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Repeatability of hematocrits and body mass of Gray Catbirds

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ABSTRACT. Hematocrits may provide information about the physiological condition of birds, but, to be a useful measure, information is needed concerning how hematocrits vary among individuals and over time. We examined the repeatability of hematocrits in a population of Gray Catbirds (*Dumetella carolinensis*) in Pennsylvania at several time scales and also examined the repeatability of body mass, another measure commonly used as an indicator of condition. Both hematocrit ($r = 0.64$) and mass ($r = 0.65$) were repeatable ($P < 0.01$) for first captures between years and between first and second captures within a year ($r = 0.41$ and $r = 0.50$, respectively; $P < 0.01$), but not repeatable ($P > 0.05$) between captures in different months within a year ($r = 0.11$ for both). Repeatability of both measures differed by sex and age. Females exhibited repeatability of hematocrit and body mass only between years, while male hematocrits were repeatable between years and between first and second captures within a season. Male mass was repeatable for all time periods. Hematocrits of younger birds were repeatable between captures within a season and their body mass was repeatable between months and weeks while hematocrits of older birds were not repeatable and their body mass was repeatable only between captures in a season. Our results indicate that hematocrits and body mass had similar repeatability coefficients overall, but that hematocrits of Gray Catbirds were a consistent trait of individuals only across years. Because repeatability between captures and months depended on sex and age, we conclude that the hematocrit is a useful measure of individual performance only in limited circumstances.

RESUMEN. **La repetibilidad del hematocrito y del peso corporal de *Dumetella carolinensis***

El hematocrito podría proveer información sobre la condición física de las aves pero para ser una medida útil se necesita información sobre como el hematocrito varia entre individuos y a través del tiempo. Examinamos la repetibilidad del hematocrito en una población de *Dumetella carolinensis* en Pennsylvania durante diferentes escalas temporales. También examinamos la repetibilidad del peso corporal, otra medida comúnmente usada como indicador de la condición del individuo. El hematocrito ($r = 0.64$) y el peso corporal ($r = 0.65$) eran repetibles ($P < 0.01$) para las primeras capturas entre años y entre la primera y segunda captura dentro del año ($r = 0.41$ y $r = 0.50$, respectivamente; $P < 0.01$), pero no eran repetibles ($P > 0.05$) entre capturas realizadas en diferentes meses dentro del año ($r = 0.11$ para los dos). La repetibilidad de las dos medidas difiere por sexo y edad. Las hembras se caracterizaron por tener repetibilidad del hematocrito y del peso corporal solo entre años, mientras que el hematocrito de los machos era repetible entre años y entre la primera y segunda captura dentro de la temporada. El peso corporal de los machos era repetible durante todos los periodos a través del tiempo. El hematocrito de las aves mas jóvenes era repetible entre capturas dentro de la temporada y su peso corporal era repetible entre meses y semanas, mientras que el hematocrito de las aves mayores no era repetible y su peso corporal era repetible solo entre capturas dentro de la temporada. Nuestros resultados indican que los hematocritos y el peso corporal en general tuvieron coeficientes de repetibilidad similares, pero que los hematocritos de *D. carolinensis* eran un rasgo consistente de los individuos solo entre años. Por la razón que la repetibilidad entre capturas y meses dependía del sexo y edad, concluimos que el hematocrito es una medida útil del performance individual solo en circunstancias limitadas.

Key words: blood parameters, condition, *Dumetella carolinensis*, individual variation, weight

Hematocrit values, the ratio of packed red blood cell volume to total blood volume, may provide information about the physiological condition of wild birds (Ots et al. 1998, Simon et al. 2005, Norte et al. 2008a; but see Dawson and Bortolotti 1997, Cuervo et al. 2007, Amat et al. 2009). High hematocrits may result from either dehydration (Biebach 1990, Carmi et al. 1992) or aerobic stress, such as that experienced during migration (Carpenter 1975), whereas low hematocrits (anemia) may indicate parasitism, chronic disease, decreased red blood cell production, or blood loss (Campbell and Dein 1984). In addition, hematocrits can vary with age, sex, season, and condition (Fair et al. 2007).

