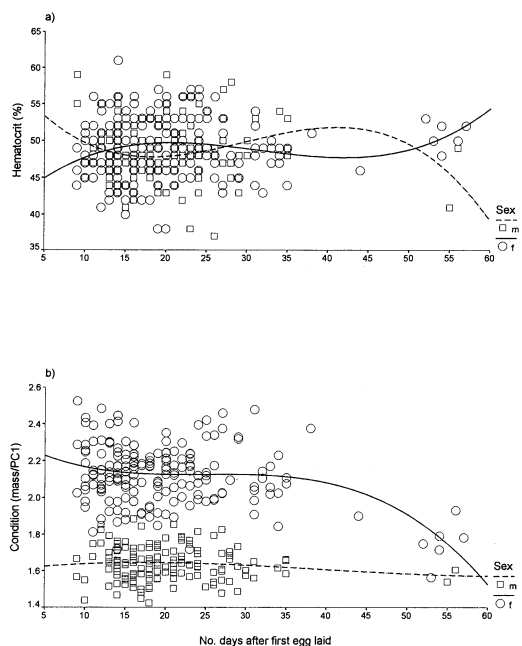


Fig. 2. Hematocrit level and condition of American kestrels in northcentral Saskatchewan from 10 days after the first egg was laid to when offspring fledged from the nest, 1994 and 1995. Lines were fitted to illustrate trends with a cubic regression function. Condition was calculated by dividing mass by the first component (PC1) of a principal components analysis.

pre-laying (females: $F = 43.79$, 1 df, $P < 0.0001$; males: $F = 13.11$, 1 df, $P = 0.0004$).

Hematocrits and condition indices of both sexes in relation to the number of days before or after egg laying that the sample was taken ("breeding chronology") were plotted (Figs. 1 and 2) for the entire breeding season, and for illustrative purposes, lines were fitted through the data using a cubic regression function. As condition indices are difficult to interpret on their own, we also report here descriptive statistics for mass to help illustrate the magnitude of variation in condition indices. Pre-laying females averaged 127.3 g (± 1.24 , range = 103–165 g, $n = 111$), while mean mass of incubating females was 136.5 g (± 0.69 , range = 113–163 g, $n = 193$). Males averaged 107.4 g (± 0.80 , range = 90–132 g, $n = 82$) and 112.7 g (± 0.57 , range = 95–128 g, $n = 146$) during pre-laying and incubation.

We compared hematocrits and condition indices of the small sample of female kestrels captured when their offspring were about to fledge to when these birds were caught during incubation using paired *t*-tests. Female condition declined significantly between these 2 periods

(mean difference = 0.37, paired $t = 7.37$, $n = 6$, $P < 0.001$; Fig. 2); however, we could not detect any difference in hematocrits between these 2 periods (mean difference = 0.33, paired $t = 0.25$, $n = 6$, $P = 0.82$; Fig. 2).

During pre-laying, hematocrit of both sexes was not related to sampling date, breeding chronology, temperature at sampling, or condition (Table 1). Hematocrits of pre-laying birds were higher earlier in the day, although not quite significantly so for females.

During incubation, hematocrit increased with sampling date in males only. This effect was seasonal, as hematocrit was not related to breeding chronology for either sex (Table 1). For both sexes, hematocrit declined throughout the day and increased with ambient temperature. Sampling time and ambient temperature at sampling were correlated for females ($r = 0.30$, $n = 197$, $P < 0.0001$) and males ($r = 0.25$, $n = 147$, $P = 0.002$) during incubation. Therefore, we performed a series of partial correlations. When we removed the effect of ambient temperature, hematocrit still correlated with sampling time for females (partial $r = -0.33$, $n = 193$, $P < 0.0001$) and males (partial $r = -0.37$, $n = 146$, $P < 0.0001$). Similarly, when the effect of time was removed, the relation between hematocrit and ambient temperature remained significant (females: partial $r = 0.27$, $n = 193$, $P < 0.0001$; males: partial $r = 0.37$, $n = 146$, $P < 0.0001$). No relation was detected between condition and hematocrit for either sex during incubation (Table 1).

Small mammal numbers ranged from 0 to 71.1 animals/100 trap nights (median = 15.4 animals/100 trap nights, $n = 168$ territories). Despite this variation, there was no relation between prey abundance and hematocrit for either sex (Table 1).

