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The carotenoid-based red cap of the Middle Spotted Woodpecker *Dendrocopos medius* reflects individual quality and territory size

KONRAD LENIOWSKI[1]* & EWA WĘGRZYN[2]
[1]*Departament of Zoology, University of Rzeszów, Rzeszów, Poland*
[2]*Faculty of Tourism and Health Sciences, University of Information Technology and Management in Rzeszów, Rzeszów, Poland*

Carotenoid-based plumage ornaments have the potential to signal individual condition and health in many species of birds. However, very little is known about the function of red plumage in woodpeckers. We assessed whether the red cap displayed by both male and female Middle Spotted Woodpeckers reflects individual quality, finding that the size of the cap is sex-dependent, whereas the brightness of the cap correlates with the body condition of an individual. Furthermore, birds with brighter caps had larger clutches, suggesting that cap coloration may be an honest signal of parental quality in woodpeckers. Interestingly, more colourful individuals also occupied smaller territories, suggesting that territory size and territory quality may be inversely related in the Middle Spotted Woodpecker.

Keywords: body condition, plumage, visual signalling.

The evolution of conspicuous plumage in birds has intrigued biologists for decades. The primary focus centres on assessing the mechanisms of maintenance of colourful feather ornaments as honest signals of quality (Zahavi & Zahavi 1997). Several studies have demonstrated that the intensity of plumage colour signals conveys information about individual condition, health and parasite resistance (e.g. Hamilton & Zuk 1982, Andersson 1994). Particular attention has been paid to red–yellow carotenoid-based ornaments, which are subject to female preference in many bird species (Hill 1999, 2002, Hill & McGraw 2006). It has been demonstrated that mating with brighter coloured males provides females with both direct and indirect benefits (Ligon 1999). Thus, carotenoid-based ornaments are thought to function as honest condition-dependent signals of phenotypic and/or genetic quality of an individual. The intensity of red coloration in woodpeckers depends on the quantity of carotenoids ingested at the time of moult (Test 1969). Thus, the intensity of red plumage colours may be an indicator of individual health and foraging ability, but could also signal greater potential reproductive success, as individuals in better condition are likely to be more effective breeders. Females in good condition may lay larger clutches (Gladbach *et al.* 2010), whereas males may invest more in feeding young (Germain *et al.* 2010), thereby fathering more offspring (Préault *et al.* 2005).

There is considerable evidence that carotenoid-based ornaments are costly to produce (Hill 2002). The costs comprise absorption, metabolic conversion, transportation and incorporation of pigments (Hill 2000, McGraw *et al.* 2005). As a result, an individual in poorer condition acquires fewer carotenoids than its superior conspecifics. Additionally, carotenoids have important antioxidant and immunostimulant properties (Møller *et al.* 2000, Blount *et al.* 2003, Stahl & Sies 2003, Sahin *et al.* 2006) and there is a trade-off between their use in biochemical processes and deposition in ornaments (Faivre *et al.* 2003, McGraw & Ardia 2003). Therefore, carotenoid-based ornaments have the potential to indicate the oxidative stress of an individual (von Schantz *et al.* 1999).

*Corresponding author.
Email: songbird.konrad@gmail.com

According to the parasite-mediated sexual selection hypothesis (Hamilton & Zuk 1982), the intensity of red–yellow coloration should be particularly sensitive to parasite load (Lozano 1994, Martinez-Padilla *et al.* 2007). Thus, the intensity of carotenoid-based plumage coloration may indicate both the condition of an individual and its genetic resistance to pathogens and/or parasites.

