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When moult overlaps migration: moult-related changes in plasma biochemistry of migrating common snipe

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~~The process of feather replacement (moulting)~~ entails considerable physiological and energetic costs to an avian organism. Even under ~~highly~~ favourable feeding conditions, endogenous body stores and energy reserves of moulting birds are usually severely depleted. Thus, most species of birds separate moult from other energy-demanding activities, such as migration or reproduction. Common snipe *Gallinago gallinago* is ~~among the~~ exceptions, as many young snipe initiate the post-juvenile moult during their first autumn migration. Here, we evaluated moult-related changes in blood biochemistry of the common snipe during a period of serious trade-off in energy allocation ~~(migration)~~. For this purpose, ~~plasma~~ concentrations of basic metabolites were evaluated in ~~over half a thousand~~ of young snipe migrating through Central Europe. We found significant changes in the plasma concentrations of total protein, triglyceride and glucose ~~over the course of~~ moult, while ~~no changes were recorded in~~ the concentrations of uric acid and albumin. Total protein concentration increased significantly in the initial stage of moult, probably as a result of increased ~~keratin~~ production, but it ~~dropped~~ ~~in the advanced stage of moulting~~ to the pre-moult level. Plasma triglyceride concentration decreased ~~over~~ the period of tertial and rectrice moult, which reflected depletion of endogenous fat reserves. By contrast, glucose concentration ~~was found to~~ increase steadily ~~over~~ the course of moult~~ing~~, which could be ~~due to~~ increased catabolism of triglycerides (via gluconeogenesis) or, alternatively, due to increased glucocorticoids as a stress response. Our results suggest that ~~considerable~~ physiological changes associated with moult may be ~~among the primary~~ determinants of the low pace of migration ~~characteristic for~~ the common snipe.

When moult overlaps migration: moult-related changes in plasma biochemistry of migrating common snipe

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ABSTRACT

The process of feather replacement (moult~~ing~~) entails ~~considerable~~ physiological and energetic costs to an avian organism. Even under highly favourable feeding conditions, endogenous body stores and energy reserves of moulting birds are usually severely depleted. Thus, most species of birds separate moult from other energy-demanding activities, such as migration or reproduction. Common snipe *Gallinago gallinago* is among the exceptions, as many young snipe initiate the post-juvenile moult during their first autumn migration. Here, we evaluated moult-related changes in blood biochemistry of the common snipe during a period of serious trade-off in energy allocation (migration). For this purpose, plasma concentrations of basic metabolites were evaluated in over half a thousand of young snipe migrating through Central Europe. We found significant changes in the plasma concentrations of total protein, triglyceride and glucose over the course of moult, while no changes were recorded in the concentrations of uric acid and albumin. Total protein concentration increased significantly in the initial stage of moult, probably as a result of increased keratin production, but it dropped in the advanced stage of moulting to the pre-moult level. Plasma triglyceride concentration decreased over the period of tertial and rectrice moult, which reflected depletion of endogenous fat reserves. By contrast, glucose concentration was found to increase steadily over the course of moulting, which could be due to increased catabolism of triglycerides (via gluconeogenesis) or, alternatively, due to increased glucocorticoids as a stress response. Our results suggest that considerable physiological changes associated with moult may be among the primary determinants of the low pace of migration characteristic for the common snipe.

Keywords Common snipe, *Gallinago gallinago*, Moult-migration overlap, Moulting, Physiology, Plasma biochemistry

INTRODUCTION

Moulting is a process by which the ~~bird~~ maintain~~s~~ feathers of ~~appropriate~~ quality, improves ~~its ability to fly~~ and enhance~~s~~ thermoregulation. However, synthesis of feathers is ~~considered~~ one of the most physiologically costly events in the annual cycle of birds and it requires substantial ~~body~~ stores ~~for completion~~ (*Murphy, 1996*). As birds increase their tissue content and ~~protein~~ synthesis during ~~the~~ moult~~ing period,~~ periodic replacement of feathers ~~demands a lots of energy~~ for whole body protein turnover (*Newton, 1968*; *Murphy & King, 1992*; *Murphy & Taruscio, 1995*).