No differences in female hematocrit could be attributed to age during either pre-laying (SY: mean = 48.5% \pm 0.46, $n = 34$; ASY: mean = 49.7% \pm 1.09, $n = 9$; $t = 1.10$, $P = 0.27$) or incubation (SY: mean = 49.2% \pm 0.58, $n = 53$; ASY: mean = 49.0% \pm 0.59, $n = 40$; $t = -0.28$, $P = 0.78$). Similarly, no age differences were found in male hematocrit during pre-laying (SY: mean = 47.0% \pm 1.27, $n = 7$; ASY: mean = 48.3% \pm 0.88, $n = 16$; $t = 0.83$, $P = 0.42$) or incubation (SY: mean = 48.1% \pm 1.47, $n = 9$; ASY: mean = 48.6% \pm 0.52, $n = 47$; $t = 0.37$, $P = 0.71$).

Kestrels generally started molting flight

feathers during incubation, and about 50% of birds we caught during this time were either missing remiges or growing new ones. We examined the potential effects of molt on hematocrit by comparing incubating birds that had begun molt with those that had not. For females, hematocrit varied (ANCOVA, $F = 5.10$; 3, 186 df; $P = 0.002$) with the time of day the sample was taken (covariate, $F = 13.82$, 1 df, $P = 0.0003$), but we could not detect a difference (main effect, $F = 0.37$, 1 df, $P = 0.54$) in hematocrits between females that had not started molting (mean = 48.6% \pm 0.50, $n = 80$) and those that had (49.3% \pm 0.36, $n = 110$). Among males, hematocrit varied ($F = 3.85$; 3, 141 df; $P = 0.01$) with the time of day the sample was taken (covariate, $F = 11.39$, 1 df, $P = 0.001$); however, there were no differences (main effect, $F = 0.12$, 1 df, $P = 0.73$) in hematocrits between males that had not started molting (mean = 48.4% \pm 0.45, $n = 81$) and those that had (48.6% \pm 0.52, $n = 64$). For both sexes, there were no interactions between time and age ($P > 0.35$ in both cases).

Among birds that were undergoing molt, we also tested whether the intensity of molt affected hematocrit. Birds with 1 or 2 remiges molting were classified as having a "low" intensity, whereas birds with 4 or more remiges molted were classified as having a "high" intensity of molt. Hematocrit of females varied (ANCOVA, $F = 2.45$; 3, 96 df; $P = 0.06$) with time of sampling (covariate, $F = 6.06$, 1 df, $P = 0.02$), but we did not detect a difference (main effect, $F = 1.16$, 1 df, $P = 0.28$) between birds with low (mean = 49.6% \pm 0.52, $n = 45$) and high (mean = 48.9% \pm 0.51, $n = 55$) intensity of molt. The interaction between time and molt intensity was not significant ($F = 0.81$, 1 df, $P = 0.37$). Male hematocrit tended to vary ($F = 2.18$; 3, 55 df; $P = 0.10$) with time of sampling (covariate, $F = 3.43$, 1 df, $P = 0.07$), although not significantly so. Males with low intensities of molt (mean = 48.1% \pm 0.70, $n = 35$) did not differ (main effect, $F = 0.29$, 1 df, $P = 0.59$) from those with high intensities of molt (mean = 49.3% \pm 0.89, $n = 24$).

The level of parasitism by *Haemoproteus* was highly variable, with some birds showing extremely high levels of parasitism (median = 53.5 parasites/100 fields, range = 1–2,000 parasites/100 fields, $n = 262$). Female hematocrit increased with the level of *Haemoproteus* infection during pre-laying ($r_s = 0.24$, $n = 78$, $P =$

0.03) but not during incubation ($r_s = 0.08$, $n = 78$, $P = 0.51$). Male hematocrit increased with the level of *Haemoproteus* infection during incubation ($r_s = 0.48$, $n = 56$, $P < 0.001$), but not during pre-laying ($r_s = 0.14$, $n = 45$, $P = 0.36$).

DISCUSSION

Hematocrits of wild kestrels in this study are higher than the 30% previously reported for captive adult kestrels during summer (Rehder and Bird 1982). Reduced activity often associated with captive conditions may be responsible for observed differences in hematocrits between captive and wild birds. For example, Snyder et al. (1981) found that captive kestrels housed in colonial pens and capable of sustained flight had higher hematocrits than those housed in pairs and constrained in their opportunity to fly. In addition, captive kestrels are provided food and water ad libitum, and so may not be as susceptible to dehydration as wild birds.

In general, male birds are thought to have higher hematocrits than females, partly due to the erythropoietic effect of androgens (Sturkie and Griminger 1976). We did not detect any differences in hematocrit between the sexes in this study (Figs. 1 and 2). Indeed, most studies have failed to demonstrate sex differences in hematocrit (Hunter and Powers 1980, Snyder et al. 1981, Lavin et al. 1992, Morton 1994, Phalen et al. 1995).

