Diversity of Nuptial Plumages in Male Ruffs Philomachus pugnax

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Johan van Rhijn[1,*], Joop Jukema[2] & Theunis Piersma[3]

Nuptial ornament diversity was studied in 1814 individual male Ruffs that were caught in their spring staging areas in Friesland, The Netherlands. Ornaments (hereafter called plumages) comprised of a ruff, two head tufts and facial wattles. Individual feathers were found to be plain (white, black or one hue), or patterned with black and *only one* hue. Patterns of feathers varied modestly within males, and greatly between males. The colour of a male's ruff plus head tufts consisted of black and/or white and/or only one other hue. Ruff, head tufts and facial wattles differed in coloration and pattern between individuals. Using seven criteria we counted 801 different plumage variants. Nevertheless, except for wattle colour, characteristics did not combine at random. Some combinations of characteristics, such as a white ruff with white head tufts, occurred much more often than expected by chance. Other combinations, such as a white ruff with black head tufts, a black ruff with white head tufts, and a regular ruff pattern with an irregular pattern, were rare. Mostly there was conformity between ruff and head tufts: they were identical or had reversed primary and secondary colours. Nuptial plumage characteristics were only weakly associated with body size. Some associations between nuptial plumage and the timing of moult were remarkable: only white males and males with a plain ruff pattern tended to have completed moult by the time of their capture in April. We discuss our findings, including the extreme diversity of nuptial plumages among individuals, in the light of development, genetics and function.

Key words: feathers, polymorphism, development, migration, moult, genetics, sexual selection, lek breeding

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Nuptial ornamentation of male Ruffs is one of the most extreme examples of intraspecific plumage variation in wild birds (e.g. van Rhijn 1991, 2013; Lank & Dale 2001; Dale 2006). These ornaments represent a third, supplemental, feather generation (for Ruffs: Jukema & Piersma 2000; for some other shorebird species: Battley *et al.* 2006, Conklin & Battley 2011). Ornamental plumage consists of a ruff (a collar of feathers around the front and the sides of the neck) and a pair of head tufts. The feathers can be coloured (black, various melanic-based hues, white) and patterned (plain, barred, spotted, patched) in a large number of ways and with a number of colours. Scapulars and tertials are also coloured and patterned in similarly varied ways, and will often match the head tufts. Finally, small wattle-like structures occur at the base of the bill extending up to the eyes and these can vary from yellowish, orange or red. Each of these characteristics re-appears year after year, with hardly any changes within individuals (JvR unpubl. data, on both wild and caged individuals).

The seasonal development of breeding plumages in Ruffs is dependent on testosterone (van Oordt & Junge 1936, Lank *et al.* 1999). Breeding plumage type is closely associated with reproductive strategy, resulting in three distinguishable males types (e.g. Hogan-

Figure 1. Two territorial independent males (left and right) and two satellite males (middle) on a lek.

Warburg 1966, van Rhijn 1991, 2013, Jukema & Piersma 2006): independent males, satellite males and faeders (female mimics). These male types and strategies become apparent on leks where males display and females select a mating partner. It has been shown that each male follows only one of these strategies during its whole life and that the different reproductive strategies in Ruffs are based on different combinations of genes (Lank *et al.* 1995, 2013, Farrell *et al.* 2013). Independent males try to defend a territory on the lek and have mostly dark coloured nuptial plumage. Satellite males do not establish their own territory but instead, to gain access to females, temporarily associate with one of the independent males. Satellites have mostly white nuptial plumage (Figure 1). However, plumage coloration sometimes fails to predict reproductive strategy, as some types of plumages may occur both among independent and satellite males (Hogan-Warburg 1966, van Rhijn 1991). Faeders do not develop conspicuous ornamentation and look like females.

Satellite males on leks are slightly smaller than independent males (van Rhijn 1983). Female mimics are considerably smaller than other males (Jukema & Piersma 2006). However, some studies suggest that even within the independents, plumage may be related to body size. Based on bodies or skins of males that had been collected in their breeding area, black independent males were somewhat larger and heavier than lighter coloured males (Dobrinskij 1969, Höglund & Lundberg 1989).

Signalling could have contributed to the evolution of plumage variation, assuming it would be advantageous for an individual to signal its reproductive strategy as opposed to hiding it (e.g. Lank & Dale 2001). Indeed, for satellites being recognizable will be important for reproductive success. Their characteristic white plumages seem to help them being tolerated in independents' territories where copulations take place (e.g. Hogan-Warburg 1966, van Rhijn 1991). In contrast, female mimics would not benefit from demonstrating their real status.

However, strategy signalling cannot explain the excessive diversity among independent males. One possibility is that diversity functions as a signal or a badge of male quality. However, such relationships appear very poor at best (e.g. Selous 1906-–1907, Hogan-Warburg 1966, van Rhijn 1991, 2013, Lank & Dale 2001). Another possibility is that individually fixed plumage polymorphism in Ruffs facilitates individual recognition (e.g. Dale *et al.* 2001, Lank & Dale 2001, Dale 2006). This is an attractive hypothesis, but it still needs to be explained why it is only in this shorebird species that males benefit from being so easily recognizable. Finally, diversity could evolve if females prefer the males that differ from all the others (e.g. Knoppien 1985, Eakley & Houde 2004, Hughes *et al.* 2013, van Rhijn 2013). This 'rare male advantage' could be an example of run-away sexual selection (Fisher 1930), in this case in several different directions.

There have been a number of studies on plumage variation in Ruffs (e.g. Drenckhahn 1975, Lank & Dale 2001). Some of the studies (e.g. Lank & Dale 2001) suggest that most plumage characteristics combine at random. However, rules exist for the distinction between independent and satellite males. Possibly, additional rules occur at other levels. They may include combinatorial rules for plumage characteristics, but also connections with other morphological features, and possibly with the timing of the moults that generate these characteristics. So far, datasets have been too small or insufficiently precise to resolve the rules that are essential for a better understanding of the biology of plumage diversity in Ruffs. In the present study, based on plumage descriptions of 1814 individuals, we aimed to detect rules and discuss them in the light of development, genetics and function.

METHODS

This study is primarily based on the descriptions of 1814 male Ruffs captured (only first time catches used) in April and May 1994–2006. A traditional netting technique was used with a 3.5 × 25 m largely wind-powered 'wilsternet' that is applied to trap Golden Plovers *Pluvialis apricaria* (details in Koopman & Hulscher 1979, Jukema *et al.* 2001). All catches (by JJ and others) were made on agricultural grasslands in the province of Fryslân, The Netherlands, chiefly near the towns of Workum and Hindeloopen (52°57'N, 05°25'E). This area used to be an important staging site for northward migrating Ruffs (Jukema *et al.* 1995, Verkuil *et al.* 2010, 2012).