Very little is known about the function of the red cap that is present in many woodpecker species. This trait is likely to be based on a carotenoid pigment because chemical analysis of carotenoid composition in some woodpecker species has demonstrated that red feathers of true woodpeckers (Picinae) contained predominantly 4-oxo-carotenoids, particularly asthaxanthin and α-doradexanthin (Stradi *et al.* 1998). Furthermore, the reflectance spectrum curve of the red cap of the Middle Spotted Woodpecker *Dendrocopos medius* is characteristic of carotenoid pigments (Fig. 1; Toral *et al.* 2008). The only study to date of the red plumage in the Middle Spotted Woodpecker concerned differences in cap length between males and females (Pasinelli 2000). In contrast to numerous studies on the signalling function of red and yellow plumage in songbirds, there has been no such research conducted on woodpeckers, although red feathers are prominent in several genera. As Passeriformes and Piciformes are not sister taxa (Hackett *et al.* 2008), it remains to be determined whether red plumage plays a similar signalling or distinct function in both taxa. The aim of our study was to test the relationship between the size and colour of the red cap in the Middle Spotted Woodpecker and its correlation with body condition, breeding success and territory size.

METHODS

The Middle Spotted Woodpecker is a medium-sized woodpecker (20–22 cm long) of the Western Palaearctic that inhabits deciduous forest, especially areas with old oaks *Quercus*, hornbeams *Carpinus* and elms *Ulmus*, as well as a patchwork of clearings, pasture and dense woodland (Pasinelli 2000, 2003). It is sedentary, socially monogamous (Michalek & Winkler 2001) and territorial in spring (Pasinelli *et al.* 2001). Both parents share breeding duties (Michalek & Winkler 2001). Each year they excavate a new cavity and raise a single brood (Pasinelli 2001, 2003).

The upperparts of Middle Spotted Woodpeckers are predominantly black with white oval wing patches and white barring on the wings. The underparts are white with a reddish area under the tail. A relatively large red crown is characteristic of both males and females (Fig. 2) but is a little

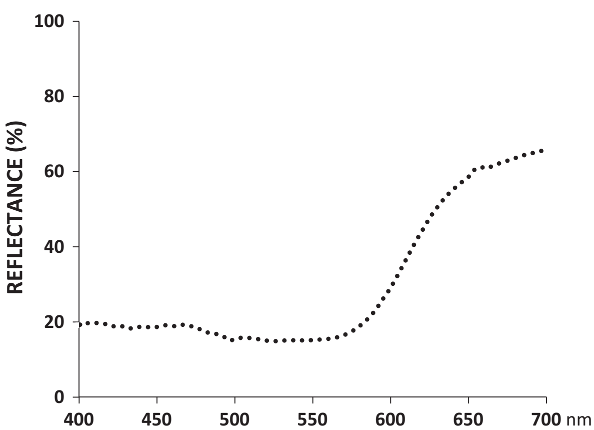

Figure 1. Spectral reflectance curve of the red cap of the Middle Spotted Woodpecker.

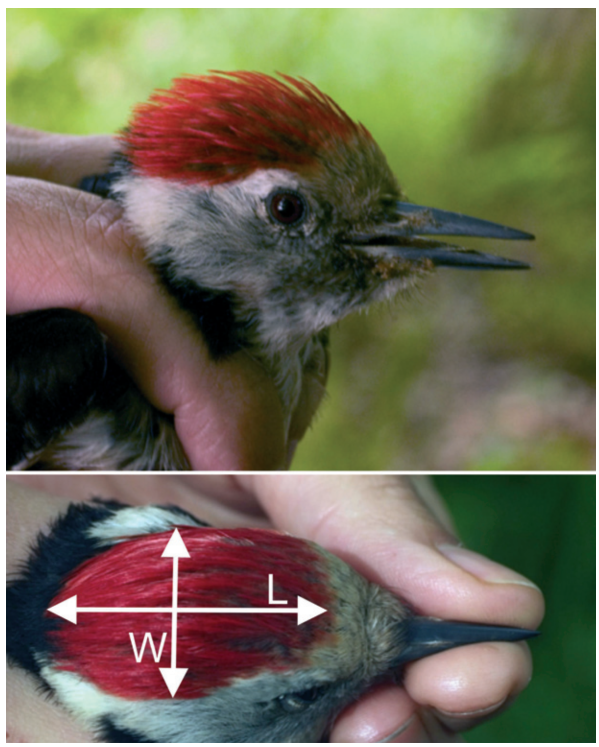

Figure 2. A photograph of the red cap of the Middle Spotted Woodpecker.

longer in males (Pasinelli 2000). No other differences between the sexes have been documented.