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Given this potential variability, determining how hematocrits vary among individuals and over time is important if they are to be useful indicators of individual health. For example, if hematocrit values are not consistent across captures (i.e., there is a greater variation in hematocrits of the same individual than those of different individuals) at any time scale, then their use as an indicator of individual performance would be limited. One such measure of consistency is repeatability.

Repeatability, or the ratio of variation among individuals to variation within and among individuals, is commonly used to determine the reliability of repeated measurements on the same object or individual and, in quantitative genetics, repeatability is used to describe the proportion of phenotypic variance in a trait that occurs among as compared to within individuals (Lessells and Boag 1987, Merilä and Sheldon 2001). Repeatability has been used in nongenetic studies to determine the time consistency of potentially highly variable characteristics such as behavior (Schwagmeyer and Mock 2003), metabolic rate (Nespolo and Franco 2000), and body condition (Hõrak et al. 2002). Measured at different time scales or life history stages, repeatability can provide information about variation in a trait and potential differences in the strength of environmental influences. A highly repeatable trait (e.g., $r > 0.5$) suggests a strong genetic as opposed to environmental component to individual variation (Boag and van Noordwijk 1987, Merilä and Sheldon 2001) and that the measure is a reliable indicator of individual performance because more than half the variation is among rather than within individuals. In contrast, traits that are not significantly repeatable or that exhibit low repeatability may have a strong environmental component, preventing useful comparisons between individuals unless environmental variation is controlled.

Despite the potential value of using hematocrits to compare the physiological state of individuals, repeatability of hematocrits has, to our knowledge, been reported for only two species of songbirds. Hematocrits of breeding adult Pied Flycatchers (*Ficedula hypoleuca*) were found to be repeatable between years for females, but repeatability at shorter time scales was not examined (Potti 2007). For Great Tits (*Parus major*), hematocrits were compared over a number of time scales, including a 45-day period, across a spring season within a year, across an autumn season within a year, across an entire year, and over 4 yr (Norte et al. 2008b). Repeatability was significant across a spring season and an entire year, but not at the other time scales (Norte et al. 2008b).

Our objective was to determine the repeatability of hematocrits of Gray Catbirds (*Dumetella carolinensis*) in northeastern Pennsylvania at various time scales to determine if hematocrits exhibit sufficient individual consistency across time (i.e., individual hematocrits vary less within than among individuals) to permit useful comparisons between individuals. We also examined repeatability of body mass, another measure used as an indicator of condition. Catbirds were recaptured over a 4-yr period and, for three of those years, were recaptured during three seasons, allowing examination of repeatability between years, between months, and between captures in the same year.

METHODS

We captured catbirds in mist-nets from mid-April to mid-July 2005 and from mid-April to September 2006, 2007, and 2008 at sites in and near Lackawanna State Park in Lackawanna County, Pennsylvania (41°34′30″N, 75°42′5″W). For a detailed site description, see Smith and Hatch (2008). Catbirds were banded with a U.S. Geological Survey aluminum band, uniquely marked with 1–3 color bands, and weighed using an electronic balance (± 0.1 g). Most catbirds were aged using plumage characteristics (second year [SY] or after second year [ASY]) and sexed using the presence of either a brood patch (females) or cloacal protuberance (males; Pyle 1997). A blood sample (50–125 μL) was collected via brachial vein puncture using a 27-gauge needle and heparinized microhematocrit capillary tubes. Samples were kept on ice in the field until taken to the lab. We determined hematocrits via centrifugation of capillary tubes for 9 min at 14,000 rpm. Using digital calipers, we measured the total volume and packed red blood cell volume to the nearest 0.01 mm.

Repeatability $[s^2_a/(s^2 + s^2_a)]$ was calculated from the ratio of the variance among individuals (s^2_a) to the variance among and within individuals ($s^2 + s^2_a$) obtained from a one-way ANOVA with individuals as the independent variable and hematocrits as the dependent variable (Lessells and Boag 1987). A trait is repeatable if the ANOVA is significant because this indicates significant differences between individuals. Standard errors were estimated following Becker (1984). Between-year repeatability was determined for all individuals captured in more than 1 yr in the same month as their previous year's capture. Between-month repeatability was determined for all individuals captured in at least two different months in a given year. For birds captured in multiple months in multiple years, data for the year with the most captures in different months were used. Finally, to determine repeatability between first and second captures, we included birds captured at least twice in 1 yr and only used the first year with two or more captures for birds caught in multiple years. All analyses were performed using SPSS version 15 (SPSS Institute 2006), and means are reported ±SE.