Upon capture, each male was ringed and weighed to the nearest g using Pesola spring-balances, and measurements were made of maximum wing length (mm), tarsus + toe (mm) and head + bill (0.1 mm). Phase of moult development of the ruff was scored as 1 = freshly shed/pin, to 5 = fully newly grown. Only the plumages of males in moult phase 2–5 could be described in terms of coloration. Phases 2 and 3 shall later be referred to as 'early', phase 4 as 'middle', and phase 5 as 'final'. In a limited number of cases age was evaluated (second calendar year or older, according to Prater *et al.* 1977). A sample of 10–15 feathers from the mid-breast in the range of the ruff was collected (details in Jukema & Piersma 2000), and a close-up sideways photo of the neck and head was made to help establish plumage characteristics.

Details of the plumages were later scored (by JJ and TP) on the basis of the photos and feather samples, making use of a scoring system for colours and patterns developed by D.B. Lank and C.M. Smith (pers. comm.). Eleven colours were distinguished (Figure 2), each coded by two digits, the first for black/white ratio (1 = pure white, 2 = straw, 3 = light brown, 4 = brown, 5 = black) and the second for admixtures (1 = none, 2 = more red, 3 = more yellow). The nine colours (21, 22, 23, 31, 32, 33, 41, 42, 43) different from white (11) and black (51) are specified as *hues*. Ruff patterns could be regular (eight types) and/or irregular (six types; Figure 3). For each male, details of the ruff coloration consisted of at least one primary colour, and if present, a secondary and tertiary colour. No males were seen with more than three ruff colours. Details of the pattern consisted of at least one regular pattern, and if recognized, a second, and at least one irregular pattern, and if recognized, also a second. For each male, details of the head tufts consisted of at least one primary colour, and if present, also a secondary colour. Head tuft patterns and wattle colours were not scored. As most colours and patterns seem to vary continuously, instead of belonging to a limited number of discrete classes, the scoring system has its limitations. In particular, choices between colours 11–21, 41–51, 22–32, 32–42, 23–33 and 33–43 may be equivocal. This may also be the case for choices between regular patterns 2–3, 3–4, 4–5, 5–6, 6–7 and 7–8, and between irregular patterns 2–3, 3–5 and 4–6.

Most analyses were performed by JvR. The first analysis, on all 1814 individuals caught at stopover sites (*Primary Dataset*), generated questions on both general and more detailed characteristics that had not yet been scored. To work this out, photos and feather samples of a *subset* of 781 males (the best accessible records) were carefully viewed, interpretations in the

Figure 2. Colour classification for nuptial feathers. Scheme and drawings developed by D.B. Lank and C.M. Smith.
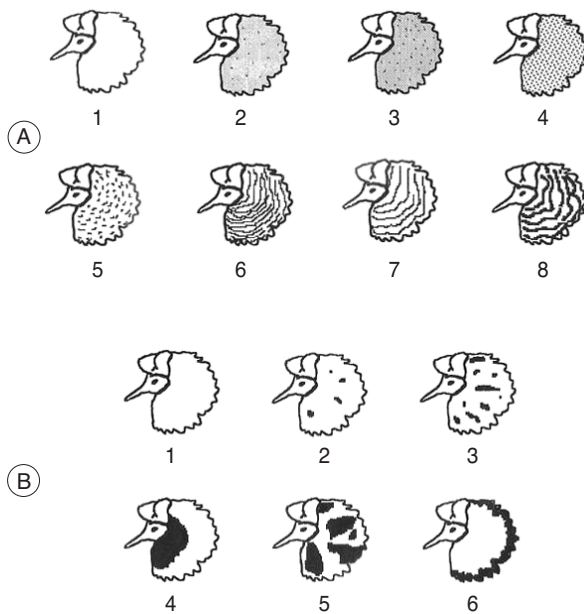
Figure 3. (A) Regular patterns of the ruff: plain (1), light flecking (2), moderate flecking (3), heavy flecking (4), broken barring (5), thin even width bars (6), uneven bars (7) and medium to wide bars (8) and (B) irregular patterns: none (1), few scattered spots or odd feathers (2), moderately spotted or lined (3), bib, a contrasting patch at top of ruff (4), patchy, large irregular areas of contrasting colours (5), and layered, with a contrasting fringe along the bottom (6). Scheme and drawings developed by D.B. Lank and C.M. Smith.

original data file were checked, alternative interpretations and extra information (wattle colour) were added (*Revisited Dataset*). As a way to summarize general broader characteristics, three categories of main colours were also scored: white (W), hue (H) and black (B) for ruff and head tufts, resulting in nine possible general 'plumage categories': WW, WH, WB, HW, HH, HB, BW, BH and BB. In addition, three pattern properties were scored for ruff in combination with head tufts: (1) The plain or almost plain parts (in Figure 3: patterns A1/B1 and B2): all, only ruff, only tufts or none. (2) The dominating pattern for ruff *and* tufts: plain (patterns A1/B1 and B2), fine (patterns A2–6), coarse (patterns A7–8) or irregular (patterns B3–6). (3) The presence of strongly contrasting parts in ruff and/or head tufts: no (patterns A1/B1 and others if contrasts between colours were weak), spots (patterns A2–6, B2–3 if contrasts between colours were strong), patches (patterns A7–8, B5 if contrasts between colours were strong), and bib (patterns B4, B6).

We also made comparisons with Ruffs that had reached their breeding area and had finished their supplemental moult. Field notes (by JvR) on the plumages of 98 males caught on leks in 1968–1972 (*Lek Dataset*) were appropriate as an *additional* source. These plumages were scored with a different scoring system, being less detailed in some respects, but giving extra information on wattle colour and head tuft pattern.

Contingency tables were interpreted by means of χ^2-statistics. Tables with empty diagonals (when colours should be different) were analysed congruent with Goodman (1968). Differences between groups in chiefly normally distributed traits were examined by *t*-tests and/or ANOVAs, followed by Games-Howell tests. Available at http://www.ardeajournal.nl/supplement/a102–005–020.pdf.

RESULTS

Feathers
Within-feather variation was an important source of diversity of nuptial plumages. Feathers differed in colour and pattern. All colours in the feather samples that were re-examined (*Revisited Dataset*) could easily be classified (examples in Figure 4) according to the scoring system (see Figure 2). Each feather had only one or two colours. Black and all hues were found in plain feathers, but more commonly in patterned ones, but pure white was never combined with any other colour. Thus, coloration of patterned feathers was always a combination of black and only one hue. No feathers with two hues were detected (although the intensity of pigmentation could gradually change from base to tip), nor with black and white, nor with black, white and a hue. Many types of patterns were found. Figure 5 shows a number of examples, not a complete series.

