

White Wagtails *Motacilla alba* showing extensive post-juvenile moult are more stressed

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Young individuals of many passerines undergo a partial moult and replace most of their body feathers and a variable number of coverts and minor wing feathers. In many species, this moult generates perceptible coloration differences, which may act as status signals. This study analyses how the extent of partial moult is related to different estimators of condition. A total of 43 young White Wagtails *Motacilla alba* caught in an urban roost in the city of Seville were analysed. The extent of their partial moult was positively correlated to the heterophil-lymphocyte ratio, but not to the abundance of leukocytes or to body mass. Individuals with more adult-like plumage may be exposed to higher stress due to the aggressiveness of territorial adults. Consequently, the increased heterophil-lymphocyte ratio found in the study is probably a consequence of the extent of moult rather than an explanation of intraspecific variation in the extent of moult.

Key words: partial moult, wagtail, stress, heterophil, lymphocyte, H/L

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INTRODUCTION

The functions of avian plumage in animal communication have attracted the attention of evolutionary biologists for many years (Darwin 1871, Butcher & Rohwer 1989, Zahavi & Zahavi 1997). Plumage characteristics may convey information such as (1) the capacity to care for young (reviewed in Andersson 1994), (2) the ability to escape from predators (Papeschi & Dessi-Fulgheri 2003), (3) genetic quality (Fitze *et al.* 2003, McGraw & Ardia 2003) or (4) social status (Badyaev & Ghalambor 1998, Senar *et al.* 2000, Velando *et al.* 2001). Additionally, many plumage characteristics have been shown to act as reliable

indicators of health status (McGraw *et al.* 2002, Papeschi & Dessi-Fulgheri 2003), parasite load in the blood (Merilä *et al.* 1999, Figuerola *et al.* 1999), ectoparasite abundance (Doucet & Montgomerie 2003) and the functioning of the immune system (Lindström & Lundström 2000, Saks *et al.* 2003).

Juvenile birds of many species present drab plumages, usually similar to those of females. Although different functions have been proposed for this delayed maturation of plumage, the most widely accepted hypothesis suggests that it may reduce aggression from adults (McDonald 1993, Muehter *et al.* 1997). Many passerines perform a partial post-juvenile moult with great intraspecific

variation in extent (Gosler 1991, Smith 1992, Jenni & Winkler 1994). Although this partial moult has been shown to be relevant in social communication (Senar *et al.* 1998b), little is known about the factors that influence its extent. Patterns of post-juvenile moult have been studied in some passerine species which showed that there is a correlation between the extent of moult among most feather tracks (Jenni & Winkler 1994, Deviche 2000). Furthermore, the extent of moult is related to the intensity of colour (Jenni & Winkler 1994). Intraspecific differences in the extent of partial moult are little studied and are mainly considered to be dependent on energetic or time constraints (Jenni & Winkler 1994). This point of view is based on the assumption that partial moult is 'the best of a bad job', that is, individuals aim to moult as much of their plumage as they can. However, partial moult generates age-related patterns of coloration that seem to have implications for sexual selection and social behaviour (Savalli 1995) and, consequently, the optimal extent of moult may depend on individual condition.

Numerous condition and health indices have been used in ornithology (Hörak *et al.* 2002). Size-corrected body mass is commonly used as an estimator of condition (Gosler *et al.* 1998); other indices, based mainly on leukocyte variables, are also good indicators of physiological/health status (Ots *et al.* 1998). Leukocytes are important components of the immune system, becoming altered in quantity and composition when an organism is exposed to pathogens or stress (Campbell 1995). Consequently, values for the total number of leukocytes (TLC) have been interpreted as an indication of an individual's current investment in immune defence (Ots *et al.* 1998, Nunn *et al.* 2000). In particular, high TLC values are characteristic of the inflammatory processes that occur in response to microbial infections and injuries (Hörak *et al.* 2002, Thrall *et al.* 2003). Heterophils and lymphocytes are the most numerous cellular lines in the immune system and they are usually responsible for the change in the total number of leukocytes. Heterophils act as the first defence barrier (Thrall *et al.* 2003), whereas lymphocytes lead