RESULTS

The mean ordinal arrival date for our Gray Catbird population as a whole (145 ± 0.7 days) was similar to the mean ordinal date of first capture for catbirds in our repeatability data set (147 ± 2 days). We found that hematocrits were significantly repeatable across first captures in each year and across first and second captures (mean interval = 16.6 ± 1.5 days), but not across months (mean interval = 34.4 ± 2.3 days) in a year (Table 1). In addition, we found that hematocrits of females were only repeatable between years, whereas those of males were significantly repeatable between years and captures (Table 1). Also, ASY birds did not have repeatable hematocrits, but hematocrits were significantly repeatable between captures for SY birds (Table 1). Overall, hematocrits were highest in May (Fig. 1).

Although body mass was significantly repeatable over more time scales and categories than hematocrits (Table 2), repeatability coefficients for all categories combined were similar for the two measures (Tables 1 and 2). Repeatability of male mass was significant over all time scales, whereas female mass was repeatable only between years (Table 2). The body mass of both SY and ASY birds was significantly repeatable between months. However, only the body mass of SY individuals was repeatable between captures. Body mass was highest in September (Fig. 2), and mass and hematocrit were negatively correlated ($r = -0.39$, $P = 0.03$, $N = 32$).

DISCUSSION

Overall, we found that the hematocrits and body mass of Gray Catbirds were repeatable between years and between captures (separated by an average of 2 weeks), but not between months. However, repeatability differed with sex and age, with the hematocrits and mass of males more repeatable than those of females and those of SY birds more repeatable than those of ASY birds. Our results suggest that

Table 1. Repeatability (± SE) of hematocrit for Gray Catbirds captured in Lackawanna County, Pennsylvania, 2005–2008. The mean number of days between captures in different months was 34.4 ± 2.3 (SE), and the mean number of days between first and second capture was 16.6 ± 1.5 (SE).

Category	Year	Month	Captures
Males	0.60 ± 0.2** ($N = 14$)	0.01 ± 0.1 ($N = 33$)	0.37 ± 0.1* ($N = 36$)
Females	0.69 ± 0.2** ($N = 8$)	0.11 ± 0.1 ($N = 19$)	0.06 ± 0.2 ($N = 22$)
SY	N/A	0.15 ± 0.2 ($N = 22$)	0.41 ± 0.1** ($N = 32$)
ASY	N/A	0.03 ± 0.1 ($N = 29$)	0.21 ± 0.2 ($N = 31$)
All categories combined	0.64 ± 0.1** ($N = 24$)	0.11 ± 0.09 ($N = 66$)	0.41 ± 0.08** ($N = 108$)

*Significant at the 0.05 level.
**Significant at the 0.01 level.