The biochemical analysis of blood is a ~~widely used~~ technique used to indicate avian body condition and to investigate physiological processes ~~occurring in~~ different life-history ~~phases.~~ In general, plasma metabolites reflect various aspects of physiological state and characterize the feeding state of birds. ~~Earlier studies have shown that~~ total protein and triglyceride levels reliably indicate nutrient status of wild~~ living~~ and captive birds (*Jenni-Eiermann & Jenni, 1998*; *Jenni-Eiermann, Jenni & Piersma,* 2002; *Albano et al., 2016*), although they may also vary in relation to environmental conditions and stress (*Artacho et al., 2007*; *Ibañez et al., 2015*). Plasma glucose level ~~is also known to~~ decrease during ~~the fasting~~ periods and~~,~~ thus~~,~~ may serve as an indicator of short-term changes in food intake (*Jenni-Eiermann and Jenni, 1998*; *Totzke et al., 1999*; *Alonso-Alvarez et al., 2002*). Numerous studies indicated that glucose levels positively correlate with different components of condition or broadly-defined individual quality (*Alonso-Alvarez et al., 2002*; *Minias & Kaczmarek, 2013*), although ~~increasing the~~ level of glucose may also be associated with increased glucocorticoids as a stress response (*Mondal et al., 2011*). By contrast, plasma concentrations of nitrogenous excretion components, such as uric acid, ~~are known to~~ increase substantially in response to starvation, ~~as~~ tissue proteins are actively mobilized as a source of energy. Plasma concentration of uric acid ~~was demonstrated as~~ a good indicator of condition especially in ~~the species~~ with low fat reserves, in which protein catabolism is rapidly activated during ~~the periods of~~ food shortage (*Villegas et al., 2002*). Finally, low albumin concentration may reflect acute diseases and chronic infection or inflammation, which may result from decreased allocation of resources to the immune function (*Hõrak et al., 2002*).

~~Taking all these into account,~~ changes in blood plasma biochemistry may well serve to evaluate physiological costs of moult~~ing~~. Earlier studies ~~have~~ investigated changes in plasma biochemistry during ~~the~~ moult~~ing process~~ in captive birds (*Dolnik & Gavrilov, 1979*; *Murphy & King, 1984*), ~~while~~ others ~~have~~ ~~examined~~ wild-living flightless birds (*Ghebremeskel et al., 1989*; *Cherel, Charrassin & Challet, 1994*). However, few, if any, papers have examined moult-related changes in plasma biochemistry ~~occurring~~ during ~~the~~ migration ~~period of wild-living~~ birds. The aim of this study is, therefore, to determine the nutritional and physiological costs of moult~~ing~~ by examining ~~the~~ changes ~~occurring~~ in blood plasma biochemistry during the moult of a migratory ~~wild-living~~ bird, the common snipe *Gallinago gallinago*. The common snipe breeds in low Arctic and boreal zones throughout entire Palaearctic, and migrates ~~for~~ wintering grounds in South-Western Europe. ~~While m~~ost avian species separate moult from other energy-demanding activities, such as migration or reproduction (*Pérez-Tris et al., 2001*; *Rohwer et al., 2009*), young common snipe typically ~~initiate~~ the post-juvenile moult during their first autumn migration (*Minias et al., 2010*). The post-juvenile moult of the common snipe is also more extensive and, thus, more energetically expensive, ~~compared to~~ other shorebirds, as it includes replacement of body feathers, lesser and median wing coverts, tertials and rectrices (*Włodarczyk et al., 2008*). In these respects, the common snipe ~~is a perfect model species~~ for study~~ing~~ moult-related changes in blood biochemistry during a period of serious trade-off in energy allocation~~, such as~~ migration.

