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ORIGINAL ARTICLE

Arrival timing and hematological parameters in Gray Catbirds (*Dumetella carolinensis*)

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Abstract Early arrival at the breeding grounds for migratory birds is associated with greater reproductive success. According to the condition-dependent arrival hypothesis, only those individuals in superior physiological condition are able to bear the costs (e.g., poor environmental conditions, limited food availability) of early arrival. Condition has usually been measured in terms of energy reserves or mass but other physiological measures of condition such as hematocrit and immune function have been gaining attention. We examined several measures of condition and their association with date of first capture in Gray Catbirds (*Dumetella carolinensis*) arriving at breeding grounds in northeastern Pennsylvania. Earlier arrivals had higher hematocrit and H/L ratios and lower lymphocyte counts. Arrival date was also negatively associated with fat score. Fat score was positively related to hematocrit, total number of leukocytes, and number of lymphocytes, but the other hematological parameters were not associated with traditional measures of condition (keel score, fat score, or a body condition index). Our results provide some support for the condition-dependent arrival hypothesis and suggest that there may be immunological differences between early- and late-arriving birds.

Keywords Condition · Hematocrit · H/L ratio · Leukocytes · Migration

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Introduction

In migratory species, early arrival at the breeding grounds is associated with fitness benefits such as acquiring high-quality territories or mates and higher seasonal reproductive success (Møller 1994; Hasselquist 1998; Lozano et al. 1996; Forstmeier 2002). However, songbirds arriving early at northerly breeding grounds often encounter poor environmental circumstances, including cold temperatures and limited food availability (Smith and Moore 2005). Consequently, the earliest arrivals must be in superior physiological condition (Kokko 1999). According to the condition-dependent arrival hypothesis (Møller 1994; Kokko 1999), only high quality individuals that are in the best condition and good physiological health are able to bear the costs of early arrival and subsequently obtain the benefits of an advanced start to breeding. A number of studies have demonstrated the advantages of arriving in superior energetic condition in terms of fat deposits (e.g., Sandberg and Moore 1996; Smith and Moore 2003), but only recently have other potential measures of condition such as hematocrit and immune function received attention (Møller et al. 2004; Ninni et al. 2004).

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Hematocrit, the ratio of red blood cells to total blood volume, has been used as an indicator of condition in many species (e.g., Jones 1983; Saino et al. 1997; Ots et al. 1998) although recently some authors have called into question its reliability given the many factors that may influence hematocrit (Dawson and Bortolotti 1997; Fair et al. 2007). Migrating birds are expected to have higher hematocrit values due to the aerobic stress of migration (Carpenter 1975) and possibly dehydration (Biebach 1990; Carmi et al. 1992). At least two studies have found that during migration individuals had higher average hematocrit (Bairlein and Totzke 1992; Prats et al. 1996), although Owen and Moore (2006) found migrating thrushes at a study site on the northern coast of the Gulf of Mexico to have lower hematocrit than those in the breeding season in Michigan. The authors suggested that the lower hematocrit may have been due to short-term food deprivation as they were capturing migrants at the completion of their trans-gulf flight. One study that examined hematocrit in relation to arrival timing in Barn Swallows (*Hirundo rustica*) found that it declined with arrival date, suggesting that earlier arrivals were in better condition (Ninni et al. 2004).