Most feathers sampled from each individual were very similar, both in colour and pattern, but some could diverge. Some samples had a combination of feathers with black with one hue plus either plain black feathers, or plain feathers of the same hue. In addition, plain white feathers were found in some samples. No samples were found that had more than one hue and had – besides plain feathers in some instances – highly differing patterns.

Ruff
In the *Primary Dataset*, 12% of the birds were scored to have only one ruff colour, 73% had two ruff colours, and 15% three. Ruffs were plain white in 4%, plain hue in 1%, and plain black in 8% of the birds. All other
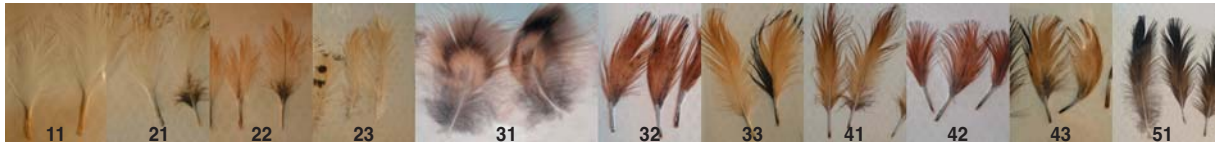
Figure 4. Samples of the colours of the feathers. The fifth panel (31) represents a sample of the second generation (alternate) plumage, as this colour is rare in nuptial plumages. All other samples are from third generation plumages.

Figure 5. Samples of different patterns of feathers. From left to right: wide bars, broken bars, two variants of fine bars, black threads, black spots, four different variants of fairly large patches at the tip, and black and hue separated by the shaft.

Table 1. Percentages in the *Primary Dataset* of (A) the primary, secondary and tertiary ruff colours, the primary and secondary head tuft colours, and (B) the first and second regular and irregular patterns.

A	Ruff				Head tufts	
	1st	2nd	3rd		1st	2nd
11: pure white	13.1	5.2	40.8	11: pure white	6.8	2.7
21: straw	10.8	13.5	3.3	21: straw	9.5	11.6
22: light rust	4.9	6.2	2.6	22: light rust	4.9	8.4
23: gold/straw	10.3	11.8	12.5	23: gold/straw	9.9	13.4
31: light brown	0.5	2.0	0.4	31: light brown	0.2	1.9
32: medium rust	8.0	7.0	4.0	32: medium rust	7.4	10.7
33: gold	2.7	1.4	1.1	33: gold	3.5	1.9
41: brown	0.5	1.2	1.5	41: brown	0.6	0.8
42: deep rust	2.0	2.1	2.6	42: deep rust	2.9	2.1
43: golden brown	2.1	1.6	0.0	43: golden brown	1.8	1.6
51: black	45.1	47.9	31.3	51: black	52.5	44.9
Total number	**1814**	**1589**	**272**		**1809**	**1496**

B	Regular			Irregular	
	1st	2nd		1st	2nd
1: plain	37.9	0.0	1: none	65.1	11.8
2: light flecking	11.5	0.0	2: few spots	11.5	35.3
3: mod. flecking	9.5	0.0	3: mod. Spotted	14.0	41.2
4: heavy flecking	5.5	0.0	4: bib	2.5	5.9
5: broken barring	12.3	20.0	5: patchy	4.9	0.0
6: thin bars	5.9	60.0	6: layered	2.0	5.9
7: uneven bars	9.1	0.0			
8: med./wide bars	8.3	20.0			
Total number	**1812**	**5**		**1809**	**17**

birds had combinations of colours. Table 1A gives percentages of colours (primary, secondary and tertiary) and Table 1B patterns (first and second regular, and first and second irregular). An example of how primary and secondary colours associated is shown in Table 2. As colours should be different, all values in the cells of the descending diagonal (from combinations of colour codes '11'–'11' to '51'–'51') are zero. The distribution in the non-diagonal cells differed from random ($\chi^2_{89} = 566$, $P < 0.001$). Combinations between black and hue, black and white, and white and hue were relatively common. In contrast, combinations between different hues (the values within the inner rectangle) were rare (zero or very low). If hues combined at random, the expected sum of the non-diagonal values in the inner rectangle is 105.5, but the observed sum was only 31. The difference is highly significant ($\chi^2_{55} = 239$, $P < 0.001$). Thus, primary and secondary colour rarely represented two hues.

Considering all ruff colours (primary, secondary and tertiary), combinations of two different hues were scored for only 3% of the birds (Tables S1–S3) and combinations of three different hues for 0.2%. Closer inspection (*Revisited Dataset*) revealed that almost all

Table 2. Frequencies (counts) in the *Primary Dataset* of combinations of primary and secondary ruff colours ($\chi^2_{89} = 566$, $P < 0.001$, according to Goodman 1968). Bold numbers in the dark grey cells are higher than expected by chance, numbers in the white cells are lower than expected. The inner rectangle represents the combinations of hues.

		Secondary colour ruff										
		11	21	22	23	31	32	33	41	42	43	51
Primary colour ruff	11	-	**17**	**10**	**29**	2	**25**	2	**5**	5	**5**	67
	21	2	-	1	1	0	0	0	**7**	0	0	**184**
	22	3	1	-	0	0	2	0	1	0	0	80
	23	5	1	0	-	0	0	0	2	0	0	**173**
	31	0	0	0	0	-	0	0	0	0	0	9
	32	2	0	0	0	0	-	0	2	1	0	**135**
	33	0	1	0	1	0	0	-	1	0	0	45
	41	0	1	1	4	2	0	0	-	0	0	1
	42	4	0	0	0	1	0	0	0	-	0	30
	43	2	0	0	0	0	0	0	0	0	-	37
	51	65	193	87	153	27	85	21	1	27	20	-

Table 3. Frequencies (counts) in the *Primary Dataset* of combinations of primary ruff colours and primary colours of head tufts ($\chi^2_{100} = 3094$, $P < 0.001$). Bold numbers in the dark grey cells are higher than expected by chance, numbers in the white cells are lower than expected by chance. The inner rectangle represents the combinations of hues.