Study area

The study was conducted in the riverine forest of Warta River Valley in Central Poland near Czeszewo (52°09′N, 17°31′E) from 2009 to 2011. The study plot consists of 222 ha of woodland (with trees of the genera *Quercus*, *Fraxinus*, *Ulmus*, *Fraxino* and *Ulmetum*) in flooded areas, and forest (of *Quercus*, *Carpinus*, *Stallario* and *Carpinetum*) on higher lying areas and in old riverbeds and meadows. The whole study area, of which about 40% is covered by mature, near-natural forest stands, has been protected as the Czeszewski Las nature reserve since 2004.

Territory mapping

Each year at the beginning of the breeding season (March–April) the entire study area was surveyed three times to search for individuals holding territories and for breeding pairs (Kosiński & Winiecki 2003, Kosiński *et al.* 2004). To make surveys more efficient we used playback of Middle Spotted Woodpecker calls. All territories were mapped and confirmed during subsequent surveys. Nesting holes were searched for within mapped territories from mid-April to the beginning of June.

Measurements

We mist-netted, ringed and collected biometric data from the red caps of 20 individuals (10 pairs). We also collected data on the clutch and brood size of each pair. Each bird was caught once during a breeding season at the late stage of incubation or within 5 days after the nestlings hatched. Birds nesting in low cavities (up to 4 m above the ground) were caught with a regular mist-net spread near the hole. For pairs nesting in higher cavities we used a trap made of mist-net spread over a metal ring fixed to a telescopic aluminium pole. With this device (and a ladder) we were able to reach holes up to 20 m high. None of the mist-netted individuals deserted their clutch during our study.

Each individual was weighted using a Pesola balance to the nearest 0.5 g. The length of a tarsus was measured using a calliper to the nearest 0.1 mm and wing length was measured with a ruler to the nearest 1 mm: all measurements were made by the same person. There was no correlation between the time of a day when a measurement was taken and an individual's body mass ($r_s = 0.15$, $P = 0.27$, $n = 20$), so this factor was not incorporated in statistical models.

The length (L) and the width (W) of the red cap were measured with a calliper to the nearest 0.1 mm (Fig. 2). The colour of the ornament was estimated by quantifying the reflectance spectra (400–700 nm) obtained from a Photon Control SPM-002 portable spectrophotometer connected to an SPL-1DH deuterium–halogen lamp, an SPA-200U reflectance probe and SPECTROSOFT PRO v. 2.3.1. software (Lightspeed Technologies Inc., Campbell, CA, USA). Colour measurements were conducted directly on mist-netted birds. Colour was measured on three randomly selected areas within the red cap. Each area was measured five times and mean values were used in further analyses (Węgrzyn *et al.* 2011). The spectrophotometer covers reflectance spectrum from 300 to 800 nm in intervals of 1 nm. Reflectance was measured with the probe placed at a constant distance touching the feathers at 90°. Measurements were relative and referred to a standard white reference and to the dark (black standard), both calibrated before the measurement of each ornament. In further analyses we used two measures of colour intensity: mean reflectance in the red spectrum (RR) and red chroma (RC). RR was calculated as the sum of the reflectance for each nanometre in the red spectral region (580–700 nm) divided by the number of nanometres sampled (120). RR is a measure of the quantity of light reflected in the range 580–700 nm and describes colour brightness. RC was calculated as the proportion of total reflectance in the red region of the spectrum: $RC = Ref_{580–700\ nm}/Ref_{400–700\ nm}$, where $Ref_{580–700\ nm}$ is the sum of the reflectance of wavelengths between 580 and 700 nm, and $Ref_{400–700\ nm}$ is the sum of the reflectance of wavelengths between 400 and 700 nm. RC describes colour saturation.