Immune function has also been considered a measure of condition, as mounting and maintaining an immune response is thought to be energetically costly (Sheldon and Verhulst 1996; Lochmiller and Deerenberg 2000; Norris and Evans 2000; Klasing 2004; but see Nilsson et al. 2007). One commonly used measure of immune status is a total and differential white blood cell (WBC) count. In captive birds, elevated WBC counts may indicate presence of an infection (Campbell and Dein 1984), while low counts may indicate reduced immunocompetence. Differential WBC counts have been used to assess the health status of wild birds (e.g., Driver 1981; Hõrak et al. 1998; Sergent et al. 2004). In particular, the ratio of heterophils to lymphocytes (H/L ratio) has been demonstrated to be a reliable indicator of stress (Gross and Siegel 1983; Maxwell 1993), as the H/L ratio has been shown to increase in response to stressors such as food deprivation (Gross and Siegel 1986), thermal stress (Dabbert et al. 1997), and injury (Vleck 2001). Heterophils are involved in innate immune function providing non-specific defense primarily against bacteria while lymphocytes are involved in acquired immune function against specific pathogens (Maxwell 1993). While several studies have examined seasonal changes in differential WBC counts (Driver 1981; Pavlak et al. 2005; Owen and Moore 2006), to our knowledge none have explicitly focused on arrival at the migratory destination.

Here, we examine several measures of condition and their relationship to arrival timing of Gray Catbirds (*Dumetella carolinensis*) at their breeding grounds in northeastern Pennsylvania. We were specifically interested in describing hematological parameters (hematocrit, total WBC count, differential WBC, H/L ratio) as birds arrived, and their relationship with more traditional measures of condition such as mass and amount of accumulated fat. If arrival timing is condition-dependent, we predicted earlier-arriving birds to have higher traditional condition measures (heavier mass, higher fat and keel scores, and higher body condition index), higher hematocrit, and higher H/L ratios (indicating greater stress experienced by early arrivals). The prediction for WBC and lymphocyte counts is less clear-cut due to the difficulty in interpreting the consequences of high or low counts (e.g., high counts may mean high immune investment or infection) and because no one has examined variation in these parameters in landbirds arriving at their migratory destination. Therefore, our objective for the leukocytes was simply to determine whether or not counts were elevated in early arrivals.

Materials and methods

We captured Catbirds in mist-nets from mid-April through mid-July at a field site near Lackawanna State Park in Lackawanna County, Pennsylvania (41°34′30″N, 75°42′5″W). Twenty-four 12-m-long nets (mesh size = 30 mm) were opened immediately prior to sunrise and closed 4–5 h later. Catbirds were banded with a USGS aluminum band and uniquely marked with 1–3 color bands, measured, and a blood sample collected (see below). Tail and wing length were recorded to the nearest 1 mm using a wing-rule, and tarsus length was measured to the nearest 0.01 mm using digital calipers. Mass was determined to the nearest 0.1 g using an electronic balance. Fat load was estimated using the Monitoring Avian Productivity and Survivorship (MAPS) six-point scale (Desante and Burton 1994), and keel was assigned a score from 0 to 3 depending on the size of the breast muscle (Bairlein 1995). We also recorded the time at which a Catbird was banded, and calculated the minutes since sunrise as the difference between banding time and official sunrise.

To determine hematocrit and differential WBC counts, we collected 50–100 μL of blood via brachial vein puncture using a 27-gauge needle and heparinized microhematocrit capillary tubes. One drop of blood was used to make a blood smear which was air dried and fixed with 100% methyl alcohol for at least 30 s in the field (per kit instructions), and later stained using a Hema3 stain kit (Fisher Diagnostics). Counts were conducted by MIH and RJS at ×1,000 using oil immersion to determine the number of lymphocytes, monocytes, heterophils, eosinophils, and thrombocytes present (Campbell and Dein 1984). Both observers used the same key and guide for distinguishing WBCs and there was no effect of observer on any

of the WBC counts or H/L ratios [generalized linear models (GLMs) with count as the dependent variable and observer as a fixed factor]. To account for aggregation of leukocytes on the smear (which typically occurs along edges) we systematically counted across an entire width of the smear, including the edges, in an effort to reduce bias and obtain a representative sample. Depending on the density of red blood cells (RBCs) in the smear, we counted 100–200 fields of view (FOV) to approximate the number of WBC per 20,000 RBCs (van Riper III et al. 1986). First, we calculated how many RBCs were in one FOV when cells formed a complete, but non-overlapping, monolayer. This was done for multiple smears until we had an accurate assessment for the particular species and microscope (both of which can attribute to variation in RBC number per FOV). We then used that calculation to determine how many FOV to count for a particular smear based on the percent coverage of the RBCs.

