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LOW OXYGEN-CARRYING CAPACITY OF BLOOD MAY INCREASE DEVELOPMENTAL INSTABILITY OF MOLT IN MIGRATING WADERS

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ABSTRACT.—The degree of asymmetry in feather replacement may be considered a reliable measure of developmental instability of avian molt. Although empirical evidence exists for the fitness consequences of molt asymmetry, the proximate cause of asymmetrical molt remains unknown. We tested for the possibility of a link between asymmetry in feather replacement and hemoglobin concentration of first-year Common Snipe (*Gallinago gallinago*) during the partial postjuvenile molt. Advancement and symmetry of molt were determined for 637 first-year Common Snipe captured at Jeziorsko reservoir, central Poland, during autumn migration. We found that the probability of asymmetrical molt did not vary with date of capture ($W = 1.66$, $P = 0.20$), but Common Snipe with lower hemoglobin concentrations had a higher probability of asymmetrical molt ($W = 5.22$, $P = 0.022$). Because Common Snipe molt during migration, high oxygen-carrying capacity of blood is presumably necessary to meet aerobic demands of the tissues during long-distance flights. We suggest that under these conditions, low hemoglobin concentrations may lead to an acute organismal hypoxia causing disruptions in developmental homeostasis, such as asymmetrical feather replacement. *Received 5 October 2012, accepted 26 December 2012.*

Key words: Common Snipe, developmental stability, fluctuating asymmetry, *Gallinago gallinago*, hemoglobin, molt asymmetry.

La Baja Capacidad de Carga de Oxígeno en la Sangre Podría Incrementar la Inestabilidad en el Desarrollo de la Muda en Aves Vadeadoras Migratorias

RESUMEN.—El grado de asimetría en el reemplazo de las plumas podría ser considerado como una medida confiable de la inestabilidad en el desarrollo de la muda en las aves. Aunque existe evidencia empírica de las consecuencias de la asimetría en la muda sobre la aptitud, la causa próxima de la muda asimétrica permanece desconocida. Evaluamos la posibilidad de que la asimetría en el reemplazo de las plumas pudiese estar ligada con la concentración de hemoglobina en individuos de *Gallinago gallinago* en su primer año, durante la muda parcial post-juvenil. El avance y la simetría de la muda fueron determinados para 637 individuos en su primer año de vida capturados en la reserva Jeziorsko, Polonia central, durante la migración de otoño. Encontramos que la probabilidad de presentar muda asimétrica no varió con la fecha de captura ($W = 1.66$, $P = 0.20$), pero los individuos con menores concentraciones de hemoglobina tuvieron una mayor probabilidad de presentar muda asimétrica ($W = 5.22$, $P = 0.022$). Debido a que *G. gallinago* muda durante la migración, se presume que necesita de una alta capacidad de carga de oxígeno en la sangre para cumplir las demandas aeróbicas de los tejidos durante los vuelos de larga distancia. Sugerimos que, bajo estas condiciones, las bajas concentraciones de hemoglobina podrían llevar a una hipoxia organísmica aguda y causar trastornos en la homeostasis del desarrollo, como un reemplazo asimétrico en las plumas.

MOLT IS AN energetically demanding stage of the avian annual cycle (Williams and Swaddle 2003). Direct energetic costs of molt are attributed to various physiological processes, such as the whole-body protein turnover, which consumes ≤30% of total energy resources needed for completion of molt (Murphy and Taruscio 1995). Apart from the costs of feather synthesis, molting also incurs indirect energetic expenses associated with impaired flight performance, especially when flight feathers are molted. For instance, the ascent angle of European Starlings (*Sturnus vulgaris*) during the complete molt was shallower than that of nonmolting individuals (Swaddle and Witter 1997). Impaired flight performance and low body mass were also observed in European Starlings in which molt was simulated by experimental reduction in the lengths of appropriate flight feathers. Swaddle and Witter (1997) therefore suggested that the decrease in body mass in European Starlings was attributable to aerodynamic costs of feather loss rather than to the physiological costs of molt.