Radiotracking and the assessment of territory size

Sixteen individuals were fitted with a 2.1-g radio-transmitter (Biotrack), which was glued onto the upperside of the base of one of the two central rectrices. The birds were followed until the chick fledged (i.e. 2–4 weeks). Tracking was conducted with a Lotec STR-1000 receiver and hand-held antennae. Each location of an individual was recorded using GPS (Garmin Colorado 300, Olathe, KS, USA). Consecutive observations of the same woodpecker were separated by at least 1 h to reduce pseudoreplication. Territory size was calculated using a fixed kernel estimator, which is considered to be the most robust of the various territory estimators (Worton 1989, Seaman & Powell 1996). We calculated the extent of the fixed kernel estimate based on 95% of the sampled locations with Home Ranger v. 1.5 software (Diehl & Larkin 1998, Walton *et al.* 2001, Matsubayashi *et al.* 2006). Due to habitat discontinuity, i.e. the presence of meadows and old riverbeds, a kernel bandwidth was chosen with a grid size of 70 × 70 m cells.

Nesting cavities were surveyed several times during each breeding season using a cavity viewer, which consisted of a micro-camera with an LED illuminator connected to a portable video recorder (Thompson Scenium, Huizhou, China). The device was fixed to a telescopic aluminium pole that enabled us to examine cavities up to 20 m high. The first survey took place after a hole was discovered and later surveys were conducted depending on the stage at which a nest was found. For holes located during egg-laying, our surveys continued until the clutch was complete and then were resumed at the predicted hatching date. Cavities discovered during incubation were monitored every 3 days until the nestlings hatched. Two of 10 nests were discovered with newly hatched nestlings, and thus we had data on clutch size for eight pairs. A second measure of breeding success of an individual was the number of its offspring aged 14–17 days (n = 10 nests). A previous study of the Middle Spotted Woodpecker demonstrated high survival rate of nestlings between 14 days of age and fledging (Kosiński *et al.* 2004, Kosiński & Ksit 2007). All surveys of breeding cavities were performed during parental feeding trips to minimize stress on birds. The last inspection of a cavity was no later than 17 days post hatching due to the risk of premature fledging of nestlings.

An individual's body condition index (BCI) was calculated on the basis of the mass of the bird as well as its wing and tarsus length (Moe *et al.* 2002). Because these variables were significantly correlated with each other ($P < 0.0001$) we used principal components analysis to calculate a single body condition score, which represented the condition of each bird. PC1 explained 75% of the variance.

It is not possible to age Middle Spotted Woodpeckers except for yearlings (K. Leniowski & E. Węgrzyn pers. obs.). All birds in our study were thus 2 years or older.

Middle Spotted Woodpeckers are highly synchronized breeders (Kosinski *et al.* 2004, Kosiński & Ksit 2007, K. Leniowski & E. Węgrzyn pers. obs.). The earliest hatching date in our study was 13 May and the latest was 15 May. Neither body mass nor reproductive success was correlated with hatching date ($r_s = -0.22$, $P = 0.18$ and $r_s = -0.29$, $P = 0.11$, respectively). Similarly, no parameter of the red cap was correlated with hatching date (cap width: $r_s = -0.12$, $P = 0.31$; cap length: $r_s = -0.07$, $P = 0.38$; RR: $r_s = 0.27$, $P = 0.12$; and RC: $r_s = -0.23$, $P = 0.16$). We took measurements of all individuals within a few days of hatching. We avoided the capture of individuals during the initial stages of incubation, as we did not want to risk clutch desertion. Parents feeding young older than 5 days did not enter a cavity for a sufficient length of time to enable us to capture them. There were no correlations between body mass and both date of measurement and the reproductive stage of an individual being measured ($r_s = -0.24$, $P = 0.16$, $n = 20$ and $r_s = -0.34$, $P = 0.07$, $n = 20$, respectively). As shown above, hatching date, measurement date and reproductive stage were not confounding factors in our study and were therefore not entered in statistical models.