We determined hematocrit via centrifugation of capillary tubes for 9 min at 14,000*g*. The total volume and packed RBC volume was measured to the nearest 0.01 mm using digital calipers. Sample sizes differ between hematocrit and WBC counts due to loss during processing or an insufficient amount of blood collected to estimate hematocrit.

Statistical analyses

We limited our analyses to 49 birds first captured prior to the mean first egg date and later verified as breeding at our site. We classified Catbirds as breeders if we recaptured or observed them after the mean first egg date for Catbirds, which was 4 June 2006 and 31 May 2007, or if they had morphological evidence of breeding (such as a brood patch) upon recapture before those dates. We determined body condition by regressing mass on the first principal component of tarsus, tail length, and wing length. Principal component 1 (PC1) accounted for 58% of the variation and was determined using a correlation matrix.

We looked for associations between ordinal date and the various hematological variables using Pearson correlations, and used Spearman rank correlations to relate condition variables to ordinal date. The differential WBC counts were not normally distributed, therefore we used a square root transformation to bring leukocyte counts into compliance with normality assumptions (Sokal and Rohlf 1981). Fat and keel scores could not be normalized, and therefore were analyzed with non-parametric tests. Year, sex, and age may influence arrival date, therefore we included them as fixed factors in GLMs with ordinal date as a covariate. Year was not a significant factor in any of the analyses (all P values > 0.3) so we combined data from both years. We also included observer as a fixed effect for analyses of WBC counts and time since sunrise as a covariate for hematocrit. We used the Kendall partial rank-order correlation coefficient (Siegel and Castellan 1988) to control for ordinal date while looking for associations between blood parameters (hematocrit, total WBC, lymphocytes) and traditional measures of condition (fat, keel, mass, body condition) since fat and keel scores were not normally distributed. All analyses were conducted in SPSS 15 (SPSS Institute 2006) and assumed to be significant at the 0.05 level.

Results

Hematocrit was negatively associated with capture date ($r = -0.59$, $n = 42$, $P < 0.001$; Fig. 1). This was not due to differential arrival by age (SY = 9, ASY = 22) or sex ($M = 22$, $F = 12$) as there was no significant relationship between hematocrit and age ($F_{1,34} = 0.67$, $P = 0.4$, Fig. 1a) or sex ($F_{1,34} = 0.65$, $P = 0.4$, Fig. 1b), although there was a significant interaction term ($F_{1,34} = 6.5$, $P = 0.02$) with later-arriving females having lower hematocrit than males (Fig. 1b). Also, time since sunrise was not a significant predictor of hematocrit and, when included in the GLM, ordinal date was still significant ($n = 42$, $F_{2,39} = 10.6$, $P < 0.001$).

Date of first capture was positively associated with number of lymphocytes ($r = 0.36$, $n = 49$, $P = 0.012$; Fig. 2a), negatively associated with the H/L ratio ($r = -0.30$, $n = 47$, $P = 0.039$; Fig. 2b) but not associated with total WBC count ($r = 0.10$, $n = 49$, $P = 0.51$). There was no age, sex or observer effect (GLM, all P-values > 0.15) and all other types of leukocytes were unrelated to arrival day.

Of the more traditional measures of condition, only fat score (Fig. 2c) was negatively associated with ordinal date ($r_s = -0.42$, $n = 42$, $P = 0.006$) while there was no relationship ($n = 42$, $P > 0.7$) with mass ($r_s = -0.02$), keel score ($r_s = 0.01$), or body condition ($r_s = 0.05$). Hematocrit, total WBC count, and lymphocytes were not significantly associated with keel score, mass, or the condition index controlling for ordinal date (Table 1), but fat score was positively associated with all three blood parameters (Fig. 3).