the specific defence in the immune system. Given that heterophils and lymphocytes are found so profusely in immune systems, their ratio (H/L) has been widely used as an estimator of stress in birds (Totzke *et al.* 1999, Thrall *et al.* 2003). In avian species, stress generates a decrease in circulating lymphocytes and an increase in circulating heterophils (Davison *et al.* 1983), leading thus to an increase in the H/L ratio. H/L acts as a reliable indicator of stress in passerines (Groombridge *et al.* 2003). Furthermore, in birds H/L is a useful measurement of stress caused by long-term changes in the environment, social rank, or the action of chronic stressors (Gross & Siegel 1983, Davis *et al.* 2000), and is even more useful than a single measurement of plasma corticosterone levels (Vleck *et al.* 2000). It is therefore a good indicator of health for use in behavioural studies in free-ranging birds (Gross & Siegel 1983).

The White Wagtail *Motacilla alba* is a partial migrant passerine which winters in Iberia in large numbers. At the end of summer, first-year birds replace part of their juvenile plumage and show great inter-individual variation in the extent of moult. This species shows both flocking and territorial behaviour during winter (Davies 1976): while some individuals (mainly adult males) defend feeding territories, most juveniles and adult females form larger flocks (Zahavi 1971, Davies 1982). Individuals with young-looking plumage are allowed by owners to feed in their territory (Davies 1981a, b), a fact that suggests that partial post-juvenile moult may play a role in communication in this species. In this study, the relationship between the extent of moult and different estimates of body condition in juvenile White Wagtails is analysed as a means of testing the hypothesis that moult extent is related to individual health status.

MATERIAL AND METHODS

Fieldwork and measurements

A total of 43 young White Wagtails were trapped in an urban roost in the city of Seville (37°23'N,

5°57'W) in November 2003. The wagtails roost in several types of ornamental trees between 5 and 10 m above the ground; the total number of wagtails using the roost has been estimated at over 500 000 birds (Vázquez *et al.* 2001). Birds were caught between 18:00 and 20:00 h in Japanese mist nests placed 8 m above ground level between the trees where the birds spent the night. For each individual, wing (to the nearest 0.5 mm, mean \pm SE: 88.35 ± 0.4) and tarsus length (to the nearest 0.1 mm, 23.32 ± 0.16) were measured. Body mass was measured with a digital scale (to the nearest 0.1 g, 21.51 ± 0.23) and age was determined from plumage characteristics (Svensson 1992). Subsequently, the number of moulted greater wing coverts (GC) on the right wing was counted in all the individuals. Given that the extent of post-juvenile moult in White Wagtails is correlated with the number of moulted GC and most of the rest of feather tracks (Jenni & Winkler 1994), this measurement was used as an indicator of the global moult appearance. All measurements were made by the same person (NV).

Sampling protocol

After measurement, a 0.25 ml sample of blood was taken from the jugular vein with 29 G sterile insulin syringes. A drop of blood was used to prepare a smear on a microscopy slide (Bennett 1970), which was air-dried and properly fixed and stained using Diff-Quick solution. The rest of the blood sample was placed into a vial without anticoagulant and then after several hours centrifuged for 10 minutes at 6000 rpm in an Eppendorf Minispin centrifuge to separate serum from cells. Both sera and cells were kept frozen at -20° C until subsequent analysis. All data was collected in the hour after capture and the time each bird was handled (less than five minutes) was almost the same in all cases, and so no important differences in circulating heterophils should have been provoked.