		Primary colour head tufts										
		11	21	22	23	31	32	33	41	42	43	51
Primary colour ruff	11	**110**	9	9	27	0	22	60	3	9	4	37
	21	4	**46**	2	4	1	0	0	1	0	0	**138**
	22	0	0	**29**	0	0	0	0	0	0	0	**60**
	23	0	4	1	**51**	0	1	2	0	0	0	**125**
	31	0	0	0	0	1	0	0	0	0	0	8
	32	0	0	0	0	0	**50**	0	0	0	0	**96**
	33	0	0	0	0	0	1	**28**	0	0	0	20
	41	0	0	1	0	2	0	0	**5**	0	0	3
	42	0	0	0	0	1	0	0	0	**15**	0	21
	43	0	0	0	0	0	0	0	0	0	**22**	17
	51	9	**112**	87	**97**	2	60	28	2	28	7	424

combinations of different hues could be classified in one of three categories: (1) including hue 21 (straw: almost white) rather than being scored as pure white, (2) including hue 41 (brown: almost black) rather than being scored as pure black, or (3) including two almost similar hues. All these could be due to ambiguity in the scoring system. In addition, small deviations of dominating colours might be caused by environmental influences during plumage development. In summary, ruff coloration consisted of one (white, hue or black), two (white + hue, white + black or hue + black) or three colours (white + hue + black), but we never observed two distinct hues in the same ruff.

Regular patterns of the ruff emerged with patterned feathers. Feather patterning in the ruff was rather uniform in these birds. Irregular patterns of the ruff appeared when (some) plain (often white) feathers diverged from the dominant feather colour. Regular and irregular patterns associated in non-random ways ($\chi^2_{35} = 501$, $P < 0.001$) (Table S4); generally, non-plain regular patterns excluded irregular patterns. Regular patterns were highly associated with the first and second colours of the ruff ($\chi^2_{70} = 738$ and 530, both cases $P < 0.001$), but not with the tertiary colours (Tables S5–S7). Irregular patterns were clearly associated with primary, secondary and tertiary colours of the ruff ($\chi^2_{50} = 342$, 250 and 92, all cases $P < 0.01$) (Tables S8–S10).

Head tufts and association with the ruff

Percentages of primary and secondary colours of head tufts are presented in Table 1A. As in the ruffs, associations between primary and secondary colours of head tufts were non-random ($\chi^2_{89} = 573$, $P < 0.001$, congruent with Goodman 1968), and combinations between different hues were rare (26 observed; 80.8 expected) (Table S11).

In many, but certainly not all, individuals, the colours and patterns of the head tufts and the ruff were similar. Most obvious were the relations *between* the colours. An example (primary colour of ruff compared with primary colour of head tufts) is shown in Table 3. It is striking that ruff and head tufts tended to have similar colours (values in the dark grey cells of the descending diagonal). In addition, various hues (code '21', '22', '23', '32') were associated with black ('51'). Almost the same associations were found in most other colour comparisons (primary and secondary colour ruff with primary and secondary colour head tufts) (Tables S12 – S15). The distributions were different from random, all cases $\chi^2_{100} > 1000$, $P < 0.001$. In most cases the values of the cells in the descending diagonal

were much higher than expected by chance. The association between black and the hues was clear for the comparison between secondary colour ruff and secondary colour head tufts, but not for the other combinations. Comparisons between the tertiary colour of the ruff and the two colours of head tufts also gave significant non-random distributions ($\chi^2_{81} = 228$ and $\chi^2_{90} = 142$, both cases $P < 0.001$), but no obvious trends (Tables S16–S17). Both primary *and* secondary colours of the ruff often reappeared as primary or secondary colours in the head tufts. Primary *and* secondary colour of the ruff might reappear in the same way in the head tufts, but they might also interchange. No associations could be established between the patterns of ruffs and head tufts, as the latter had not been scored in the *Primary Dataset*. The regular and irregular pattern of the ruff, however, appeared to be associated with the primary and the secondary colour of the head tufts (Tables S18–S21). In all four comparisons the distributions were different from random ($\chi^2_{70} = 579$ and 382, $\chi^2_{50} = 290$ and 246, all cases $P < 0.001$).

General 'plumage category' as scored in the *Revisited Dataset* was significantly associated with the properties 'plain parts', 'general pattern for ruff and head tufts' and 'presence of strongly contrasting parts' ($\chi^2_{21} = 555$, 566 and 251, all cases $P < 0.001$) (Tables S22–S24). The major associations are summarized in Table 4. Three of the nine possible plumage categories appeared to be rare or absent. Portraits and feather samples of typical representatives of the six remaining categories are displayed in Figure 6.

Table 4. Major associations (combinations that occur remarkably more often than expected by chance) of plumage categories (ruff + head tufts) with 'parts that remain plain', 'general pattern' and 'presence of contrasting parts' (*Revisited Dataset*).

Plumage category		Percentage	Major trends		
Ruff	Tufts		Plain	Pattern	Contrast
White	White	6.3	All	Plain	Spots
White	Hue	6.4	Ruff	Irregular	Patches
White	Black	0.4			
Hue	White	0			
Hue	Hue	18.3	None	Coarse	Bib
Hue	Black	23.4	Tufts	Fine	Spots
Black	White	0.6			
Black	Hue	21.6	Ruff	Irregular	Patches
Black	Black	22.9	Tufts	Fine	No
	Total number	781			

Figure 6. Portraits and feather samples of six males, typical representatives of the general plumage categories: 1461959 (white–white), 1337634 (white–hue), 1337636 (hue–hue), 1353498 (hue–black), 1353460 (black–hue) and 1409083 (black–black).

Combined nuptial plumage coloration and diversity

For birds in complete nuptial plumage, we rarely scored more than one distinct hue (ruff and head tufts together, see Table 3). In the central part of the table, within the inner rectangle, the values in cells are zero or very low,

Figure 7. Head and feather sample of male 149101, apparently with two different hues in its nuptial plumage.

except for the diagonal. The sum of these non-diagonal values (combinations of different hues) is 18, which is below the expected value of 253.0 if the hues associated at random ($\chi^2_{55} = 1737$, $P < 0.001$). Similar trends were found in the other colour comparisons between ruff and head tufts (Tables S12–S17). In all cases the observed values were considerably lower than the expected ones. This indicates that, as with the finding for ruffs alone (see above), in the large majority of cases only one hue is found besides black and/or white. This can also be concluded from the *Lek Dataset* (15 males had no hue – only black and/or white, 78 males had one hue, and 5 were scored with two hues that were almost identical in all cases). The *Revisited Dataset* revealed that the original descriptions (*Primary Dataset*) in which two or – in very rare cases – three hues had been distinguished, quite often referred to hues that were very similar and could fade into each other within one and the same feather. Almost all cases with more than one hue could be due to measurement error (see Methods). In fact, only one out of 781 photos seems to represent a case of a male with two distinct hues in its nuptial feathers (Figure 7). All other plumages could easily be classified as pure white, white with one hue, white with black, white with one hue and black, one hue with black, or pure black. In a few cases 'white' seemed to be close to a very light hue, and in a few other cases 'black' seemed to be close to a very dark hue. Plumages with only one pure hue (without any white or black patterning) were not seen, and thus seem to be very rare among Ruffs, but do exist (D.B. Lank, pers. comm.).