Discussion

Our results partially support the hypothesis of condition-dependent arrival (Møller 1994; Kokko 1999) as hematocrit and fat score were negatively associated with arrival date in Gray Catbirds at our study site. Total WBC count was unrelated to capture date but lymphocyte count was positively associated with capture date, which may indicate later birds were either fighting infection or investing more

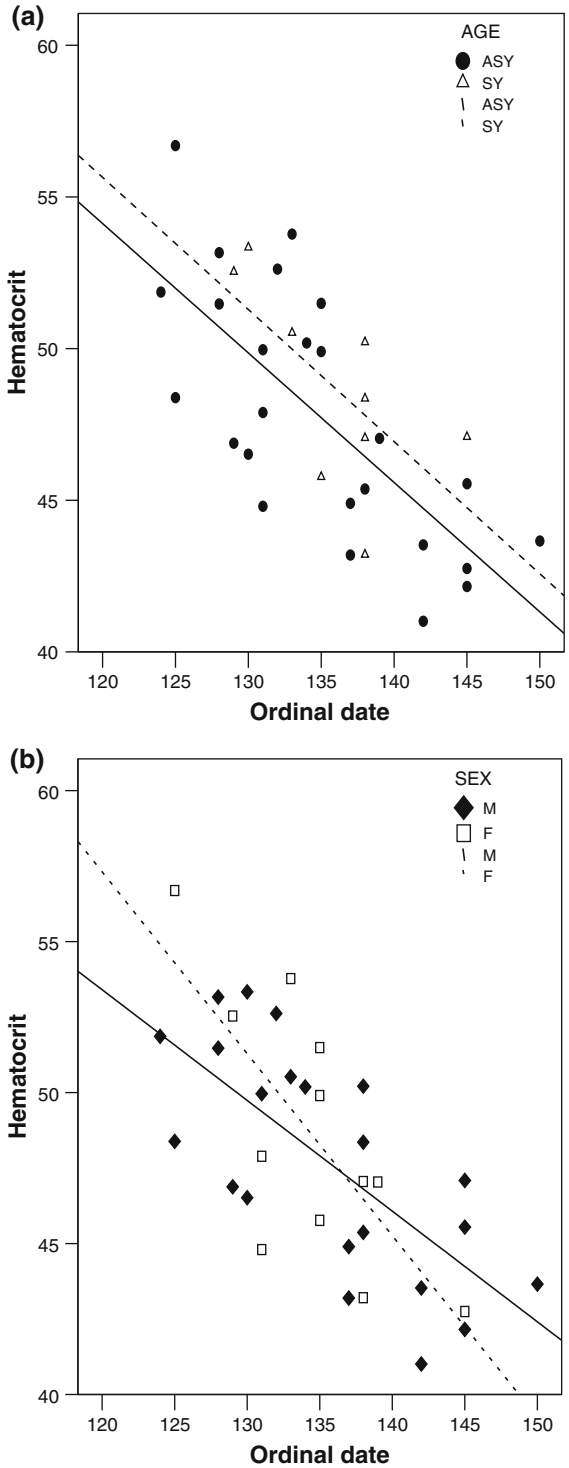

Fig. 1 Scatterplots of hematocrit and ordinal date based on **a** age and **b** sex for Gray Catbirds (*Dumetella carolinensis*) arriving at breeding grounds in northeastern Pennsylvania in 2006 and 2007 combined. Age ($F_{1,34} = 0.67$, $P = 0.4$) and sex ($F_{1,34} = 0.65$, $P = 0.4$) were not significantly related to hematocrit, although there was a significant interaction ($F = 6.5$, $P = 0.02$). *Lines* represent best fit and are included only to help visualize the patterns

in acquired immunity. Interestingly, H/L ratio was higher in earlier-arriving Catbirds which suggests that early-arriving individuals are experiencing more stress, even though they are in better energetic condition than late-arriving individuals.