Molecular sexing

The cellular fraction of the blood sample, which was obtained without anti-coagulants, was used to sex the birds. Sex was determined from blood cell

DNA, using polymerase chain reaction (PCR) amplification of the CHD genes (Ellegren 1996, Griffiths *et al.* 1998). All the birds were successfully sexed by this method; in 98% of individuals these results agreed with sexing in the field based on plumage characteristics.

Blood smear analysis

TLC was estimated by the method of Lane (1996), that is, by counting the number of leukocytes on twenty 400 \times light microscope monolayer fields and selecting those with a similar cell density. The total number of white blood cells per microliter was calculated by multiplying this value by 100. This method of estimation is well correlated with estimates obtained by counting in chambers (Wiskott 2002). For each smear, the cellular type (heterophils, lymphocytes, eosinophils, monocytes and basophils) of 100 leukocytes was identified according to Campbell (1995), and the H/L was calculated as the ratio of the numbers of heterophils and lymphocytes (Fig. 1). Blood parasites (intraerythrocytic protozoa and circulating protozoa and nematodes) were searched for at low (100 \times ; 5 min), medium (400 \times ; 10 min) and high (1000 \times ; 10 min) magnification (Deviche *et al.*

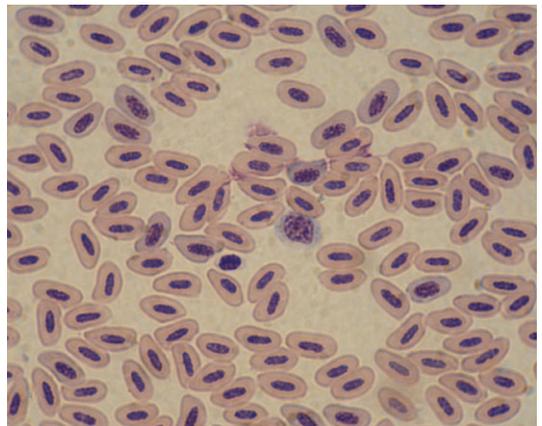


Figure 1. Blood smear of White Wagtail showing abundant erythrocytes and a single lymphocyte (in the middle of this photo by G. López). Stress was estimated from the ratio of numbers of heterophils (not in this picture) and lymphocytes.

2001). In the case of intraerythrocytic protozoa infection, a total of 1500 erythrocytes were counted, getting the genus identification and the intensity of infection. Only one individual (2.3%) was infected by the intraerythrocytic haematozoan *Haemoproteus* sp., with an infection intensity of 0.03% of erythrocytes; the exclusion of this individual from subsequent analyses had no qualitative effect on the results. The repeatability of leucocyte variables was estimated by counting the smears of ten individuals twice and subsequently calculating the intra-class correlation (Lessells & Boag 1987). Repeatabilities were very high for both TLC ($r = 0.95$, $F_{9,10} = 35.31$, $P < 0.0001$) and H/L ($r = 0.90$, $F_{9,10} = 18.87$, $P < 0.0001$).

Statistical analyses

In order to discover the effects that the extent of partial moult could have on different condition indices, a MANOVA was used with TLC, H/L and body condition as dependent variables, sex as a factor and number of moulted GCs as a covariate; the interaction between sex and number of moulted GCs was also included. We followed a stepwise backwards selection procedure until all the independent variables increased significantly the fit of the model. We chose tarsus instead of wing length as a measure to standardise body mass for bird size because of its independence from moult processes; the tarsus grows in the nest long before the post-juvenile moult takes place. Nevertheless, results did not change qualitatively when using body condition estimated in relation to wing length. Body condition was estimated as the result of the regression of body mass on tarsus length ($r^2 = 0.44$). We used the Shapiro-Wilk test to test the fit of the different variables to a normal distribution. Body condition, TLC and log transformed H/L were normally distributed. The distribution of the number of moulted GCs could not be normalised and analyses were done using ranked values (see Conover & Iman 1981). Ranks were assigned to each value as a consecutive number from 1 to 43, from lower to higher values, and whenever identical values occurred we assigned the average of the ranks to each one.