Although the nine plumage characteristics presented in Table 1 can combine to an impressive number of different phenotypes (about 5×10^6), most of these possibilities did not actually occur. As we have seen, combinations of different hues are excluded. Nevertheless, in our sample of 1814 males we observed 801 different combinations: 565 combinations were scored only once, but various combinations more often, some of them even more than a dozen of times. Three examples: (1) 31 males plain white ruff and head tufts, (2)

24 males gold straw ruff with black moderate flecking, head tufts black with gold straw, and (3) 11 males black ruff and head tufts with light rust broken bars.

Wattles in association with feather coloration

Almost all males that were caught on leks in late April and May had well developed wattles (*Lek Dataset*). In contrast, males caught on migration in early and mid-April did not have visible wattles. Thus, wattles develop after most nuptial feather growth is completed. All wattles of an individual had the same colour, but there was variation between individuals. Colours ranged from bright yellow (lower male in Figure 6), to orange (second male in Figure 6), and bright red (third male in Figure 6). This might suggest that wattle colour is associated with the yellowish and reddish hues of the feathers. In the *Revisited Dataset*, wattle colour could be scored in 375 cases and thus be related to plumage colour. Three categories of wattle colours (yellow, orange, red) were tabulated against five categories of plumage colours: white (code: '11'), brown ('21' + '31' + '41'), red ('22' + '32' + '42'), yellow ('23' + '33' + '43'), and black ('51'). An example (wattle colour compared with primary colour of ruff) is shown in Table 5. The distribution of the frequencies was different from random ($\chi^2_8 = 17.3$, $P = 0.027$ with primary colour of ruff, and $\chi^2_8 = 22.5$, $P = 0.004$ with primary colour of head tufts) (Tables S25–S26). However, there were no indications of an association between wattle colour and plumage hue. Instead, white plumages co-occurred with red wattles about twice as often as expected.

Associations between plumage type and body size

Body mass and wing length in the *Primary Dataset* varied considerably among individuals (resp. 120–335 g,

Table 5. Frequencies (counts) in the *Revisited Dataset* of combinations of wattle and primary ruff colours ($\chi^2_8 = 17.3$, $P = 0.027$). The bold number in the dark grey cell is higher than expected by chance, numbers in the white cells are lower than expected.

Wattle colour	Primary colour ruff				
	11	Brown	Red	Yellow	51
Yellow	15	18	24	21	83
Orange	15	9	13	19	54
Red	**25**	8	10	22	39

Table 6. Average (A) body mass (g) and (B) wing length (mm) for birds with the same primary colours of ruff, primary colours of head tufts, regular pattern of ruff, and irregular pattern of ruff (*Primary Dataset*). Bold values in the dark grey cells are significantly higher than at least one of the values in the same series, values in the white cells are significantly lower ($P < 0.05$, *t*-tests for comparisons between the first and second column, Games-Howell post-hoc tests for comparisons among all colours or patterns. ANOVAs are based on the complete range of colours (including white) or patterns (including pattern 1).

Mass	(A)		Primary colour										ANOVA
	White	Non-white	21	22	23	31	32	33	41	42	43	51	
Ruff	227.4	**233.7**	231.7	230.2	232.4	236.4	236.0	237.9	235.8	230.5	223.2	234.9	$P = 0.022$
Tufts	227.9	233.3	228.8	228.6	228.9	244.0	230.8	240.0	226.5	237.0	232.8	235.2	$P = 0.005$
	Absent	Present	Pattern										
			2	3	4	5	6	7	8				
Regular	233.0	233.0	236.7	230.9	232.0	229.3	235.9	235.5	231.6				$P = 0.156$
Irregular	**234.9**	229.4	234.1	229.1	222.2	223.1	230.6						$P < 0.001$

Wing	(B)		Primary colour										ANOVA
	White	Non-white	21	22	23	31	32	33	41	42	43	51	
Ruff	191.6	**192.3**	192.5	191.6	192.7	193.4	192.4	191.8	191.9	192.1	191.5	192.3	$P = 0.207$
Tufts	191,5	192.3	191.6	191.3	191.8	191.3	191.7	192.4	190.7	192.5	191.1	192.7	$P < 0.001$
	Absent	Present	Pattern										
			2	3	4	5	6	7	8				
Regular	191.8	**192.5**	192.7	192.4	192.2	192.5	**193.2**	192.1	192.3				$P = 0.033$
Irregular	**192.5**	191.7	191.9	191.8	191.5	191.7	189.8						$P < 0.001$

mean = 233; 163–207 mm, mean = 192). Average body mass and wing length also differed between groups of individuals with similar colour or pattern (mass: 222–244 g, SD = 20–40; length: 190–193 mm, SD = 2–5; Table 6). However, differences were small, in the order of 10 g for body mass (less than 5% of the total), and about 1 mm for wing length (less than 1% of the total). Body mass was lower and wing length shorter in birds that had white as the primary ruff colour (code: '11') than in the non-white birds (t-tests, $P = 0.001$ and 0.017, resp.). For birds that had white as the primary tuft colour this trend was not significant (t-test, $P = 0.066$ and $P = 0.052$, resp.). Birds with regular patterns had the same body mass as those without (t-test, $P = 0.995$), but had longer wings (t-test, $P = 0.002$). Birds with irregular patterns had a lower body mass and shorter wings than the birds without (t-tests, $P < 0.001$ both cases, Table 6). Variation in body mass and wing length in most cases differed significantly among the colours and patterns (ANOVAs body mass: between primary ruff colour $F_{10,1762} = 2.10$, $P = 0.022$; primary tuft colour $F_{10,1757} = 2.51$, $P = 0.005$; regular ruff pattern $F_{7,1763} = 1.52$, $P = 0.156$; irregular ruff pattern $F_{5,1762} = 5.40$, $P < 0.001$; ANOVAs wing length: between primary ruff colour $F_{10,1800} = 1.33$, $P = 0.207$; primary tuft colour $F_{10,1795} = 3.24$, $P < 0.001$; regular ruff pattern $F_{7,1801} = 2.18$, $P = 0.033$; irregular ruff pattern $F_{5,1800} = 5.01$, $P < 0.001$), but the separate colours did not statistically differ from each other and only a few patterns appeared to differ from other patterns (Games-Howell post-hoc tests, Table 6).