Aerodynamic costs of flight in molting birds may be further increased when the process of molt proceeds asymmetrically. Different times of shedding the corresponding feathers from the left and right sides create asymmetry in the lengths of growing feathers, which has consequences for an individual's flight abilities

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(Swaddle et al. 1996). Asymmetry in flight feathers may negatively affect turning performance (Thomas 1993), and asymmetric lengths of rectrices are known to reduce general flight maneuverability. In Barn Swallows (*Hirundo rustica*), both the degree of asymmetry in rectrices caused by experimental treatment as well as the natural degree of asymmetry negatively affected flight maneuverability (Møller 1991). Lower maneuverability was also recorded in Streamertails (*Trochilus polytmus*) with experimentally elongated, asymmetrical tail feathers (Evans et al. 1994).

Asymmetry in molting of the corresponding left- and right-side feathers may be classified as fluctuating asymmetry (FA; i.e., the random deviation from perfect symmetry in bilateral traits; Watson and Thornhill 1994). It is widely accepted that FA of morphological characters indicates the magnitude of developmental instability, which occurs under environmental and genomic stress (Parsons 1992). For this reason, FA was proposed as a reliable measure of individual phenotypic and genotypic quality (Thornhill and Sauer 1992). Because asymmetry reflects an inability to cope with stressful situations—which, in the case of flight feathers, hampers locomotion—it presumably reflects important fitness components of birds. In fact, comparative analyses indicate that strong relationships exist between FA and growth, fecundity, and survival of individuals (Møller 1999). In the present study, we used the degree of asymmetry in feather replacement as a measure of developmental instability of molt (see also Brommer et al. 2003).

Although fitness consequences of molt asymmetry have been recognized in birds (Brommer et al. 2003), the proximate cause of asymmetrical feather replacement remains unknown. The ultimate causes of asymmetrical development may include both genetic factors (inbreeding homozygosity, mutations, and chromosomal anomalies) and environmental factors (food shortage, pollutants, parasitism, and infections) (Møller and Thornhill 1998), but the physiological background of asymmetry in feather replacement has never been investigated. Here, we hypothesize that low hemoglobin concentration resulting in low oxygen-transport performance may, under certain conditions, lead to disruptions in developmental homeostasis, such as asymmetrical feather replacement. Because flying is an energetically expensive activity that often takes place at high altitudes with low oxygen pressure (Piersma et al. 1996), birds are especially prone to hypoxic stress during long-distance migration (Carpenter 1975). Studies on freely flying birds in wind tunnels demonstrated that oxygen consumption may increase as much as 15-fold during a flapping migratory flight (Faraci 1991). Thus, we would expect hemoglobin concentrations to affect the degree of molt asymmetry, especially in species in which the period of feather replacement coincides with annual migration. To test this prediction, we assessed the hematological state of a migratory shorebird, the Common Snipe (*Gallinago gallinago*), during the first prebasic molt.

Methods

Field work was conducted at the Jeziorsko reservoir (51°40′N, 18°40′E), central Poland, where Common Snipe were trapped from mid-July to mid-September in 2008–2011. In total, 637 first-year Common Snipe were captured and banded. Birds were aged by plumage (Kaczmarek et al. 2007, Włodarczyk et al. 2008) and measured according to standard procedures described by Meissner (2000). Wing length was measured with a stopped ruler to 1 mm; head (from tip of bill to back of skull), bill, and tarsus lengths were measured with calipers to the nearest 0.1 mm. All birds were weighed with an electronic balance to the nearest 1 g. Fat loads were assessed in the furculum and in the axilla according to the five-point scale developed for waders (Meissner 2000). Mean values of furculum and axilla fat scores were calculated to express the size of fat loads of each individual. Additionally, we measured biometrical traits that differ between the sexes in Common Snipe: the length of the outermost rectrix (R7) and the difference in the length of two outermost rectrices (R6–R7). On the basis of these measurements, the sex of the individual was determined according to discriminant equations developed by Włodarczyk et al. (2011). We also reduced three basic biometrical traits (wing, head, and tarsus lengths) to the first principal component (PC1) using principal component analysis, because the multivariate metric is likely to express the overall structural size of birds more reliably than any single measurement (Freeman and Jackson 1990). All biometrical traits were standardized to equal unit variances (*z*-scores) prior to the analysis and had similar loadings on PC1 (0.30–0.36). PC1 accounted for 55.3% of variation in all reduced biometrical traits.