RESULTS

The number of moulted GC did not differ between males and females (mean \pm SE: 6.56 ± 0.47 ; males: 7.67 ± 0.41 , $n = 15$; females: 5.96 ± 0.66 , $n = 28$; $t_{41} = 1.29$, $p = 0.20$). An overall relationship between the number of moulted GCs and the indices of condition ($F_{3,35} = 5.25$, $P = 0.004$) was found. There were no significant effects of sex ($F_{3,34} = 0.6$, $P = 0.62$) or of the interaction between sex and the number of moulted GCs ($F_{3,33} = 1.28$, $P = 0.29$). Univariate *a posteriori* tests suggest that H/L (1.63 ± 1.3) was significantly correlated with the number of moulted GCs ($r^2 = 0.243$, $F_{1,37} = 12.01$, $P = 0.01$, Fig. 2), which indicates that individuals with a larger extent of post-juvenile moult had an increased presence of heterophils in relation to lymphocytes. The number of moulted GCs was not significantly related to TLC ($F_{1,37} = 3.06$, $P = 0.09$) or to body condition ($F_{1,37} = 0.78$, $P = 0.38$).

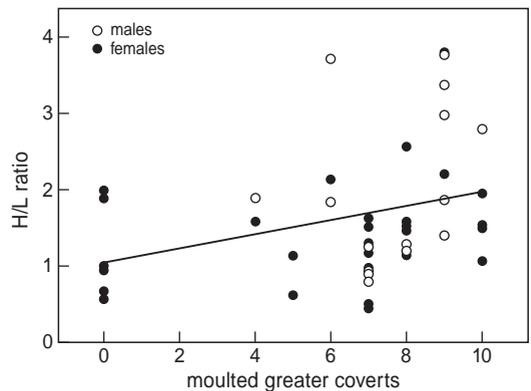


Figure 2. Relationship between H/L and the number of moulted greater coverts in male and female White Wagtails.

DISCUSSION

In this study a correlation was found between the extent of partial moult and H/L. Interestingly, this correlation was positive and contrary to the

hypothesis that the individuals in best condition invest more in moulting. There are at least two possible explanations for this correlation between an indicator of stress and the extent of partial post-juvenile moult. Firstly, individuals in worse condition may invest a relatively greater amount of energy in moulting. Secondly, individuals with more extended moult suffer increased levels of stress during the winter. Contrary to the first explanation, feather moult is directly related to the amount of resources available (Grubb 1991, Carrascal *et al.* 1998). On the other hand, Senar *et al.* (1998a, b) demonstrated that juvenile Siskins *Carduelis spinus* with adult-like plumage received greater aggression from adults than those with delayed moult. As in Siskins, the demonstrated higher permissiveness of territorial adult White Wagtails towards juveniles (Davies 1981b) could explain the increased levels of stress that individuals with more complete moults seem to suffer, since H/L has been shown to correlate better with social stress than with any other estimator (Gross & Siegel 1983). These data suggest that the extent of post-juvenile moult may not only be regulated by energetic or time constraints, but also by social interactions, which could greatly reduce the potential benefits of larger moult extension. Several melanin-derived badges of status are under social control and birds displaying experimentally enlarged badges are exposed to increased levels of aggression and/or mortality (Senar *et al.* 1993, Veiga 1993). Since H/L responds rapidly to food deprivation (Gross & Siegel 1986), both social rank stress and alimentary stress generated by adult intolerance could be responsible for increases in the H/L. Nevertheless, the negative effect of advanced partial moult derived from stress may be the cost paid for obtaining benefits during the breeding season. Accordingly, females prefer to pair with adult individuals rather than with juvenile-looking ones (Samson 1976, Middleton 1979). Consequently, the extent of moult in juveniles could suffer a trade-off between stress

derived from social interactions during the winter and pairing success in the next breeding season.