Timing of the moult
In the Primary Dataset, primary colour of the ruff was the only characteristic that varied significantly with moult phase ($\chi^2_{30} = 48.6$, $P = 0.017$, Table 7) (Tables S27–S33), because the sample of final phases had more white males than expected by chance. Yet, there were no differences between catching date distributions of the different primary colours (ANOVA, $F_{10,1803} = 1.24$, $P = 0.26$). We examined the association between moult phase and the *presence* of secondary and tertiary colours, and regular and irregular patterns (Tables S34–S38), and found that only the presence of secondary ruff and head tuft colours varied with phase ($\chi^2_3 = 24.5$ and 28.0, $P < 0.001$ in both cases). In particular, secondary colours tended to occur more often than expected by chance in the samples of the early phases.

In the *Revisited Dataset*, the distributions of moult phase against plumage category, plain parts of plumage, general pattern, and presence of contrasting parts differed significantly from random (respectively $\chi^2_{21} = 37.8$, $P = 0.014$; $\chi^2_9 = 30.6$, $P < 0.001$; $\chi^2_9 = 24.4$, $P = 0.004$; $\chi^2_9 = 17.0$, $P = 0.049$) (Tables S39–

Table 7. Frequencies (counts) in the *Primary Dataset* of combinations of moult phase and primary ruff colours ($\chi^2_{30} = 48.6$, $P = 0.017$). Bold numbers in the dark grey cells are higher than expected by chance, numbers in the white cells are lower than expected.

Moult phase	Primary colour of ruff										
	11	21	22	23	31	32	33	41	42	43	51
2	23	14	7	20	0	17	7	1	7	3	85
3	41	50	26	37	2	39	9	0	**15**	13	**229**
4	**110**	**91**	38	**93**	5	62	22	2	12	13	325
5	**61**	39	18	35	2	27	10	5	2	8	169

Table 8. Major associations of moult phase with 'plumage categories' (ruff + head tufts), 'parts that remain plain', 'general pattern' and 'presence of contrasting parts' (*Revisited Dataset*).

	Moult phase		
	Early (2-3)	Middle (4)	Final (5)
Categories	Hue–hue, black–hue	Hue–black	White–white, white–hue, black–black
Plain	None		Only ruff, only head tufts, all
Pattern	Coarse		Plain
Contrast	Patches		Spots

S42). Similarly to the *Primary dataset*, the white–white and white–hue plumage categories, and the plain patterns were most frequent amongst birds with almost completed ruff feather growth (Table 8). The coarse patterns and contrasting patches were most common in birds in the early stages of moult, whereas plain plumages were most common in birds in final moult stages. This could mean that plain birds arrived later, or, that the plain feathers grow later and cover the patterned ones.

DISCUSSION

Despite the fact that there were many recurring associations between the different levels of plumage variability, the overall diversity in nuptial plumages of Ruffs is impressive. On the basis of this study we can clearly reject the general idea of Lank & Dale (2001) that plumage properties combine at random, either between colours, or between patterns, or between colours and patterns. Some combinations occurred quite often, others were rare or non-existing. The individual feathers that bring about colour and pattern of ruff and head tufts were: plain white, plain black, plain hue, or have a pattern with black and only one hue. The feathers within a male's plumage showed modest variations. However, between males differences in feather patterning were considerable.

The colour of a male's nuptial plumage consisted of one, two or three of the following elements: (1) black, (2) white and (3) only one hue. This last finding is consistent with the pattern shown by Lank & Dale (2001, their figure 2) on how shades of ruff and head tufts (grey scale) combine, but they did not highlight this limitation. It may be that in very rare cases two hues are really present, but in nearly all cases there existed close conformity between ruff and head tufts. They may either look the same, or – more or less – reversed. Only one feature, the colour of the wattles at the base of the bill (red, orange or yellow), seems to be completely independent of other plumage characteristics. This could be an indication of different underlying mechanisms, for instance different pigments (see Development).

We propose six main categories of plumages (see Table 4, Figure 6). Based on field experience on leks, and on the *Lek Dataset*, it is most likely that the first category (white–white) entirely consists of satellite males. Probably, the second category (white–hue) also consists mainly of satellite males. The third category (hue–hue) has few satellite males, most of them with a white bib. Males of the fourth (hue–black), fifth (black–hue), and sixth (black–black) category are certainly almost all independent males.

Our results are consistent with earlier findings (Dobrinskij 1969, van Rhijn 1983, Höglund & Lundberg 1989) that body size in males with white plumages tends to be smaller than in dark males. Yet, the differences, especially in wing length, were considerably smaller than in earlier studies (about 1 mm or less than 1% of the total, compared to about 4 mm or 2% of the total in earlier studies). The differences in body mass between the current and earlier studies were in the same range, although the data of the staging areas are not fully comparable with those collected on leks. In the staging areas males undergo considerable mass changes between arrival and departure (Koopman 1986, Verkuil *et al.* 2012), whereas body mass does not reach such high values in lekking males.

Development

The third feather generation (supplemental plumage) of a Ruff appears in the course of April (e.g. Drenckhahn 1968, Jukema & Piersma 2000), starting with feathers of breast and shoulders (ruff) and followed by feathers of the head (head tufts). By the end of the moult, after the small feathers near the bill are lost, the temporarily enlarged facial wattles become visible. Before that time, between January and April, the large wing coverts, mantle, scapulars, tertials and, commonly, half of the number of rectrices are moulted, partly in the wintering area (e.g. Schmitt & Whitehouse 1976, Pearson 1981). These feathers most probably represent the second plumage generation (alternate plumage), directly replacing the basic plumage (Jukema & Piersma 2000). Nevertheless they are quite colourful, more so than the second generation feathers of breast, ruff and tufts. Bar-tailed Godwits (*Limosa lapponica baueri*) also grow an alternate plumage of barred feathers, which after just 3–5 weeks is replaced with supplemental red feathers (Conklin & Battley 2011).

During pre-supplemental moult plumages gradually change. Coarse patterns and contrasting patches tend to become rare and plain, and white plumages become more common (see Timing of the moult). This seems to reflect the process of plumage perfection during moult. Initially, the male's plumage is 'sloppy' because of the mixing of feathers of both the alternate and supplemental plumage. This sloppy appearance is strengthened because the growth schedules of various feathers differ. By the end of moult the plumage looks well-cared for. It is possible that plain feathers, especially the black ones, develop somewhat later or slower than

feathers that are patterned. Observations on males that were kept in captivity suggest that the process of plumage perfection also occurs from year-to-year during their first years of life (JvR unpubl. data). Moults seem to proceed more smoothly with increasing age, and nuptial plumages seem to become less patterned and more brilliant.