Statistical analyses

We used Student's t-tests to assess whether females differed in cap parameters from males (independently of which female was paired to which male) and paired t-tests to determine whether there were significant differences in cap parameters within breeding pairs. The relationship between ornament and body condition was analysed using general linear mixed models (GLMMs) with the ornament parameters (L, W, RR and RC) of each bird as dependent variables, nest as a random factor, sex as a fixed factor and BCI as covariate. To investigate the relationship between reproductive success, body condition and ornament, we used GLMMs with clutch size and number of offspring as dependent variables, nest as a random variable, sex as a factor, and BCI and ornament parameters (L, W, RR and RC) as covariates. Differences between male and female territory size were determined using a non-parametric Mann–Whitney *U*-test. K-means cluster analysis with two cluster centres allowed us to divide all territories into two groups, small and large. Next we used a Mann–Whitney *U*-test to compare colour parameters of the red cap (RR and RC) between individuals that occupied small and large territories. The relation between cap colour and territory size was determined using Spearman's rank correlation coefficient. All analyses were conducted in SPSS 20 software (SPSS Inc., Chicago, IL, USA).

RESULTS

On average, males had significantly longer and wider caps than females (Table 1), but the colour parameters of the red cap (RR and RC) did not differ significantly between the sexes (Table 1). However, when analysing sexual differences in cap parameters within pairs of woodpeckers, females had not only smaller but also less colourful caps than their partners (Table 1).

General linear mixed models revealed that the size of the red cap (L and W) was not related to BCI, but depended on the sex of an individual (Table 2). Individuals in better condition had brighter caps irrespective of their sex (Table 2, Fig. 3). Saturation of the cap (RC) was unaffected by either BCI or sex (Table 2). GLMM analyses suggested an effect of cap brightness (RR) on clutch size and an effect of BCI on the number of offspring just before fledging (Table 3). Individuals with brighter caps had larger clutches (Fig. 4) and birds in better condition produced more offspring (Fig. 5). Both parameters of reproductive success (eggs and nestling number) were unaffected by RC.

The mean size of a male territory was 1.2 ha ± 0.53 (min = 0.41, max = 1.74, n = 8) and a female territory 0.81 ha (min = 0.35, max = 1.47, n = 8) but the difference was not statistically significant (Z = −0.87, P = 0.38). Using K-means cluster analysis with two cluster centres we divided all territories (n = 16) into small (0.59 ha ± 0.19, n = 8) and large (1.45 ± 0.16 ha, n = 8). Individuals that occupied small territories were characterized by brighter caps (RR = 0.34 ± 0.09, n = 8) than the owners of large territories (RR = 0.24 ± 0.05, n = 8; Z = −2.02, P = 0.042, n = 16). RC of a cap did not differ between birds on small and large territories (Z = −0.16, P = 0.87, n = 16). Red cap brightness was significantly and inversely correlated with territory size (r_s = −0.5, n = 16, P = 0.026; Fig. 6).

DISCUSSION

Our study indicated that the size of the red cap in the Middle Spotted Woodpecker is sex-dependent, whereas the brightness of this trait is related to individual body condition. Pasinelli (2000) also established that the red cap of the Middle Spotted Woodpecker is significantly longer in males, but did not determine whether the sex of an individual is the only factor affecting ornament size. We found that both the length and the width of a red cap in the Middle Spotted Woodpeckers are sexually dimorphic and unrelated to individual condition, whereas the brightness of the red cap may reflect individual condition. We also found that birds with brighter caps had larger clutches, suggesting that the colour of the red cap may provide an honest signal

Table 1. General (t) and within-pair (t_p) differences in the size and colour of the red cap between male (n = 10) and female (n = 10) Middle Spotted Woodpeckers.