For all captured first-year Common Snipe, we quantified the progression of the partial prebasic molt, which typically includes replacement of all body and wing coverts, tertials, and rectrices (Włodarczyk et al. 2008). Birds were classified into one of three molt categories: before molt (n = 324), in the initial stage of molt (only body/wing coverts in active molt; n = 216), or in the advanced stage of molt (tertials or rectrices in active molt; n = 97). We assigned a molt score for each tertial and rectrix, following the standard approach of Ginn and Melville (1983): 0 = an old unmolted feather, 5 = a new fully grown feather, and 1–4 = successive stages of feather growth. The molt index of birds in the advanced stage of feather replacement was expressed as the sum of molt scores of all tertials (from both wings) and rectrices. We also calculated the differences between molt scores of the left and right feathers for each pair of rectrices and tertials, and the absolute values of these differences were totaled for all pairs of feathers (molt asymmetry index). For the purpose of analysis, molt asymmetry was coded binomially, where "0" represented symmetrical molting (molt asymmetry index = 0), and "1" represented asymmetrical molt (molt asymmetry index > 0).

We measured hemoglobin concentration for more than half of all captured first-year Common Snipe (n = 347). The birds were randomly chosen for the analysis. For this purpose, we collected ~5 µL of blood from the ulnar vein of each bird. The concentration of hemoglobin was determined using a portable HemoCue Hb 201+ photometer (HemoCue Hb, Ängelholm, Sweden). Although this technique for measuring avian hemoglobin was not validated against more conventional methods, it has been demonstrated that measurements obtained with the HemoCue photometer were highly proportional to the packed cell volume of birds, and the character of this relationship was consistent across nine avian orders (Velguth et al. 2010). Thus, the HemoCue photometer is acknowledged to reliably measure hemoglobin concentration in avian blood and is widely used in both field (Murphy et al. 2010, Prinzinger and Misovic 2010) and experimental bird studies (Burness et al. 2000, Pryke et al. 2007, Pryke and Griffith 2009). In the present study, we measured hemoglobin level for 167 Common Snipe that had not yet started molting, 117 in the initial stage of molt, and 63 in the advanced stage.

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We used general linear models to investigate the influence of different independent variables on hemoglobin concentration in Common Snipe. To assess the effects of hemoglobin concentration, date of capture, and molt index on the probability that a bird exhibited asymmetrical molt, we used a generalized linear model with the logit link function, and the significance of each independent variable was evaluated with the Wald statistic. Spearman correlation was used to test for the relationship between hemoglobin concentration and molt asymmetry index. All values are presented as means ± SE. Statistical analyses followed Zar (1996) and were performed using STATISTICA, version 10.0 (StatSoft, Tulsa, Oklahoma).

RESULTS

The mean hemoglobin concentration of juvenile Common Snipe was 175.7 ± 0.85 g L^{-1} (n = 347). There were no differences in hemoglobin concentration between the sexes (F = 1.15, df = 334, P = 0.28). We also did not find any relationship between hemoglobin level and the structural size of birds (F = 1.48, df = 335, P = 0.22). On the other hand, after accounting for the effect of year (F = 7.05, df = 338, P < 0.001), hemoglobin level of Common Snipe increased with date of capture (F = 3.96, df = 338, P = 0.047; β = 0.09 ± 0.05) and with fat stores (F = 20.86, df = 338, P < 0.001; β = 4.51 ± 0.99; Fig. 1). Fat stores were significantly related to stage of molt (F = 5.71, df = 629, P = 0.003), with lowest values during the advanced stage of feather replacement (trend analysis: F = 10.81, df = 629, P = 0.001). By contrast, hemoglobin level did not change along the molt progression (F = 1.82, df = 336, P = 0.16). For Common Snipe in the advanced stage of molt, we found no relationship between molt index and hemoglobin concentration (F = 0.39, df = 66, P = 0.54). The relationship remained nonsignificant even after accounting for the effects of date of capture and fat stores (F = 0.09, df = 64, P = 0.76).