New feathers are created by the same feather follicles (e.g. Prum 1999, Yu *et al.* 2004) at the same feather tracts as the feathers of the previous plumage. Yet, the new feathers differ in size, shape, pattern and colour from second generation feathers. The old were short and striped, the new feathers are longer and more colourful (Jukema & Piersma 2000). These differences are the result of changing physiological factors, in particular the amount of circulating testosterone (e.g. Kimball & Ligon 1999, Bókony *et al.* 2008, McGraw 2008, Roulin & Ducrest 2011). For instance, the production of melanin pigments is enhanced by testosterone. Although the relationship between testosterone and plumage in the Ruff has been demonstrated by castrating males (van Oordt & Junge 1936) and by implanting testosterone in females (Lank *et al.* 1999), in this species the female mimics are strikingly deviant. These males have very large testes in comparison to other males, but do not develop large and showy feathers and do not have a dark (melanised) appearance (Jukema & Piersma 2006). It is possible that they use a mechanism that neutralizes the effects of testosterone on growing feathers, and maybe, also on their behaviour. This happens, for instance, in male ducks, that aromatize testosterone into oestrogen at the time they moult into eclipse plumage (e.g. Kimball & Ligon 1999).

In shorebirds melanins are the major (possibly the only) feather pigment (e.g. Toral *et al.* 2008, Stoddard & Prum 2011). There are two groups of melanin: eumelanin (black and dark brown) and pheomelanin (reddish and yellowish hues). They are produced in cells called melanocytes, stored in small cell organelles (melanophores), that can be transferred to other cells, for instance to the cells of the developing feather (keratinocytes). Melanocytes are distributed over the skin, quite often in particular patterns. As older satellite males keep an increasing area of white head feathers during the whole year (van Rhijn 1983, 1991, D.B. Lank pers. comm.), some regions appear to lose their melanocytes in the course of years. It is plausible that pheomelanin and eumelanin are formed in succession at the same site and are subsequently packed as a core consisting of several particles of pheomelanin surrounded by a layer of eumelanin (Bush *et al.* 2006,

Ito & Wakamatsu 2008). Pigments have to be distributed in a particular way within a growing feather to create the feather pattern. With rather simple reaction-diffusion models the complex patterns that have been found in feathers can be simulated (Prum & Williamson 2002).

The variety of ruff and head tuft colours seems to be sufficiently explained by the existence of feathers without pigments (white feathers) and feathers with eumelanins and/or pheomelanins (black and various hues). Although the mechanistic details are unknown, it is possible that different types of pheomelanins are involved in the different hues, as has been established for human hair (e.g. Piletic *et al.* 2010). It is also possible that they arise by different blends between pheomelanin and eumelanin (e.g. McGray *et al.* 2005), as has been shown for human hair too (e.g. Ito & Wakamatsu 2011). Most probably an individual male produces only one type of pheomelanin (or perhaps one blend of pheomelanin with eumelanin) that causes its characteristic hue.

In addition, some males with plain black feathers stand out on leks and in the staging areas because of a bluish or greenish gloss over their feathers (iridescent structural coloration). These glosses have not been scored because they cannot reliably be detected on photos. Whereas colours from melanins are hardly affected by health and food availability at the time the feather grows (but see McGraw 2007, 2008), structural coloration seems to be strongly influenced by these factors (McGraw *et al.* 2002). Similarly, the colours from some other pigments, such as carotenoids, are related to the condition of the animal (e.g. Hill 1999). These pigments have not yet been found in the plumage of shorebirds, but the bright coloration of the wattles near the bill base (yellow, orange and red) suggest that carotenoids are involved. Condition in male Ruffs was not found to be related to wattle coloration, but instead to the extent of the area with wattles (Lank & Dale 2001).

Genetics
Breeding experiments have shown that variation in mating strategies in Ruffs is based on genetic factors (Lank *et al.* 1995, 2013), but the genetic factors underlying nuptial plumage variation remains unknown. Although our analysis was restricted to phenotypic variation, our data may help to generate hypotheses on genetic control of nuptial plumage. In fact, we tried to derive a number of general properties from our results that may together define an individual-specific nuptial plumage: (1) whiteness (presence of skin areas without

melanocytes), (2) blackness (proportion of eumelanin among the melanins produced in melanocytes), (3) hue (type of pheomelanin or blend of pheomelanin with eumelanin), (4) feather pattern (diffusion characteristics of pigments in growing feathers), (5) plumage category (combination of ruff and head tufts), and (6) wattle colour. The observation that individual nuptial plumage patterns do not change with age suggests that the molecular processes of feather and wattle growth are fixed within an individual, but it remains unclear whether and how the underlying genes or gene expression varies between individuals. Below we review what is known so far, but bear in mind that nuptial plumage development involves an unknown number of coding and regulatory genes.

The first property, whiteness, is the most likely candidate for separating satellite males from independent males. Most satellite males have areas of skin, possibly without (active) melanocytes, that produce white feathers. This is not necessarily restricted to the supplemental plumage, but may also happen in the other plumages. Areas of skin that produce white feathers, for the supplemental plumage are either absent or relatively small in independent males. Satellite males have been shown to possess one or two dominant satellite alleles (Lank *et al.* 1995). The finding that all pure white males (see Figure 1) observed on leks were satellite males, suggests that 'a large area of frontal skin without (active) melanocytes' is a pleiotropic effect of the satellite allele. Alternatively, the 'whiteness' factor is closely linked to the satellite allele. However, reproductive strategy is not fully associated with white plumages (Figure 8). Apparently, in addition to the 'satellite allele', size and position of the areas without (active) melanocytes are also under control of other genes.

The second and third properties, blackness and hue, are regulated by the proportion of eumelanin among the melanins and by a type of pheomelanin or an unknown number of blends of pheomelanin with eumelanin, and might be quantitative traits under influence of a number of genes of which the effects are added. The potentiality of these properties could appear from the highly variable melanocortin-1 receptor (MC1R) gene (Mundy 2005). Differences between the hues may also relate to variations in the intensity of pigmentation (McGraw *et al.* 2005).

The fourth, patterning of feathers, has been simulated with reaction-diffusion models (Prum & Williamson 2002). These simulations suggest that the number of (molecular) instructions is not necessarily high for creating a complicated colour pattern in a

Figure 8. Reproductive strategy is not fully associated with white plumages. The two males at the right side are both independent males. Their ruffs are (almost) white and their head tufts black. The male at the left side of the picture is a satellite male with a white ruff and light brown head tufts. The male on the background is probably a satellite male.

feather. The way that pheomelanin pigments are packed together in granules with eumelanin (Ito & Wakamatsu 2008) could facilitate this process.

The fifth, plumage category, is constrained by the factors discussed above. Possibly only for the non-white plumages extra information is required to control the relationship between ruff and head tufts. Ruff and head tufts may have almost similar feathers or somewhat reversed characteristics, especially in blackness. A possible cause is variation in the density of (active) melanocytes in the skin.