	Females (n = 10)		Males (n = 10)		
	Mean ± sd	Min–max	Mean ± sd	Min–max	t-test (n = 20)
L (cm)	2.76 ± 0.36	2.28–3.40	3.37 ± 0.22	3.09–3.78	t = −4.63, **P < 0.001** t_p = −4.92, **P = 0.001**
W (cm)	1.86 ± 0.24	1.55–2.35	2.21 ± 0.35	1.73–2.91	t = −2.67, **P = 0.016** t_p = −3.78, **P = 0.004**
RR	0.26 ± 0.09	0.16–0.41	0.32 ± 0.10	0.19–0.45	t = −1.42, P = 0.172 t_p = −3.90, **P = 0.004**
RC	0.6 ± 0.1	0.39–0.74	0.66 ± 0.11	0.46–0.91	t = −1.27, P = 0.22 t_p = −2.30, **P = 0.047**

L, cap length; W, cap width; RR, colour brightness; RC, colour saturation. Significant P values are shown in bold.

Table 2. Results of General Linear Mixed Models testing the effects of body condition (BCI) and sex of individual on the four parameters measured from a red cap (L, W, RR, RC), *n* = 20.

	BCI			Sex			Covariance parameters	
	F	*P*	d.f.	*F*	*P*	d.f.	Estimate	se
L (cm)	0.005	0.94	17	19.29	**< 0.001**	17	0.093	0.032
W (cm)	2.44	0.137	17	5.47	**0.032**	17	0.082	0.028
RR	7.54	**0.014**	17	0.97	0.339	17	0.006	0.002
RC	1.53	0.233	17	2.37	0.142	17	0.012	0.004

L, cap length; W, cap width; RR, colour brightness; RC, colour saturation. Significant *P* values are shown in bold.

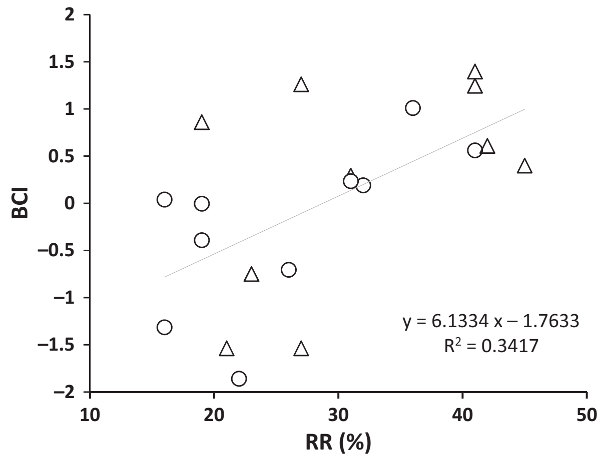

Figure 3. Relationship between cap brightness (RR) and body condition (BCI) in male (Δ) and female (○) Middle Spotted Woodpeckers.

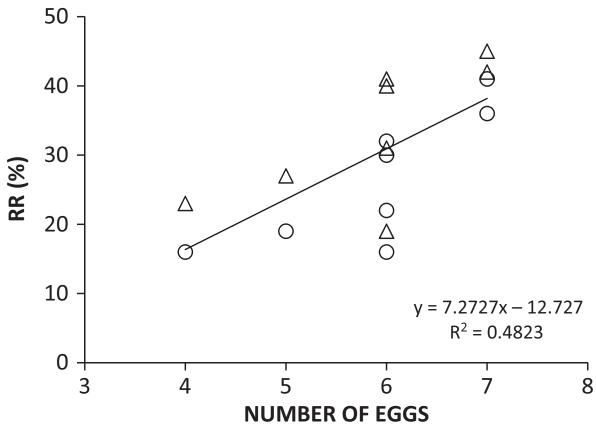

Figure 4. Relationship between cap brightness (RR) and clutch size in male (Δ) and female (○) Middle Spotted Woodpeckers.

Table 3. Results of General Linear Mixed Models testing the effects of body condition (BCI), ornament brightness (RR) and saturation (RC) on two parameters of breeding success (the number of eggs and nestlings) in Middle Spotted Woodpeckers.