The lower hematocrit observed in late-arriving Catbirds may be due to multiple factors. Hematocrit may vary with age, sex, season, and body condition (reviewed by Fair et al. 2007) as well as time of day (Dawson and Bortolotti 1997). In our study, age, sex, time since sunrise, and condition were not significantly associated with levels of hematocrit. Hematocrit can also be elevated by dehydration (Biebach 1990; Carmi et al. 1992), something for which we could not control. However, we have no reason to expect birds arriving earlier to the breeding grounds to be more dehydrated than those arriving later. Effects of energetic condition on hematocrit are varied (Fair et al. 2007), but at least one study found decreased levels in nutritionally stressed Red Knots (*Calidris canutus*) (Piersma et al. 2000), and another study in migrating Blue Tits (*Cyanistes caeruleus*) found that hematocrit increased with fat score (Svensson and Merilä 1996). Therefore, poorer nutritional status may be a reasonable explanation for low hematocrit in late-arriving birds. Ninni et al. (2004) also found a negative correlation between arrival date and hematocrit in Barn Swallows. Although they did not directly relate body condition to hematocrit, later arrivals in 1 of 2 years were in significantly poorer condition than earlier arrivals, suggesting a potential relationship between hematocrit, arrival date, and condition. In our study, hematocrit was not correlated with body condition but was correlated with fat score when controlling for date. Since hematocrit and fat score were negatively related to ordinal date, this suggests that some measures of condition are related to arrival timing while others are not, and that hematocrit may be indicative of aerobic capacity but not body condition.

The positive relationship between lymphocyte number and arrival date is surprising as lymphocyte count has been positively related to energetic and nutritional condition in non-migratory contexts (Bachman 2003; Lochmiller et al. 1993; Råberg et al. 2003; Stinnett 1983). Additionally, Owen and Moore (2008) found that thrushes arriving at a migratory stopover site in poor energetic condition had lower lymphocyte counts. We also found a positive relationship between fat score and lymphocytes, controlling for date, which suggests that lymphocytes increase with date due to something other than condition. The spleen, which is a major site for lymphocyte storage and differentiation, is reduced during or immediately following the migratory period (Fänge and Silverin 1985; Deerenberg et al. 2003), which may explain the low lymphocyte counts of early-