The sixth, colour of wattles, has been suggested to be based on one gene with two non-dominant alleles (van Rhijn 1991). Heterozygotes would develop orange wattles, one homozygote red wattles and the other yellow wattles. Their frequencies agreed with the Hardy-Weinberg law (van Rhijn 1991, p. 62). Wattle colour remains largely constant over years, but seems to be independent of other plumage characteristics. For that reason it is likely to be under control of independent genes. Considering the brightness of these colours, pigmentation by carotenoids is more likely than pigmentation by melanins (e.g. Grether *et al.* 2004); also, carotenoids are the major pigments in the skin of birds (e.g. Olson & Owens 2005). Carotenoids have to be obtained from food resources, implying that not all individuals possess these pigments at any time (e.g. Olson & Owens 2005). As in melanins, pigmentation by carotenoids may be under control of testosterone (e.g. Blas *et al.* 2006). In addition, the intensity of the

carotenoid pigmentation is expected to depend on the condition of the male (e.g. Hill 1999, Simons *et al.* 2012). In some cases the variation in carotenoid pigmentation could be ascribed to genetic differences (e.g. Eriksson *et al.* 2008, Walsh *et al.* 2011).

We suggest that the molecular regulation of wattle colour operates independently of plumage, but consider it plausible that the regulatory factors for plumage are interdependent, except those for whiteness.

Evolution

The diversity in the plumage of Ruffs continues to raise evolutionary questions (e.g. Roulin 2004). Generally breeding plumages are thought to be an effect of mate choice for quality, or attractiveness (e.g. Endler & Basolo 1998, Ryan 1998, Arnqvist 2006). A choice for quality has direct benefits for the fitness of the offspring (health and status) and may be regarded as a case of natural selection. A choice for attractiveness has only indirect effects on the fitness of the offspring (attractive sons) and should be regarded as a pure case of sexual selection. In Ruffs, only very few plumage characteristics may indicate quality (e.g. Lank & Dale 2001). So far it has proved impossible to correlate plumage characteristics with female interest or mating success (Shepard 1975, Hill 1991).

Two other explanations have been given for plumage diversity in Ruffs: (1) to signal status (satellite or independent male), and (2) to signal individual identity (van Rhijn 1983, Dale *et al.* 2001, Lank & Dale 2001, Dale 2006). Clearly, satellite males will benefit from signalling their mating strategy. Their white plumage provides a "passport" for admission to mating sites and in combination with particular postures, restrains the territory holders to attack them (Hogan-Warburg 1966, van Rhijn 1991, Lank & Dale 2001). It is less clear why an individual male benefits from displaying his identity in such a conspicuous way. It may be helpful for a satellite male to recognize its tolerant host, or for a territory owner to recognize its neighbour (and vice versa). However, the central question is whether male reproductive success is improved by being identifiable. Females may make the decision to mate with a particular male after several visits to various males. If these visits are scattered over days and over locations, easy identification of males is advantageous for females. But is it also advantageous for males? It may be advantageous for the one that was finally chosen, but certainly not for the others that were not chosen for mating.

Being identifiable is beneficial for territorial males that have settled on a lek. Their neighbours have tested their fighting abilities and will avoid their territory. This will minimize violence to ritual attacks or very short fights. The extreme plumage diversity among Ruffs may be useful for individual identification because they do not sing (Lank & Dale 2001). After all, individual recognition is also widespread in largely monomorphic birds and other animals that live in groups (e.g. van Rhijn & Vodegel 1980). However, identification may not be beneficial for a territorial male that is newly settling on a lek. A new male is vigorously attacked by all neighbouring males and has to fight heavily for a long time before it is tolerated by the others. Only a very small number of males get settled without such fighting; in these cases the settling male closely resembled the previous owner of the territory or another territorial male that had recently left the lek (JvR unpubl. data). Thus, it is questionable whether a male benefits from being identifiable.

Thus, and perhaps hardly surprisingly, even after our detailed description and analysis of nuptial plumage variation, the evolutionary drivers of the extreme diversification in Ruffs remain beyond our grasp. Yet, we suggest that sexual selection is involved in major ways. If, as seems to be the case for Ruffs, females do not select males with particular colours or patterns, they might still select males with odd plumages as these are most stimulating for their sensory system (e.g. Knoppien 1985, Eakley & Houde 2004, Hughes *et al.* 2013, van Rhijn 2013). Also, odd males are conspicuous, and for that reason alone they could be attractive mating partners. A preference for odd mates creates diversity within a species without direct fitness advantages of 'being different from most others', but it could initiate a self-propelling, 'run-away' process. But why would such selection for diversity be so rare?

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SAMENVATTING

Kemphanen *Philomachus pugnax* ruien drie keer per jaar. De derde rui, die in april of mei wordt voltooid, voltrekt zich grotendeels op de pleisterplaatsen tijdens de trek naar de broedgebieden. Deze rui levert bij mannetjes een broedkleed op dat individueel sterk verschilt. Tussen 1994 en 2006 werden van ruim 1800 in Friesland gevangen mannetjes met een gedeeltelijk of geheel ontwikkeld broedkleed verschillende veerkarakteristieken beschreven. Het broedkleed wordt gekenmerkt door een kraag, twee pluimen op de kop en gekleurde wratjes bij de snavel. Individuele veren daarin zijn effen wit, zwart of gekleurd of ze hebben een patroon met zwart en nog een kleur. Hoewel er veel variatie is tussen mannetjes in kleuren en patronen van kraag en pluimen, heeft elk mannetje van jaar op jaar vrijwel hetzelfde broedkleed. Met uitzondering van de kleur van de wratjes, blijken de kleuren en patronen niet volgens toeval te combineren. Sommige kenmerken, zoals een witte kraag met witte pluimen, komen veel vaker samen voor dan verwacht. Andere combinaties, zoals een witte kraag met zwarte pluimen, een zwarte kraag met witte pluimen of een regelmatig met een onregelmatig patroon in de kraag, komen juist minder vaak voor. Er is een verband tussen sommige kenmerken van het broedkleed en lichaamsgrootte. Witte mannetjes en mannetjes met een onregelmatig patroon in de kraag zijn doorgaans wat kleiner dan andere Kemphanen. Sommige verbanden tussen ruistadium en broedkleed zijn opmerkelijk. De witte mannetjes en de mannetjes met effen kragen op de pleisterplaatsen hebben doorgaans hun rui al voltooid en dat kan niet worden verklaard door verschillen in vangdata. Onze resultaten, met inbegrip van de enorme diversiteit die onder Kemphanen te vinden is, worden uitvoerig besproken in samenhang met ontwikkeling, erfelijkheid en functie.