Asymmetrical first prebasic molt was recorded in 52.3% of molting birds (n = 97). Whether a bird exhibited asymmetrical molt was independent of its molt index (W = 1.12, P = 0.29). The probability of asymmetrical molt did not vary with the date of capture (W = 1.66, P = 0.20), but Common Snipe with lower hemoglobin concentrations were more likely to exhibit asymmetrical molt (W = 5.22, P = 0.022; β = −0.040 ± 0.018; Fig. 2). As indicated by the odds ratio of the logistic regression, the probability of asymmetrical molt decreased by 4.1% for each increase of 1 g L^{-1} in the concentration of hemoglobin. We also found a significant negative relationship between hemoglobin concentration and degree of molt asymmetry as estimated by the molt asymmetry index (R = −0.32, P = 0.012, n = 63). However, when individuals with symmetrical molt were excluded from the analysis, the relationship lost its statistical significance (R = 0.06, P = 0.75, n = 32).

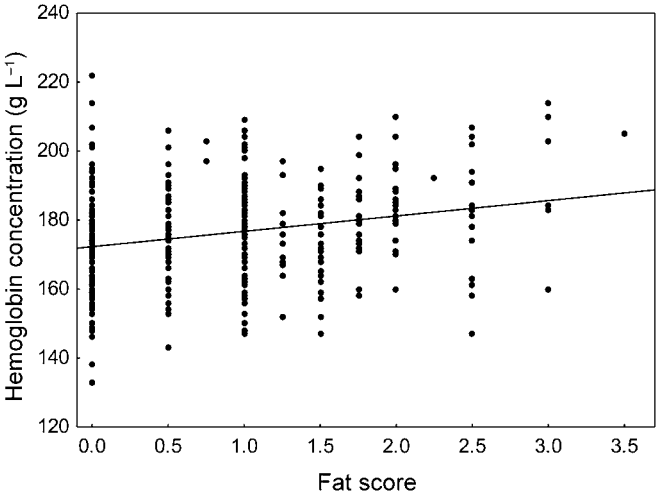


FIG. 1. Relationship between hemoglobin concentration and accumulated fat stores in first-year Common Snipe migrating through Jeziorsko reservoir, central Poland, 2008–2011.

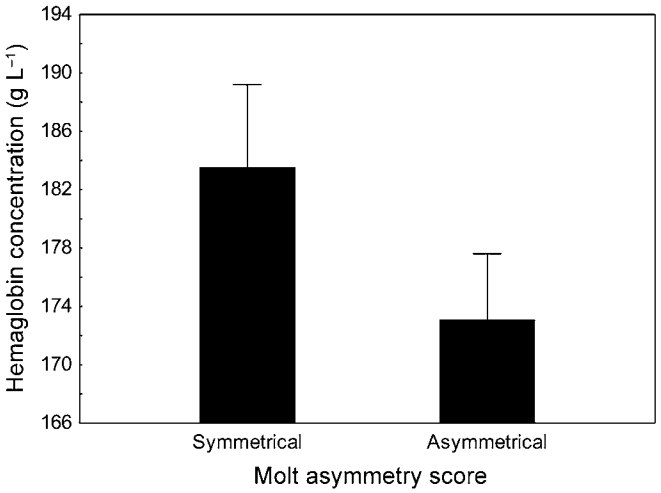


FIG. 2. Hemoglobin concentration of migrant first-year Common Snipe with symmetrical and asymmetrical prebasic molt (bars = 1.96*SE). Migrating individuals were captured during autumn at Jeziorsko reservoir, central Poland, 2008–2011.

DISCUSSION

Blood profile parameters are widely acknowledged to reflect aspects of physiological status in many taxa of animals. Hemoglobin concentration (mass of hemoglobin per unit of blood) is a fairly simple measure of the oxygen-carrying capacity of blood (Campbell 1995). In mammals, an organism's potential to satisfy its demands for energy is more reliably measured by the amount of oxygen supplied to the tissues per unit of time than by the oxygen capacity of blood (Kostelecka-Myrcha 2002). This is measured by the amount of hemoglobin per unit surface area of erythrocytes, which determines opportunities for full use of hemoglobin during the course of oxygen transport. By contrast, the amount of hemoglobin per unit surface area of erythrocytes remains constant among all avian species, as well as among individual birds in different physiological and environmental situations (Kostelecka-Myrcha 1997). Changes in total surface area of erythrocytes of birds are proportional to changes in hemoglobin concentration, which is an adaptation to the constant oxygen conditions in the lungs that are maintained by air sacs and the cross-current gas exchange (Schmidt-Nielsen 1975, Kostelecka-Myrcha 1997). Consequently, among several other physiological factors, hemoglobin level may indicate a bird's potential to satisfy its oxygen demand.