Under this scenario, the correlation between stress and the extent of moult should be negative or not significant at the time of moult. Unfortunately, similar data during the start of moult could not be obtained from our study area because birds come from a variety of different European breeding areas (Belgium, Germany, The Netherlands, Czech Republic and United Kingdom, according to ringing recoveries and subspecies assignment). Nonetheless, a similar study on Siskins showed that the correlation between the extent of moult and body condition was positive just after moult, but negative at the end of the winter (Senar *et al.* 1998b).

The other two estimators, TLC and body mass, have been described as reliable indicators of condition in passerines (Ots *et al.* 1998, Hōrak *et al.* 2002), although no correlation between these factors and the extent of partial moult was found in our study. In the case of TLC, it is known that interstitial liquid variations may strongly alter this value (Campbell 1995, Thrall *et al.* 2003) and that numerous factors may modify the interstitial liquid volume (Sturkie 1986). Another possibility could be the proliferation of certain cellular lines due to injuries, parasites or infections (Campbell 1995). Body mass is also affected by many factors and this could explain the lack of correlation with other variables. For instance, current nutritional status, distances covered to spend the night in the roost, or exposure during the day to different levels of predator abundance (Adriaensen *et al.* 1998, Gosler 1996, Vázquez *et al.* 2001) could be responsible for these changes.

In conclusion, our results suggest that intraspecific variation in the extent of post-juvenile moult is related to health status well after moult completion. Further understanding on how social interactions may affect the costs of moult should clarify the cost-benefit balance faced by juvenile passerines.

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SAMENVATTING

Veel jonge zangvogels ruien voor de winter een deel van de lichaamsveren. De mate waarin dit gebeurt, verschilt sterk van individu tot individu – ook binnen een soort – zonder dat bekend is wat deze variatie veroorzaakt en wat de gevolgen ervan zijn. Er wordt wel verondersteld dat de ruitoestand in de winter te maken heeft met beperkingen in beschikbare energie of tijd tijdens de rui. Individuen die toegang hebben tot meer of beter voedsel, zouden minder last van stress hebben en daardoor in staat zijn meer veren te vervangen dan individuen die in minder gunstige omstandigheden leven. Als dit zo is, dan zou de ruitoestand van jonge vogels een negatief verband moeten laten zien met de mate waarin ze in stress verke-

ren. Resultaten in de vogelwereld zijn niet eenduidig, want onderzoekers hebben zowel positieve als negatieve trends gevonden.

Om meer duidelijkheid omtrent dit probleem te scheppen vingen de auteurs overwinterende Witte Kwikstaarten *Motacilla alba* op een grote slaappleaats in Sevilla, Zuid-Spanje. Daartoe werden mistnetten op 8 m hoogte tussen de bomen gespannen. Van de gevangen vogels werden biometrische gegevens verzameld en het aantal geruide grote dekveren werd bepaald als maat voor de ruitoestand. Verder werden bloedmonsters genomen om de aantallen te bepalen van witte bloedlichaampjes, waaronder die van heterofielen en lymfocyten. De verhouding van deze twee typen cellen (H/L) wordt wel gebruikt als maat voor de stress waaronder dieren leven (hogere ratio meer stress). In de Witte Kwikstaarten bestond een positief verband tussen de mate van rui en de H/L verhouding, terwijl er geen verband aantoonbaar was tussen de ruitoestand en het totaal aantal witte bloedlichaampjes of het gewicht van de vogel. De verklaring voor de waarnemingen wordt gezocht in het effect van de ruitoestand van de dieren op hun sociale status. Jonge vogels die nog het meest het juveniele kleed hebben, worden het minst door oude vogels lastig gevallen. Jonge vogels die in de winter al het adulte kleed hebben, profiteren daar mogelijk van als ze terugkeren in het broedgebied (onder andere Nederland), maar de prijs daarvoor is een stressvol bestaan in de winter. (CB)

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