We did not detect any differences in hematocrit between the pre-laying and incubation periods in either sex (Figs. 1 and 2). In addition, there was no relation between hematocrit and the date of sampling for females during pre-laying or incubation, although there was a weak positive relation between male hematocrit and date of sampling during incubation (Table 1). In contrast, both Morton (1994) and deGraw et al. (1979) found seasonal declines from May to August in both sexes of white-crowned sparrows (*Zonotrichia leucophrys*). Female kestrels are rather sedentary during both pre-laying and incubation, with the male undertaking nearly all of the hunting duties (Balgooyen 1976), so it seems likely that females have little need to alter their oxygen-carrying capacity.

Although it might be expected that male kestrels should increase their oxygen-carrying capacity as the breeding season progresses, there were no apparent changes in hematocrit. Even

though there was an increase in hematocrit with sampling date during incubation, hematocrit did not vary with the number of days before or after the initiation of egg laying that the sample was taken (Table 1). As breeding chronology might be considered a crude measure of the energy expenditure of males because it reflects the length of time the male has provided for the female, these results suggest that males breeding later in the season have slightly higher hematocrits than those breeding earlier. However, although Breuer et al. (1995) found no seasonal changes in hematocrits of Australian passerines, there were significant changes in the volume and numbers of erythrocytes, suggesting alterations of oxygen-transport capabilities and levels of aerobic respiration. Further investigation is required to ascertain whether kestrels may alter oxygen-carrying capacity by more subtle means than changes in hematocrit.

Stresses associated with egg laying have been hypothesized as causing the rate of erythropoiesis to decline, which in turn results in reduced female hematocrit during egg laying (Jones 1983). Alternatively, Morton (1994) argued that declines in hematocrit around the time of egg laying result from dilution of the cellular components because of an influx of protein, lipid, and calcium into the plasma. Hematocrits of female white-crowned sparrows declined sharply during laying, and then increased after laying was complete (Morton 1994). In contrast, hematocrits of female kestrels did not show any relation with the number of days before or after egg-laying that the sample was taken (Table 1). However, to minimize disturbance, birds in the process of laying were not trapped actively, and so our sample may have been inadequate to detect influences of egg laying on hematocrits if they existed.

During pre-laying, hematocrits of both sexes did not vary with ambient temperature; however, hematocrit increased with ambient temperature during incubation for both sexes. From the results of previous studies, we would have predicted a negative correlation, as erythrocyte production has been shown to decline as air temperature increases (Moye et al. 1969, Kubena et al. 1971). Moreover, we would have predicted that if trends were to emerge, they would appear more likely during pre-laying when mean daily temperatures are lower and daily fluctuations are more extreme. For example, Rehder et al. (1982a) and Rehder and

Bird (1982) found temperature correlated negatively with hematocrits of captive kestrels. Many studies comparing hematocrits between seasons with different ambient temperatures have found higher hematocrits associated with colder temperatures (deGraw et al. 1979, Hunter and Powers 1980, Clemens 1990, Swanson 1990, Abelenda et al. 1993), presumably in response to thermogenic demands associated with cold temperatures (Carey and Morton 1976). Our results may be the consequence of plasma water being used to help dissipate body heat through evaporation, therefore concentrating red blood cells and elevating hematocrits. Hematocrits of pre-laying birds may not be affected by evaporative water loss because of lower ambient temperatures at sampling (mean = 12.1 C, range = -0.3–24.3 C, $n = 195$) compared to incubation (mean = 21.5 C, range = 6.9–33 C, $n = 344$).

Hematocrit of both sexes declined with the time of day the sample was taken during both pre-laying and incubation (Table 1). We would expect that deterioration and removal of red blood cells from the circulatory system would be reduced during the night when kestrels are inactive and their metabolism likely approaches basal rates. Alternatively, recent research suggests that dehydration resulting from normal overnight fasting may be sufficient to cause elevated hematocrits in kestrels (Lyons 1996). The decline in hematocrit throughout the day that we observed may result from birds replenishing their plasma water as more water is derived from their prey. Many previous investigators have not addressed specifically diurnal changes in hematocrit; rather they have assumed the existence of such patterns, and have attempted to control for them by sampling birds at the same time during each day (e.g., Balasch et al. 1976, Gee et al. 1981, Rehder and Bird 1982). Studies that have examined diurnal changes have found little evidence for time of day effects on hematocrit. For example, Rehder et al. (1982a) did not detect a time of day effect on hematocrit in captive kestrels, and although Rehder et al. (1982b) showed hematocrits of red-tailed hawks (*Buteo jamaicensis*) declined during the day, they could not eliminate hemodilution resulting from repeated sampling as the causal factor (see also Sturkie and Newman 1951).