High metabolic demands of feather synthesis require that increased amounts of oxygen must be supplied to the tissues. For

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instance, oxygen consumption of molting White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) was substantially higher than that of nonmolting individuals (Schieltz and Murphy 1995), and metabolizable energy requirements of both Eurasian Kestrels (*Falco tinnunculus*; Dietz et al. 1992) and King Penguins (*Aptenodytes patagonicus*; Cherel et al. 1994) were higher during molt than during nonmolt episodes. Therefore, when molting coincides with other energetically expensive activities such as migration, we might expect significant tradeoffs in energy allocation. Birds are known to adjust the oxygen-carrying capacity of their blood during premigratory preparation by increasing hemoglobin concentration, in order to cope more effectively with the high energetic burden of long-distance flights (Piersma et al. 1996). We recorded significantly higher hemoglobin levels in Common Snipe with higher fat reserves at the stopover site, which suggests that hematological adjustments occurred in fat individuals that were ready to depart on migration. On the other hand, there was strong variation in hemoglobin concentration within the migratory population of Common Snipe that we studied, with individual values ranging from 138 to 222 g L^{-1}, which suggests that some birds may be unable to make the ecophysiological adjustment necessary for migration and molting. As a consequence, individuals with low oxygen-carrying capacity of blood may temporarily fail to meet the oxygen demand of the tissues, which could lead to acute organismal hypoxia. Under such hypoxic or energetic stress, the developmental stability of molt is likely to be substantially reduced, which may explain the negative correlation between hemoglobin concentration and molt asymmetry in migrating Common Snipe. To our knowledge, this is the first empirical demonstration of possible links between hematological status and molt stability in birds.

To date, the only study that has tested for an association between energetic constraints and stability of feather development has been Swaddle and Witter's (1994) study of captive European Starlings, in which experimentally induced energetic stress during molt increased the level of asymmetry in fully grown primary feathers. In the same study, primary-feather asymmetry decreased as the amount of subcutaneous fat stored during molt increased. In a nonexperimental study, the causal effect of food limitation on molt asymmetry was demonstrated for a group of Hawaiian forest avian species (Freed and Cann 2012). It was also found that Common Whitethroats (*Sylvia communis*) starting molt late in the season showed a higher degree of asymmetry in feather replacement than early-molting individuals (Hall and Fransson 2001), and the authors suggested that this pattern could be attributed to high metabolic rate caused by the stress of molting late in the year.

Although we suggest that oxygen-carrying capacity of the blood may exert direct causal effects on the degree of molt asymmetry, we acknowledge that our data are correlational. In ecological studies of birds, hemoglobin concentration is commonly used as an indicator of an individual's condition, health, or quality. Several studies have indicated that the concentration of hemoglobin varies with the parasite load of birds. Increased hemoglobin levels were recorded in nestling Common Starlings reared in nests with reduced mite loads (Clark and Mason 1988). A similar physiological response was observed in nestling Blue Tits (*Cyanistes caeruleus*) reared in parasite- and pathogen-free artificial nests (Słomczyński et al. 2006). Apart from parasite-related effects, variation in the hemoglobin concentration of nestling Blue Tits and Great Tits (*Parus major*) reflected differences in trophic conditions between seasons and sites (Bańbura et al. 2007, Kaliński et al. 2009). Similarly, the experimental study of Pryke and Rollins (2012) demonstrated positive effects of diet quality on hemoglobin concentrations in nestling Blue-faced Parrot Finches (*Erythrura trichroa*). Unusually low hemoglobin concentrations were also recorded in Great Tit chicks exposed to high environmental pollution (Nyholm et al. 1995). Therefore, Common Snipe with lower hemoglobin concentrations may be of generally lower physical condition or inferior genetic quality and, for this reason, exhibit reduced developmental stability resulting in a high degree of molt asymmetry. To unequivocally determine whether the relationship between hemoglobin level and molt asymmetry is of a causal or a correlative nature, experimental studies on the physiological state of molting birds are needed.

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