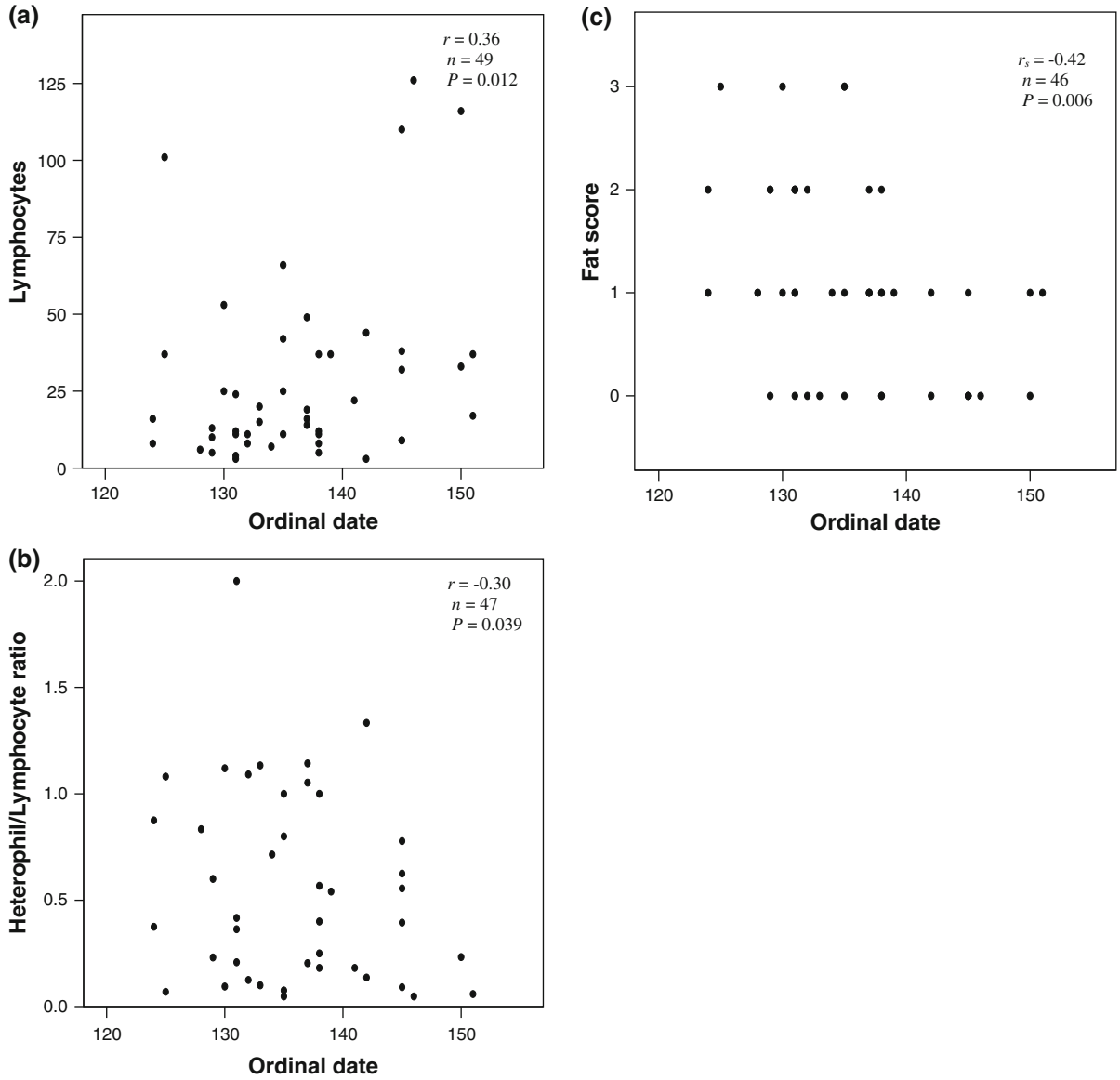

Fig. 2 Correlations between ordinal date and **a** number of lymphocytes, **b** H/L ratio, and **c** fat score of Gray Catbirds arriving at breeding grounds in northeastern Pennsylvania in 2006 and 2007 combined

Table 1 Partial correlations between hematocrit, total WBC count, or number of lymphocytes and traditional condition factors controlling for ordinal date for Gray Catbirds (*Dumetella carolinensis*) arriving on breeding grounds in northeastern Pennsylvania

Variable	*n*	Fat *T*	Keel *T*	Mass *T*	Body condition *T*
Hematocrit	38	0.20*	0.06	−0.08	−0.05
Total WBC	44	0.17*	−0.05	0.09	0.08
Lymphocytes	44	0.19*	−0.005	0.07	0.17

Body condition was calculated from the residuals from a regression of mass on the first factor of a principal components analysis (using tarsus, wing, and tail lengths). Partial correlation coefficients (*T*) are Kendall partial rank-order correlation coefficients

* Significant at the 0.05 level

arriving birds. Furthermore, the early-arriving birds appear to be experiencing more stress as indicated by the higher H/L ratios. Dhabhar and McEwen (1996) suggest acute stress may actually cause lymphocytes to leave circulation and sequester into peripheral organs and tissues, but as migratory birds are experiencing chronic stress, this is unlikely to be the case. We acknowledge that, without a direct test of immune response (such as an immune challenge or experimental infection), we cannot definitively determine the consequences of low lymphocyte counts. An intriguing possibility is that low lymphocyte counts may reflect a trade-off between increased speed of migration and reduced immune function in early-arriving Catbirds,