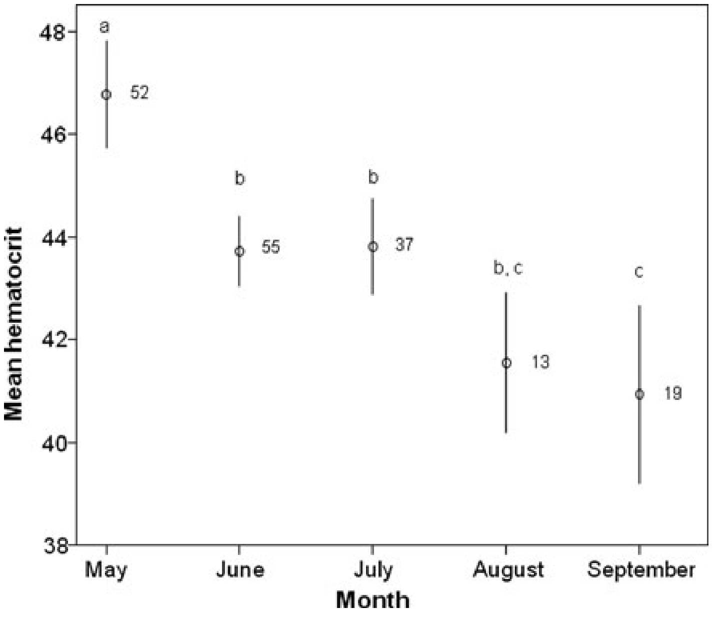

Fig. 1. Mean monthly hematocrit for Gray Catbirds captured in or near Lackawanna State Park, Pennsylvania. Bars represent 95% confidence limits, numbers represent sample size, and letters indicate means that are significantly different (Tukey post-hoc test).

the hematocrits of individual Gray Catbirds are sufficiently similar across years to compare individuals on an annual basis, but that within-year comparisons, especially for females, should not be made unless it is possible to control for the considerable environmental variation.

Repeatability of hematocrits for Gray Catbirds in our study was higher than that reported for either Pied Flycatchers (across years: $r = 0.23 \pm 0.09$ for females, $r = 0.17 \pm 0.11$ for males; Potti 2007) or Great Tits (same spring: $r = 0.32 \pm 0.15$; same year: $r = 0.24 \pm 0.11$; Norte et al. 2008b). One possible explanation for such differences among species is that body size may affect hematocrits because larger species, with greater blood volume, may be better able to mediate variation in hematocrits. Gray Catbirds are approximately twice as large

Table 2. Repeatability (± SE) of body mass for Gray Catbirds captured in Lackawanna County, Pennsylvania, 2005–2008. The mean number of days between captures in different months was 34.4 ± 2.3 (SE), and the mean number of days between first and second capture was 16.6 ± 1.5 (SE).

Category	Year	Month	Captures
Males	$0.67 \pm 0.1^{**}$ ($N = 14$)	$0.48 \pm 0.1^{**}$ ($N = 33$)	$0.46 \pm 0.1^{**}$ ($N = 36$)
Females	$0.55 \pm 0.2^{*}$ ($N = 8$)	0.04 ± 0.1 ($N = 19$)	-0.13 ± 0.2 ($N = 21$)
SY	N/A	$0.56 \pm 0.1^{**}$ ($N = 22$)	$0.64 \pm 0.1^{**}$ ($N = 32$)
ASY	N/A	$0.31 \pm 0.1^{**}$ ($N = 29$)	0.26 ± 0.2 ($N = 30$)
All categories combined	$0.65 \pm 0.1^{**}$ ($N = 24$)	0.11 ± 0.09 ($N = 66$)	$0.50 \pm 0.08^{**}$ ($N = 100$)

*Significant at the 0.05 level.
**Significant at the 0.01 level.

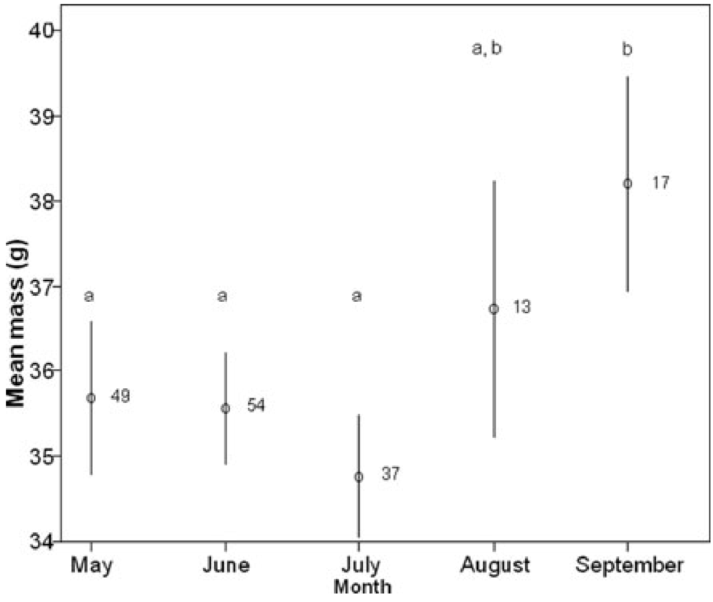

Fig. 2. Mean monthly body mass for Gray Catbirds captured in or near Lackawanna State Park, Pennsylvania. Bars represent 95% confidence limits, numbers represent sample size, and letters indicate means that are significantly different (Tukey post-hoc test).