METHODS

General field procedures

Common snipe were captured at the Jeziorsko reservoir (51°40'N, 18°40'E), central Poland, during autumn migration (04 August – 25 September). Jeziorsko reservoir is one of the most important stopover sites for migrating waders in inland Poland and the maximum concentrations of common snipe at the site ~~can~~ exceed a thousand of individuals in August (*Janiszewski et al., 1998*). In total, we caught 1007 first-year common snipe during seven ~~migratory~~ seasons (2009-2015). Snipe were captured in walk-in traps and mist nets, vocal stimulation ~~was occasionally used~~. All birds were ringed and aged ~~by~~ plumage (*Kaczmarek et al., 2007*; *Włodarczyk et al., 2008*). Sex of birds was determined either molecularly (~~only~~ in 2009), following ~~methods described by~~ *Kahn, John & Quinn* (*1998*), or by morphological measurements, using discriminant equations developed for the same migratory population of common snipe (*Włodarczyk et al., 2011*). For ~~the purpose of~~ sexing by morphology, bill length and distance between tips of two outermost rectrices were measured with calipers (± 0.1 mm), ~~while~~ vane length of the outermost rectrix was measured with a ruler (± 1 mm). Fieldwork was performed under the annual permissions ~~of~~ the Regional Environmental Protection Directorate in Łódź, Poland (nos. RDOS-10-WPN.I-6630-12/09/db; RDOS-10-WPN.I-6630-23-10/kb; WPN-I.6205.4.2011HG; WPN.6205.13.2012.DB.4; WST-SI.6205.6.2013.MJ; WST-SI.6205.6.2014.MJ; WPN.6205.63.2015.HG). Catching, ringing, and handling ~~of~~ birds was performed under individual annual permissions for ringers ~~issued~~ by the Polish Academy of Sciences, with an approval of the Ministry of the Environment in Poland and General Environmental Protection Directorate (nos. DOPozgiz-4200/III-173/622/09/ls - DZP-WG.6401.03.36.2015.km).

~~Moult~~

In all captured snipe we quantified the stage of post-juvenile moult. During post-juvenile moult snipe change their natal feathers (body feathers, lesser and median wing coverts, tertials, and rectrices) to an adult-~~like~~ plumage (Fig. 1). Thus, when post-juvenile moult is completed, first-year birds become indistinguishable from adults based on the plumage characteristics. However, ~~very~~ few young birds (if any) finish their post-juvenile moult before ~~reaching~~ wintering grounds ~~and~~ throughout ~~all~~ seven years we captured only 43 individuals in fresh (recently moulted) adult-~~like~~ plumage, most of which were ~~likely~~ adults. All these birds were ~~excluded from further study procedures~~. The remaining young birds were classified into one of three moult categories: 1) ~~before~~ moult (no feathers moulted); 2) initial stage of moult (only body/wing coverts in active moult); 3) advanced stage of moult (tertials or rectrices in active moult). An exact moult progress was also quantified for birds that moulted tertials or rectrices. For this purpose, each tertial (n = 8) and rectrix (n = 14) was given a moult score according to the feather scoring system developed by ~~*Ginn & Melville (1983)*~~, where: 0 – old feather ~~remaining,~~ 1 – old feather missing or a new feather ~~completely~~ in a pin, 2 – new feather up to one third grown, 3 – new feather between one and two thirds grown, 4 – new feather more than two thirds grown, 5 – new feather fully developed. A sum of all individual feather ~~moult scores~~ was used as a general moult score (max. 110, when all tertials/rectrices ~~are fully~~ renewed).

Plasma biochemistry

~~Ca.~~ 50% of captured young snipe (n = 538 individuals) were selected for plasma biochemistry measurements. Between 20 and 40 µl of blood was collected ~~into heparinized capillary tubes~~ from the ulnar vein of each bird. Blood sampling was performed under the permission of the Local Bioethical Commission in Łódź, Poland (no. Ł/BD/278). Samples were centrifuged at 6000 rpm for 5 min within an hour of collection. Plasma ~~was separated~~ from blood cells and kept at -20°C until analysis. Concentrations of the following ~~plasma~~ metabolites were measured (methods in parentheses): total protein (biuret reaction), albumin (bromocresol green), triglycerides (glycerol phosphate oxidase/peroxidase), glucose (glucose oxidase/peroxidase), and uric acid (uricase/peroxidase). All parameters were analysed with a spectrophotometer (BTS-330, BioSystems Reagents & Instruments, Barcelona, Spain) using commercial kits and reagents recommended by the manufacturer. The applied biochemical methods followed the standard methodology used in avian studies (e.g. *Artacho et al.,* *2007*). Since the amount of plasma collected from each bird~~s~~ was often not sufficient to measure all five plasma biochemistry parameters, ~~we obtained varying~~ sample sizes for each parameter (Table 1).