	Number of eggs			Number of nestlings		
	F	*P*	*df*	*F*	*P*	*df*
BCI	0.23	0.640	12	7.27	**0.016**	16
RR	5.99	**0.031**	12	0.13	0.720	16
RC	0.43	0.524	12	3.54	0.078	16

BCI, body condition index; RR, colour brightness; RC, colour saturation.

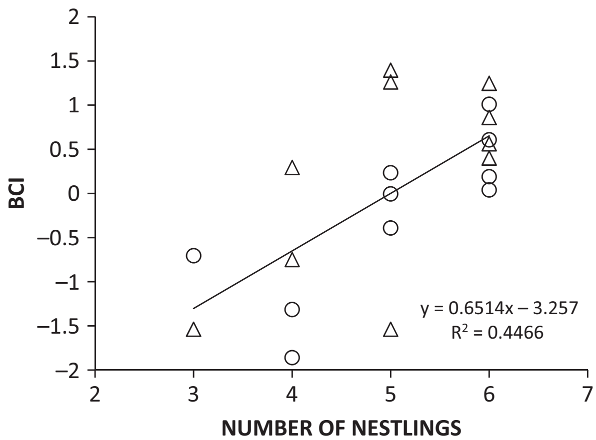

Figure 5. Relationship between individual body condition in male (Δ) and female (○) Middle Spotted Woodpeckers and the number of nestlings just before fledging.

of parental quality in woodpeckers. This is in accordance with other studies, which have demonstrated that highly ornamented females lay larger clutches (Gladbach *et al.* 2010). As high-quality females are frequently paired with superior males the relationship between the colour of the red cap and clutch size may be present for both sexes. The number of nestlings just

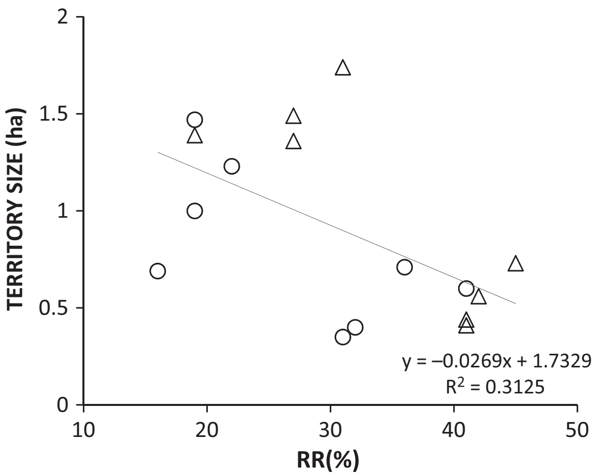

Figure 6. Relationship between cap brightness (RR) and territory size in male (Δ) and female (○) Middle Spotted Woodpeckers.

before fledging was related more to parental body condition than to the colour of the red cap. This indicates that not all aspects of reproductive success are directly associated with the brightness of the red cap. However, we cannot completely rule out the possibility that our results were confounded by the age of individuals. Nonetheless, the lack of yearlings in the study reduces the likelihood of age effects altering our results.

Our study also revealed that individuals with brighter caps occupied smaller territories. This may suggest that that the two territory traits, size and quality, may be inversely related in the studied species, a result found in other studies of woodpeckers (Pasinelli 2000, Wood *et al.* 2008). It is likely that woodpeckers increase territory size as its quality decreases, to help ensure sufficient food supplies are available. In such a scenario, individuals in better condition and with brighter caps should occupy smaller territories of higher quality.