(21–24 cm, 23–56 g; Cimprich and Moore 1995) as Pied Flycatchers (13 cm, 10–15 g; Robinson 2005).

One possible explanation for the repeatability in hematocrits across years in our study is that we captured most Gray Catbirds soon after completing migration and arriving on the breeding grounds. Individuals may attain maximum hematocrits during migration (Bairlein and Totzke 1992, Prats et al. 1996), and hematocrits have also been found to be highest in April and early May for wild and captive White-crowned Sparrows (*Zonotrichia leucophrys*, deGraw et al. 1979) and in April for captive American Kestrels (*Falco sparverius*, Rehder and Bird 1983). White-crowned Sparrows and American Kestrels are migratory, but Great Tits, a non-migratory species, also exhibited the greatest repeatability of hematocrits in the spring (April–early July, Norte et al. 2008b). Thus, hematocrits appear to be highest and most repeatable early in the breeding season, regardless of migratory status.

The mass and hematocrits of female Gray Catbirds in our study varied more within a year than did the mass and hematocrits of males, with values for females repeatable at only one time scale and male hematocrits repeatable for two time scales and male mass for all three time periods examined. We found similar results for SY versus ASY birds, with the hematocrits of ASY birds not repeatable and mass exhibiting low repeatability between months and, for SY birds, mass repeatable across months and captures and hematocrit repeatable across captures. For Pied Flycatchers, hematocrits of males and females did not differ, and the repeatability of hematocrit was similarly low for males and females (Potti 2007). Also, hematocrit did not differ with age, but repeatability was not examined separately for the two age classes (Potti 2007). The greater variability for female Gray Catbirds (hence lower repeatability) in our study may be due to the physiological changes associated with egg laying (see Discussion below). However, reasons for the greater repeatability of the hematocrits of younger (SY) catbirds, given that both SY and ASY birds are capable of breeding, are unclear.

The lack of repeatability of hematocrits and mass of Gray Catbirds at an intermediate time scale (across months) indicates that within-individual variation is greater than among-individual variation at this time scale. This suggests that variation in hematocrit across months has a large environmental component, likely due to seasonal changes in the avian life cycle such as the onset of breeding. For example, several investigators have reported that the hematocrits of female birds are lower during egg laying than at other times during the breeding season (Silverin 1981, Jones 1983, Morton 1994, Williams et al. 2004, Wagner et al. 2008), and male American Kestrels had higher hematocrits during some stages of reproduction (i.e., copulation and laying first clutches) than others (Rehder et al. 1982). Seasonal variation in ambient temperature may also reduce repeatability because hematocrits are known to vary with temperature (deGraw et al. 1979, Rehder et al. 1982). Most studies where seasonal changes have been examined have revealed that hematocrits were higher during the winter and spring than during summer (reviewed by Fair et al. (2007)).

Despite the consistency in hematocrit values that we recorded and the repeatability of body mass at most time scales, hematocrit was unrelated to body condition (a principle component of wing, tail, and tarsus regressed on mass) in our population (Hatch et al., in press) and negatively related to body mass. This may be due to the greater influence of short-term environmental variation on body condition than hematocrits (Ots et al. 1998, Hõrak et al. 2002). Other studies, primarily involving nestlings, have also revealed no relationship between either body condition and hematocrits (Dawson and Bortolotti 1997, Villegas et al. 2002, Cuervo et al. 2007) or nutritional condition and hematocrits (Amat et al. 2009). However, hematocrit values may be related to, and may influence, other measures of fitness. For example, we found that the hematocrits of earlier-arriving Gray Catbirds were higher than those of catbirds arriving later in the spring (Hatch et al., in press), and, in several other species of birds, early arrival is associated with greater reproductive success (e.g., Lundberg and Alatalo 1992, Møller 1994, Forstmeier 2002, Smith and Moore 2005).