Statistical analyses

Differences in plasma biochemistry parameters between consecutive stages of post-juvenile moult were analysed with the general linear models (GLMs), separately for each parameter. In each model, we controlled for the ~~confounding~~ effects of sex, year, date of capture, and hour. Date was standardize within each season to account for annual variation in the timing of migration. To obtain more parsimonious reduced models, we removed non-significant (p > 0.15) predictors from initial full models. All statistical analyses were performed with Statistica 10.0 (StatSoft, Tulsa, OK, USA). All values are presented as means ± SE.

RESULTS

43.7 % of young common snipe showed signs of post-juvenile moult (n = 538). Most moulting snipe (74.9 %, n = 235) were ~~in~~ the initial stage of moult ~~(moulting body/wing coverts, no tertials or rectrices moulted)~~, while the remaining 25.1 % were ~~in~~ the advanced stage of moult ~~(moulting tertials and rectrices).~~

~~We found significant differences in~~ plasma concentrations of total protein and glucose between the consecutive stages of post-juvenile moult (Table 2, 3). Total protein concentration ~~increased~~ significantly in the initial stage of moult, ~~when compared to~~ the level before moult (35.57 ± 0.52 g/l vs. 33.33 ± 0.42 g/l; Tukey: p < 0.001; Fig. 2a). ~~Afterwards, it significantly dropped~~ in the advanced stage of moult (32.62 ± 0.90 g/l; Tukey: p = 0.011), ~~returning to the low~~ pre-moult level (Tukey: p = 0.67; Fig. 2a). By contrast, glucose concentration ~~increased from before moult~~ the advanced stage of moult (454.8 ± 7.1 mg/dl vs. 511.6 ± 20.6 mg/ dl; Tukey: p = 0.039; Fig. 2b). Snipe ~~in~~ the initial stage of moult ~~showed~~ an intermediate ~~level~~ of glucose ~~concentration~~ (Fig. 2b). Other plasma parameters showed no variation with moult stage (Table 4). Only ~~plasma~~ triglyceride concentration changed with moult score of snipe that moulted tertials or rectrices ($F_{1,31}$ = 4.10, p = 0.047), and ~~we found that~~ it significantly decreased ~~over the course of tertial/rectrice moult~~ (β = -0.29 ± 0.14; Fig. 3). All other plasma parameters showed no variation with moult score of tertials and rectrices (all p > 0.05).

DISCUSSION

~~Changes were observed~~ in the total protein, triglyceride and glucose concentrations ~~of~~ plasma during the post-juvenile moult of the common snipe. ~~While total protein concentration increased significantly in the initial stage, it significantly dropped in the advanced stage of moult. Glucose concentration was found to increase over the course of moulting, with higher values observed in the more advanced stages. In contrast, plasma triglyceride concentration significantly decreased over the period of tertial and rectrice moult.~~ At least some of these changes in blood plasma biochemistry are ~~likely~~ associated with the energy ~~required by~~ the process of feather replacement. ~~No moult-related changes were found in plasma concentrations of uric acid and albumin.~~

~~Total protein concentration increased significantly in the initial stage of moulting but fell later during the advanced stage, returning to the low pre-moult level.~~ The snipe has probably the highest protein demand at the beginning of the moult, ~~with~~ whole body protein turnover accelerating during successive stages of feather replacement. Deposition of protein as keratins ~~can~~ equal ~~one-~~quarter or more of the total protein mass of the bird (*Newton, 1968*; *Murphy & Taruscio, 1995*; *Roman et al., 2009*). However, ~~as well as~~ playing a role in ~~plumage replacement~~, plasma proteins ~~perform~~ a variety of immunological and transport ~~duties~~ and are important indicators of nutritional state and health (*Jenni-Eiermann & Jenni, 1996*). Plasma proteins also carry a range of metabolites. Reduction of total protein content is an indicator of many pathological changes (malnutrition), as proteins contribute to a pool of amino acids for protein synthesis and can act as a source of energy.