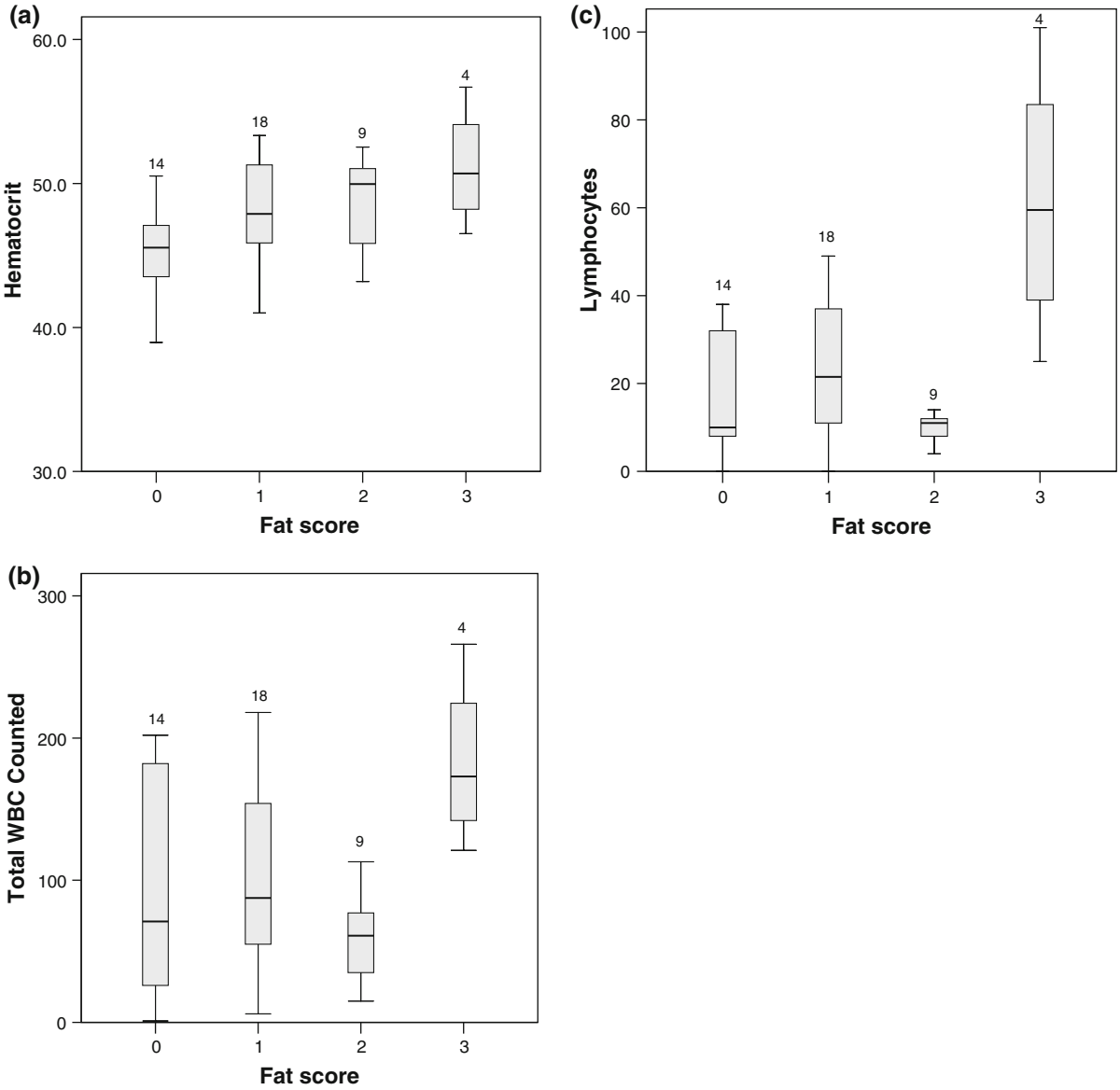

Fig. 3 *Boxplots* of fat score and **a** hematocrit, **b** total WBC count, and **c** number of lymphocytes for Gray Catbirds arriving at breeding grounds in northeastern Pennsylvania in 2006 and 2007 combined. *Bar* equals the median, *whiskers* encompass the range. *Numbers* above are sample sizes

but tests of this idea must first determine whether low lymphocyte counts represent lower investment in immune function or lower infection rates.