Our results indicate that hematocrits of Gray Catbirds can be compared on an annual basis if individuals are sampled early in the season, but that within-year comparisons should not be made without accounting for seasonal variation (particularly for females). Thus, before being used as a measure of physiological condition or as a proxy for other measures of fitness in other species of birds, we recommend that investigators determine the extent to which hematocrits vary among individuals and over time.

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LITERATURE CITED

Amat, J. A., M. A. Rendón, J. M. Ramírez, F. Hortas, G. M. Arroyo, A. Garrido, M. Rendón-Martos, and A. Pérez-Hurtado. 2009. Hematocrit is related to age but not to nutritional condition in Greater Flamingo chicks. European Journal of Wildlife Research 55: 179–182.

Bairlein, F., and U. Totzke. 1992. New aspects on migratory physiology of trans-Saharan passerine migrants. Ornis Scandinavica 23: 244–250.

Becker, W. A. 1984. Manual of quantitative genetics, 4th edition. Academic Enterprises, Pullman, WA.

Biebach, H. 1990. Strategies of trans-Sahara migrants. In: Bird migration (E. Gwinner, ed.), pp. 352–367. Springer-Verlag, Berlin, Germany.

Boag, P. T., and A. J. van Noordwijk. 1987. Quantitative genetics. In: Avian genetics. (F. Cooke and P. A. Buckley, eds.), pp. 45–77. Academic Press, London, UK.

Campbell, T. W., and F. J. Dein. 1984. Avian hematology. Veterinary Clinics of North America: Small Animal Practice 14: 223–248.

Carmi, N., B. Pinshow, W. P. Porter, and J. Jaeger. 1992. Water and energy limitations on flight duration in small migrating birds. Auk 109: 268–276.

Carpenter, F. L. 1975. Bird hematocrits: effects of high altitude and strength of flight. Comparative Biochemistry and Physiology 50A: 415–417.

Cimprich, D. A., and F. R. Moore. 1995. Gray Catbird (*Dumetella carolinensis*). In: The Birds of North America, No. 167 (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C.

Cuervo, J. J., A. P. Møller, and F. de Lope. 2007. Haematocrit is weakly related to condition in nestling Barn Swallows *Hirundo rustica*. Ibis 149: 128–134.

Dawson, R. D., and G. R. Bortolotti. 1997. Are avian hematocrits indicative of condition? American Kestrels as a model. Journal of Wildlife Management 61: 1297–1306.

DEGRAW, W. A., M. D. KERN, AND J. R. KING. 1979. Seasonal changes in blood composition of captive and free-living White-crowned Sparrows. Journal of Comparative Physiology B129: 151–162.

FAIR, J., S. WHITAKER, AND B. PEARSON. 2007. Sources of variation in haematocrit in birds. Ibis 149: 535–552.

FORSTMEIER, W. 2002. Benefits of early arrival at breeding grounds vary between males. Journal of Animal Ecology 71: 1–9.

GAUNT, A. S., AND L. W. ORING. 1999. Guidelines to the use of wild birds in research. <www.nmnh.si.edu/BIRDNET/GuideToUse>.

HATCH, M. I., AND R. J. SMITH. In press. Arrival timing and hematological parameters in Gray Catbirds (*Dumetella carolinensis*). Journal of Ornithology.

HÕRAK, P., L. SAKS, I. OTS, AND H. COLLIST. 2002. Repeatability of condition indices in captive Greenfinches (*Cardeulis chloris*). Canadian Journal of Zoology 80: 636–643.

JONES, P. J. 1983. Hematocrit values of breeding Red-billed Quelas *Quelea quelea* (Aves: Ploceidae) in relation to body condition and thymus activity. Journal of the Zoological Society of London 201: 217–222.

LESSELLS, C. M., AND P. T. BOAG. 1987. Unrepeatable repeatabilities: a common mistake. Auk 104: 116–121.

LUNDBERG, A., AND R. V. ALATALO. 1992. The Pied Flycatcher. Academic Press, San Diego, CA.

MERILÄ, J., AND B. C. SHELDON. 2001. Avian quantitative genetics. In: Current ornithology, vol. 16 (V. Nolan AND C. F. Thompson, eds.), pp. 179–255. Plenum Publishers, New York, NY.