Similar to the present study, *Dolnik & Gavrilov* (*1979*) found total protein level to increase in the initial state of moulting, which was associated with much more intensive synthesis of protein as material for new feather production. This initial rise was followed by a decrease over the next stages. Similar ~~findings have been made~~ in ~~a number of~~ other bird species, with decreases in total protein content observed during moult~~ing~~ in sea birds (*Work, 1996*), passerines (*Newton, 1968*; *DeGraw & Kern, 1985*) and ~~a~~nseriforms (*Driver, 1981*; *Roman et al., 2009*). In waterfowl, accumulation of muscle protein occurred simultaneously with the growth of new wing feathers (*Ankney, 1984*). Other studies show that the level of total protein ~~is~~ significantly higher after moult~~ing~~ than during feather replacement (*Thompson & Drobney, 1996*). Nevertheless *Ghebremeskel et al.* (*1989*) found total plasma protein to be significantly lower in the post-moult than the pre-moult stage in rockhopper *Eudyptes crestatus* and Magellanic penguins *Spheniscus magellanicus*. ~~Differentiation~~ in protein level ~~can be seen between species,~~ and this may result from variations in the supply of amino acids and energy. Most species rely mostly on their diet to meet the growing demand for protein during moulting, but some birds, such as penguins, use endogenous nutrients to synthesize feathers (*Cherel, Charrassin & Challet, 1994*). While it remains unknown whether the common snipe primarily use endogenous or exogenous nutrients for feather synthesis, it ~~has been~~ found that snipe depend on endogenous energy from adipocyte cells during moult period (*Minias et al., 2010*). The ~~falling~~ levels of total protein observed in blood serum are believed to occur as a result of protein accumulation in the muscles and feathers ~~while~~ moult~~ing~~ and in response to less intensive synthesis in the liver; the protein requirement is also greater at the beginning of the moulting period than at the end (*Murphy & King, 1984*). In an advanced state of feather replacement, some proteins ~~delivered~~ with food could be catabolized ~~for~~ amino acids and keto acids, and then used primarily as energy or for fatty acid ~~synthesis~~ (*Artacho et al., 2007*).

Plasma triglyceride level is a well-known indicator of malnutrition or fasting, and the level ~~has been found to~~ decrease rapidly~~,~~ even during overnight fasting (e.g. *Jenni-Eiermann & Jenni, 1996*; *Jenni & Schwilch, 2001*; *Jenni-Eiermann, Jenni & Piersma, 2002*). ~~In the present study,~~ plasma triglyceride levels ~~were found to significantly~~ decrease ~~over the course of~~ moult~~ing. This ~~is consistent with the previous findings ~~showing~~ that ~~the~~ fat reserves of snipe decreased by ~~approximately~~ 50% between the initial stage and the end of the advanced stage of the post-juvenile moult (*Minias et al., 2010*). The ~~falling~~ plasma triglyceride level observed ~~over the course of the~~ moult is probably an indicator of increasing problems with food supply. To ~~compensate for~~ energy demand, snipe rely on their fat reserves and probably catabolised protein obtained from dietary sources. ~~It is known that~~ birds catabolise fat reserves to compensate for energy deficiencies in food intake and moult~~ing~~ is a highly demanding energetic process (*Jenni-Eiermann & Jenni 1996*; *Klasing 1998*; *Jenni & Schwilch, 2001*; *Jenni-Eiermann, Jenni & Piersma, 2002*; *Artacho et al., 2007*). For example, ~~considerable energy usage has been observed in~~ moulting chaffinches *Fringilla coelebs* (*Dolnik & Gavrilov, 1979*). A number of studies ~~have found~~ metabolized energy ~~level to~~ increase during the first part of ~~the~~ moult, but then ~~fall~~ during moult~~ing~~, finally ~~settling~~ at a level below initial values upon completion (*Newton, 1968*; *Myrcha & Pinowski, 1970*; *Dolnik & Gavrilov, 1979*; *Jenni-Eiermann & Jenni, 1996*; *Artacho et al., 2007*).

In contrast to plasma triglyceride levels, ~~our findings indicate that~~ glucose concentration steadily increases from the start of the moult~~ing period~~ until ~~the~~ advanced stage. Glucose is the main ~~metabolite~~ of the carbohydrate metabolism and is obtained from the diet. Some studies indicate that better body condition is associated with increased glucose level (*Minias & Kaczmarek, 2013*). ~~It is also known that a falling~~ glucose level in birds could be an indicator of short fasting periods (*Jenni-Eiermann & Jenni, 1994, 1997),* however, in some species plasma glucose concentration ~~has been reported to~~ negatively correlate with body mass (*Kaliński et al., 2014*). During starvation, glucose is produced from stored glycerol and amino acids or by gluconeogenesis (*Herzberg et al., 1988*) and may also occur with increased glucocorticoids ~~as stress-induced hyperglycaemia~~ (*Remage-Healey & Romero, 2001*).