Red chroma, which describes the saturation of colour, in our study was unrelated to sex, condition or reproductive success of an individual. Because red plumage is the result of carotenoid deposition, quantification of red chroma is frequently treated as a measure of the relative accumulation of carotenoids in feathers (e.g. Saks *et al.* 2003, Quesada & Senar 2006, Shawkey *et al.* 2006). Although some studies confirmed the relationship between chroma and the amount of carotenoids in the plumage (Isaksson & Andersson 2008), the correlation holds only in the case of unsaturated colours, such as yellow and orange (Andersson & Prager 2006). In saturated colours, chroma is unrelated to pigment concentration (Andersson & Prager 2006: 82). Thus in the case of red, which is a saturated colour, chroma is not a reliable indicator of the amount of carotenoids deposited in feathers. The lack of a correlation between red chroma and condition or breeding success in the Middle Spotted Woodpecker may not therefore reflect the lack of a relationship between feather carotenoid content and measures of individual quality. However, to support this assumption the extraction of plumage carotenoids needs to be quantified.

The other measure of colour in our study was cap brightness, which was significantly related to body condition and the clutch size of individuals. The reflectance of an object, resulting in colour brightness, depends not only on the amount of pigment but also on the texture of the surface (Wyszecki & Stiles 1982). Glossiness increases colour brightness (Butler *et al.* 2011) and is related to surface smoothness (Stamm *et al.* 1977, Rasmussen & Dyck 2000, Andersson & Prager 2006). Thus, differences in cap brightness in Middle Spotted Woodpeckers are likely to result from variability in feather structure and glossiness, which, in turn, is enhanced by preen wax (Hochleitner *et al.* 1996). Waxed feathers look brighter and more vivid (Andersson & Amundsen 1996, Blanco *et al.* 1999, Delhey *et al.* 2007 but see López-Rull *et al.* 2010 and Pérez-Rodriguez *et al.* 2011 for the opposite effect). The malfunction of the uropygial gland results in matt feathers (Hochleitner *et al.* 1996, Moyer *et al.* 2003). Preen wax also improves feather resistance to abrasion (Moreno-Rueda 2011).

Feather brightness also depends on the background white structural components of barbs (Shawkey & Hill 2005), as carotenoid-based colours need structural colours to shine. The shape of a reflectance curve is due to carotenoids, whereas the amount of reflected light, perceived as brightness, depends on the structural components of the feathers.

Another factor affecting feather reflectance and consequently brightness is dirt (Zampiga *et al.* 2004). Experimental cleaning of feathers enhances their brightness (Surmacki & Nowakowski 2007) and females prefer males with bright, clean feathers (Zampiga *et al.* 2004). Birds assign a considerable amount of their daily time budgets to grooming (Cotgreave & Clayton 1994, Walther & Clayton 2005) and its energetic cost is twice as high as the basal metabolic rate (Goldstein 1988). Birds suffering from infection devote less time to feather maintenance (Yorinks & Atkinson 2000) and thus plumage brightness can act as an honest signal of the current condition of an individual. Feather maintenance may be as important as pigment accumulation in the context of sexual selection. Individuals of high-quality plumage are in better condition, have greater breeding success and are preferred by females (Fitzpatrick & Price 1997, Ferns & Lang 2003, Ferns & Hinsley 2004, Zampiga *et al.* 2004).

The feathers that make up the red cap in the Middle Spotted Woodpecker are particularly exposed to abrasion and dirt accumulation due to frequently fitting through a relatively small hole (Kosiński & Ksit 2007). Excavating cavities mostly in dead, rotten wood also makes it hard to keep a red cap clean. It seems quite likely that higher reflectance in some individuals may be the result of better feather maintenance. The significant correlation between cap brightness and individual body condition in the Middle Spotted Woodpeckers suggests that birds with a higher reflectance of the red cap were better nourished. This might have influenced the production of preen wax and the ultrastructure of feathers. The inverse correlation between cap brightness and territory size may also result from the fact that owners of smaller, but at the same time more resource-rich, territories may save time from territory defence and foraging in favour of preening. Irrespective of whether cap brightness in the Middle Spotted Woodpecker is linked to feather structure, the amount of preen wax or the frequency of preening, we demonstrate that it is a useful predictor of individual condition. We suggest that the expression of red plumage in woodpeckers may be an honest signal of quality. However, we acknowledge that our study is descriptive and an experimental approach would be needed to confirm this suggestion.

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