Habitat quality frequently has been implicated as a causal factor determining differences in

hematocrits of mammals (Hellgren et al. 1989, 1993), but few studies of avian blood variables have examined this relation. We could not detect any difference in hematocrits among kestrels occupying territories differing in quantity of food. Similarly, previous studies of nestling kestrels (Dawson and Bortolotti 1997) and house sparrows (*Passer domesticus*; Gavett and Wakeley 1986) showed no food-related differences in hematocrit. Previous work on our study area suggests that kestrel reproduction is sensitive to population fluctuations of their prey (Bortolotti et al. 1991; Wiebe and Bortolotti 1992, 1994).

Declines in avian hematocrit resulting from experimentally induced starvation have been well-documented (Le Maho et al. 1981, Boismenu et al. 1992). The effects of normal variation in condition of birds has received less attention. The condition of kestrels is significantly better during incubation than pre-laying in both sexes; however, hematocrits did not differ between pre-laying and incubation (Figs. 1 and 2). Similarly, females lost condition between incubation and when their young fledged (Fig. 2), but no significant differences in hematocrit could be detected. During both pre-laying and incubation, there also was considerable variation in condition of both sexes but no significant correlations between hematocrit and condition indices could be detected (Table 1). Even though Rehder and Bird (1982) found some correlations between hematocrit and mass in captive kestrels, our results suggest that when body condition is within the normal range found in wild kestrels, hematocrits do not vary with condition.

Second-year kestrels are often in poorer condition than after second-year birds (R. D. Dawson and G. R. Bortolotti, unpubl. data), presumably because they are less experienced foragers or are less dominant than older birds. Therefore, we expected that if there were differences between age classes in hematocrit, it would be the result of age-related differences in condition, rather than being a function of the age of a bird per se. Even though there is abundant evidence to suggest that hematocrits increase with age in growing birds (Hemm and Carlton 1967, Campbell and Dein 1984, Hughes 1984, Puerta et al. 1989), our results are consistent with other studies of adult birds that have found no age effect (deGraw et al. 1979, Rehder et al. 1982a, Gessaman et al. 1986, Puerta et al. 1990,

Abelenda et al. 1993, Phalen et al. 1995). These results provide additional evidence that excludes hematocrit as being a condition-related variable when body condition is within the normal range.

Both deGraw et al. (1979) and Rehder and Bird (1982) assert that one of the most important factors influencing avian hematocrit is molt. Growing quills become extensively vascularized and the resulting increases in plasma volume are not accompanied by a corresponding increase in erythrocyte number (Chilgren and deGraw 1977), causing a decline in hematocrit. Hematocrits have been shown to decline both with the presence of molt (deGraw et al. 1979, Morton 1994) as well as the intensity of molt (Chilgren and deGraw 1977, Rehder and Bird 1982); however, we could not detect a relation with either presence or absence, or intensity, of molt in wild kestrels.

Blood parasitism should result in depressed hematocrits as a result of destruction of erythrocytes by the parasite (Wintrobe 1981), and also presumably by the immune system removing infected cells. Contrary to expectation, the intensity of infection by the blood parasite *Haemoproteus* was correlated positively with hematocrit of females during pre-laying and males during incubation. Birds may be compensating for the loss of oxygen-carrying capacity by producing erythrocytes faster than the immune system is capable of removing parasitized blood cells. However, why the relation between hematocrit and parasite load is specific to pre-laying for females and incubation for males is enigmatic, and requires further investigation.

MANAGEMENT IMPLICATIONS

Many authors have stated that reduced hematocrits may be indicative of the disease status of an animal, and measuring hematocrits is a standard procedure when birds are admitted for clinical treatment (Cooper 1975, Mauro 1987). The results of this study clearly demonstrate that in a normal population of American kestrels, hematocrit is not a condition-dependent variable. In addition and contrary to expectation, we found that kestrels with high levels of infection by blood parasites actually had higher hematocrits, demonstrating the need for future studies to consider the effects of hematozoa on blood variables.

In a survey of 21 species of East African raptors, birds suffering from injury or disease gen-

erally had reduced hematocrits (Cooper 1975). Similarly, measures of body condition were related to hematocrit in red-billed queleas (*Quelea quelea*; Jones 1983). Birds in Cooper's study were often in poor physical condition, and the colony of queleas in Jones' investigation were under such stress that all birds either died or abandoned the colony. These observations, coupled with the results of this study, suggest that birds may only show marked deviations in hematocrit levels from normal values when birds are in extremely poor physical condition. When this stage is reached, however, hematocrits may be unnecessary as a simple external examination of the bird will reveal an advanced stages of malnutrition or disease (Messier et al. 1987).

Although blood studies may provide useful information on the nutritional status of birds, future investigations need to employ experimental techniques to determine if, and which, blood variables are reliable for predicting the general condition and health of birds. Similarly, it is also necessary to document and test factors, both intrinsic and extrinsic, that could potentially affect hematocrit values.

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