There are two ~~likely~~ explanations for the increasing levels of plasma glucose ~~over the course of~~ moult in the common snipe. First, snipe use a ~~considerable amount of~~ their fat reserves ~~in the final stages~~ of moult~~ing~~ (*Minias et al., 2010*), which is supported by decreasing plasma triglyceride concentrations, ~~as shown in this study.~~ Thus, the increasing glucose level may ~~occur as~~ an effect of the catabolism of triglycerides~~, which are~~ stored in adipocyte cells. During lipolysis, the triglycerides are split into monoacylglycerol units which are then converted to free fatty acids and glycerol. Glycerol can be then ~~converted~~ into glucose by conversion into dihydroxyacetone phosphate and then into glyceraldehyde 3-phosphate~~;~~ the process of gluconeogenesis (*Herzberg et al., 1988*). Consequently, we cannot exclude that the increased catabolism of fat may lead to higher plasma glucose levels in the advanced stage of moult.

~~A~~ second reason for ~~rise~~ in glucose levels may be an increase in the levels of corticosteroids, ~~as these~~ can ~~raise~~ the level of glucose and ~~increase~~ the rate of protein breakdown. Glucocorticoids increase glucose level by working as an insulin antagonist, and stimulating lipolysis in adipose tissue, resulting in an increase in plasma free fatty acids and glycerol levels (*Remage-Healey & Romero, 2001*). This scenario seems ~~likely,~~ as migrating birds ~~are known to~~ express higher levels of baseline corticosterone that may be related to the development or maintenance of migratory condition (*Ramenofsky, Piersma & Jukema, 1995*; *Holberton, 1999*). This may also explain why moult-related glucose level ~~increase has not been~~ recorded in the studies on blood biochemistry of moulting birds ~~kept~~ in captivity (*Romero & Remage-Healey, 2000*).

In conclusion, our study indicates ~~considerable~~ changes in blood plasma biochemistry during the post-juvenile moult in the common snipe. ~~We believe that t~~hese nutritional and physiological costs of moult~~ing could be among~~ the primary determinants ~~of~~ the low pace of migration in this species. The common snipe ~~is known to~~ minimize energy expenditure during autumn migration, a strategy characterized by low refuelling rates, accumulation of small fat reserves, and short ~~migratory flights with~~ a large number of stopover sites (*Włodarczyk et al., 2007*). Our results ~~may~~ suggest that ~~considerable~~ physiological changes associated with moult and a trade-off in energy allocation between moult and migration may prevent the common snipe from adopting migration strategy of energetically-expensive long-distance migratory flights.

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Competing Interests

The authors declare that they have no competing interests.

Author Contribution

Patrycja Podlaszczuk performed the experiments, contributed materials/analysis tools, wrote the paper, prepared the figures or/and tables, reviewed drafts of the paper.

Radosław Włodarczyk performed the experiments, reviewed drafts of the paper.

Tomasz Janiszewski designed the experiments, performed the experiments, reviewed drafts of the paper.

Krzysztof Kaczmarek designed the experiments, performed the experiments, reviewed drafts of the paper.

Piotr Minias designed the experiments, performed the experiments, analyzed the data, contributed materials/analysis tools, reviewed drafts of the paper.

Data Deposition

The raw data has been supplied as a Supplemental Dataset.

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Table 1 ~~Sample sizes~~ for different plasma parameters ~~of young common snipe in relation to the stage~~ of post-juvenile moult.

Plasma parameter	Moult stage			Total
	Before	Initial	Advanced	
Total protein	299	171	58	528
Triglycerides	267	146	49	462
Glucose	213	103	37	353
Albumin	191	96	35	322
Uric acid	75	37	21	133

Table 2 ~~Plasma~~ total protein concentration in relation to post-juvenile moult and confounding variables in young common snipe migrating through central Poland. Reduced model $R^2 = 0.41$ ($F_{10,517} = 35.85$, $p < 0.001$).