The higher H/L ratio of early-arriving Catbirds can indicate chronic stress (Gross and Siegel 1983; Maxwell 1993). However, it is likely that the early Catbirds may be better equipped to deal with the stress, as indicated by the higher hematocrit and fat score for early arrivals. The difference in H/L ratio between earlier and later arrivals is a result of changes in lymphocyte number and not changes in heterophil counts, as heterophil number was not related to arrival date in our population. It is difficult to make comparisons with other studies as none have reported H/L ratios in relation to arrival, and only one (Owen and Moore 2006) examined H/L ratio in relation to migration. The authors found that migrating thrushes had higher H/L ratios than conspecifics captured during the breeding season and suggest this may be due to the heightened energetic stress of long-distance migration.

Further study of the arrival period, including experimental challenges to the immune system, is needed to clarify the relationships between immunocompetence and arrival timing. The evidence so far suggests early arrivals have allocated resources to migration (higher hematocrit and energetic condition) rather than one aspect of immune function (lymphocyte count). Unfortunately, we do not

know what these hematological variables mean in terms of a bird's ability to resist disease (proximate concerns) or the impacts on fitness (ultimate concerns). It may be that fluctuations in immunity have short-term advantages in terms of allocating resources to where they are currently most needed (e.g., earlier arrival traded off for survival risk). Given the evidence that arrival timing and reproductive success are linked, reducing immune function for earlier arrival may be beneficial in the long run because early-arriving individuals may be able to allocate more resources towards their reproductive success in the short-term even with the greater susceptibility to disease.

Zusammenfassung

Timing der Ankunft und hämatologische Parameter von Katzendrosseln (*Dumetella carolinensis*)

Bei Zugvögeln steht eine frühe Ankunft im Brutgebiet mit einem höheren Fortpflanzungserfolg in Zusammenhang. Gemäß der Hypothese der konditionsabhängigen Ankunft können lediglich solche Individuen, die in besonders guter physiologischer Kondition sind, die Kosten einer frühen Ankunft (z. B. schlechte Umweltbedingungen, begrenzte Nahrungsverfügbarkeit) tragen. Kondition wird normalerweise in Form von Energiereserven oder Masse gemessen, doch andere physiologische Konditionsmaße wie Hämatokritwert und Immunfunktion erhalten verstärkt Beachtung. Wir haben mehrere Konditionsmaße von in ihrem Brutgebiet in Nordost-Pennsylvania eintreffenden Katzendrosseln und ihre Verbindung mit dem Datum des Erstfangs untersucht. Früher eintreffende Vögel hatten höhere Hämatokritwerte und H/L-Verhältnisse und niedrigere Lymphozytenzahlen. Das Ankunftsdatum stand außerdem in negativem Zusammenhang mit dem Fettwert. Der Fettwert stand in positiver Beziehung zum Hämatokritwert, der Gesamtleukozytenzahl und der Lymphozytenanzahl, doch die anderen hämatologischen Parameter zeigten keinen Zusammenhang mit traditionellen Konditionsmaßen (Kielwert, Fettwert oder Körperkonditionsindex). Unsere Ergebnisse bieten gewisse Unterstützung für die Hypothese der konditionsabhängigen Ankunft und deuten darauf hin, dass es immunologische Unterschiede zwischen früh und spät eintreffenden Vögeln gibt.

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