MØLLER, A. P. 1994. Phenotype-dependent arrival time and its consequences in a migratory bird. Behavioral Ecology and Sociobiology 35: 115–122.

MORTON, M. L. 1994. Hematocrits in montane sparrows in relation to reproductive schedule. Condor 96: 119–126.

NESPOLO, R. F., AND M. FRANCO. 2000. Whole-animal metabolic rate is a repeatable trait: a meta-analysis. Journal of Experimental Biology 210: 2000–2005.

NORTE, A.C., J. A. RAMOS, P. M. ARAUJO, J. P. SOUSA, AND B. SHELDON. 2008a. Health-state variables and enzymatic biomarkers as survival predictors in nestling Great Tits (*Parus major*): effects of environmental conditions. Auk 125: 943–952.

———, B. SHELDON, J. P. SOUSA, AND J. A. RAMOS. 2008b. Repeatability and method-dependent variation in blood parameters in wild-caught Great Tits *Parus major*. Acta Ornithologica 43: 65–75.

OTS, I., A. MURUMÄGI, AND P. HÕRAK. 1998. Haematological health state indices of reproducing Great Tits: methodology and sources of natural variation. Functional Ecology 12: 700–707.

POTTI, J. 2007. Variation in hematocrit of a passerine bird across life stages is mainly of environmental origin. Journal of Avian Biology 38: 726–730.

PRATS, M. T., L. PALACIOS, S. GALLEGO, AND M. RIERA. 1996. Blood oxygen transport properties during migration to higher altitude of wild quail, *Coturnix coturnix coturnix*. Physiological Zoology 69: 912–929.

PYLE, P. 1997. Identification guide to North American birds: Part I. Slate Creek Press, Bolinas, CA.

REHDER, N. B., D. M. BIRD, AND P. C. LAGUË. 1982. Variations in blood packed cell volume of captive American Kestrels. Comparative Biochemistry and Physiology 72A: 105–109.

———, AND D. M. BIRD. 1983. Annual profiles of blood packed cell volumes of captive American Kestrels. Canadian Journal of Zoology 61: 2550–2555.

ROBINSON, R. A. 2005. BirdFacts: profiles of birds occurring in Britain and Ireland. BTO Research Report 407, BTO, Thetford, UK. <http://www.bto.org/birdfacts> (accessed 17 January 2009).

SCHWAGMEYER, P. L., AND D. W. MOCK. 2003. How consistently are good parents good parents? Repeatability of parental care in the House Sparrow, *Passer domesticus*. Ethology 109: 303–313.

SMITH, R. J., AND F. R. MOORE. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. Behavioral Ecology and Sociobiology 57: 231–239.

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

SIMON, A., D. W. THOMAS, P. BOURGAULT, J. BLONDEL, P. PERRET, AND M. M. LAMBRECHTS. 2005. Between-population differences in nestling size and hematocrit level in Blue Tits (*Parus caeruleus*): a cross-fostering test for genetic and environmental effects. Canadian Journal of Zoology 83: 694–701.

SMITH, R. J., AND M. I. HATCH. 2008. A comparison of shrub-dominated and forested habitat use by spring migrating landbirds in northeastern Pennsylvania. Condor 110: 682–693.

SPSS INSTITUTE. 2006. SPSS for Windows, version 15.0. SPSS Institute, Inc., Chicago, IL.

VILLEGAS, A., J. M. SÁNCHEZ, E. COSTILLO, AND C. CORBACHO. 2002. Blood chemistry and haematocrit of the Black Vulture (*Aegypius monachus*). Comparative Biochemistry and Physiology 132A: 489–497.

WAGNER, E. C., C. A. STABLES, AND T. D. WILLIAMS. 2008. Hematological changes associated with egg production: direct evidence for changes in erythropoiesis but a lack of resource dependence? Journal of Experimental Biology 211: 2960–2968.

WILLIAMS, T. D., W. O. CHALLENGER, J. K. CHRISTIANS, M. EVANSON, O. LOVE, AND F. VEZINA. 2004. What causes the decrease in haematocrit during egg production? Functional Ecology 18: 330–336.