~~Predictor~~	F	P
Full model		
Moult stage	**3.46**	**0.032**
Sex	2.30	0.13
Year	**7.47**	**<0.001**
Date	1.51	0.22
Hour	**9.68**	**0.002**
Reduced model		
Moult stage	**3.13**	**0.045**
Sex	2.12	0.15
Year	**7.54**	**<0.001**
Hour	**9.14**	**0.003**

Table 3 Plasma glucose concentration in relation to post-juvenile moult and confounding variables in young common snipe migrating through central Poland. Reduced model $R^2 = 0.16$ ($F_{8,344} = 7.96$, $p < 0.001$).

~~Predictor~~	F	p
Full model		
Moult stage	**3.60**	**0.028**
Sex	0.41	0.52
Year	**14.21**	**< 0.001**
Date	**4.59**	**0.033**
Hour	3.23	0.07
Reduced model		
Moult stage	**3.74**	**0.025**
Year	**14.35**	**< 0.001**
Date	**4.82**	**0.029**
Hour	3.38	0.07

Table 4 Plasma concentrations of albumin, triglycerides, and uric acid in relation to post-juvenile moult and confounding variables in young common snipe migrating through central Poland.

~~Predictor~~	Albumin		Triglycerides		Uric acid	
	F	p	F	p	F	p
Moult stage	1.42	0.24	0.12	0.89	0.44	0.65
Sex	1.58	0.21	0.09	0.77	0.01	0.92
Year	**9.01**	**< 0.001**	**10.23**	**< 0.001**	0.30	0.58
Date	0.02	0.88	0.27	0.60	**22.03**	**< 0.001**
Hour	**15.77**	**< 0.001**	**3.87**	**0.049**	2.50	0.12

Figure 1 The extent of the post-juvenile moult in wing and tail of the common snipe. Plumage areas ~~bounded~~ by white contours~~ are moulted~~. LC – lesser wing coverts, MC – median wing coverts, TR – tertials, R – rectrices.

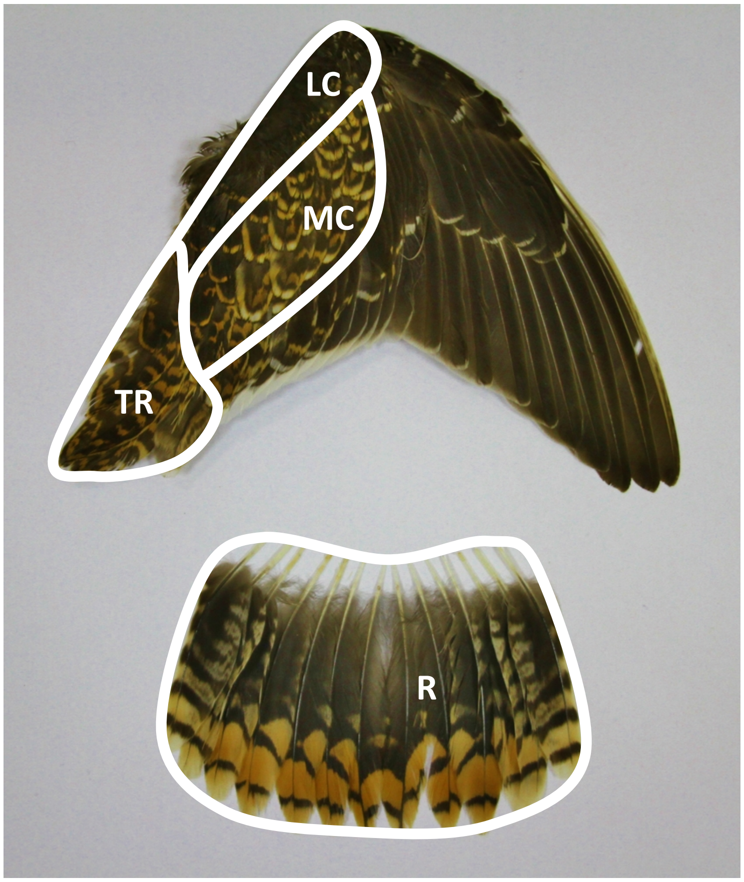
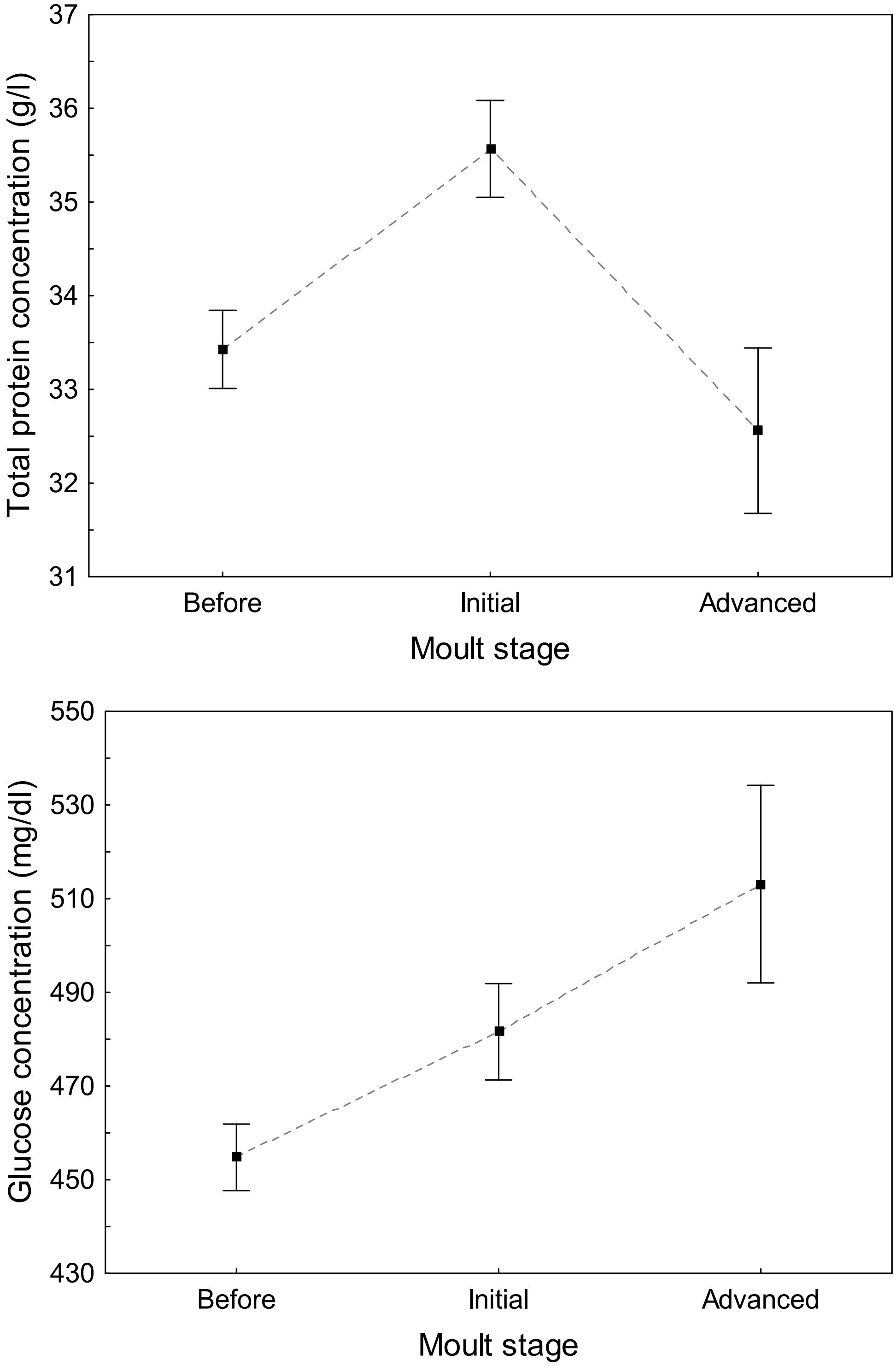


Figure 2 Changes in plasma concentrations of total protein (a) and glucose (b) between the consecutive stages of post-juvenile moult in young common snipe migrating through central Poland. Means ± SE are presented.



412 **Figure 3** Changes in plasma triglyceride concentration with moult score of young common snipe in the
413 advanced stage of post-juvenile moult.