

Plumage ornaments in male Northern Lapwings *Vanellus vanellus* may not be a reliable indicator of their mating success

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Conspicuous morphological traits that signal aspects of physical state of the owner may be used as cues in mate choice, leading to sexual selection of ornamental traits. In birds, colour patterns as well as structural attributes may constitute ornaments affecting mate choice. In the breeding season, Northern Lapwing *Vanellus vanellus* males possess long crests, contrast-rich black and white facial markings, a black breast, and a shining greenish dorsal side. In non-breeding and juvenile plumages, and in females, crests are shorter, facial patterns have less clear contrasts, and breast and dorsal side possess varying amounts of light fringes. Depending on moult energetics in late winter/early spring, when males acquire their breeding plumage, the state of these characters could potentially signal male condition to females prospecting for mates. We examined if these traits correlated with male mating success in this polygynous species, predicting males with the most expressed ornamental characters (a) to mate earlier and (b) to gain more mates. Trait states were ranked for 31 males of which breeding phenology and number of mates were known. No correlation was found between trait expression and date of first egg laid on the territory and number of mates did not correlate with trait expression. Thus, the study did not confirm that females use crest length, breast blackness and face contrasts or lack of dorsal fringes as cues in their mate choice. This could be because the elaborate traits do not have an ornamental function important for female mate choice, but experimental studies would be needed to rigorously test this hypothesis.

1. Introduction

Female mating preferences for males that express sexually dimorphic traits are known from a wide range of animal taxa (Andersson 1994). Males showing the most exaggerated traits may acquire higher reproductive success than less ornamented males. In birds, sexually selected ornaments have

been found in relation to long tails, striking plumage patterns and long crests (Møller 1988, Andersson 1992, Jones & Hunter 1993, Daunt *et al.* 2003). Presumably the states of ornaments convey information about a male's quality as a mate and thus correlate with male mating success (e.g., Petrie *et al.* 1991). The Polygyny Threshold Model (PTM) in its classical form (Verner 1964,

Orians 1969), which is an ideal free distribution model (Fretwell 1972), predicts the most attractive males to be chosen first, and male mating success to be positively related to degree of ornament expression.

Male Northern Lapwings *Vanellus vanellus* (hereafter Lapwings) are frequently found to be polygynous with about 20–50% of males having more than one female breeding simultaneously on their territory (Byrkjedal *et al.* 1997, Parish *et al.* 1997, Lislevand 2003). Like other species of Vanellinae (Piersma 1996), Lapwings possess conspicuous plumage traits, following a similar pattern in both sexes. Male plumage, however, differs from that of females by showing more distinct black and white head patterns, fewer white feathers and fringes in the black breast patch, and a longer crest (Glutz von Blotzheim 1975, Cramp & Simmons 1983, Meissner *et al.* 2013). Adult males also have fewer buff feather fringes on their back than females.

All these traits show a considerable individual variation (Glutz von Blotzheim *et al.* 1975, Byrkjedal *et al.* 1997), and they have characteristics typical for many sexually selected traits (Andersson 1994) by being less expressed in immature birds and in birds in non-breeding plumage, most developed in the male breeding plumage and being regularly displayed towards potential mates or sexual rivals (e.g., Cramp & Simmons 1983). The examined characters are determined by pre-breeding moult (e.g., Meissner *et al.* 2013), and as feather growth incur costs, ornaments can indicate individual quality of the owner (Møller 1988, Lindström *et al.* 1993, Piersma & Jukema 1993, Mulder & Magrath 1994, McNamara & Houston 2008).

We studied crest length, face and breast contrasts, and back feather fringing as male ornamentation in Lapwings, presumed to be indicators of individual breeding quality, and we wanted to see if the state of these characters would be related to timing of breeding and mating success. We predicted males with long crests and well developed plumages to acquire mates and breed earlier than males with poorly developed plumages, consequently expecting crest length to correlate negatively, and the amount of facial and breast spots and dorsal fringes positively, with date of mating. Assuming no restraints on female mate choice, we

also expected the number of mates to be positively correlated with male crest length but negatively with the amount of white plumage spots on face and breast and with the number of pale fringes on back feathers. Support for any of these predictions would indicate that crest length, unspotted face and/or breast patterns, or lack of dorsal fringes, could act as ornaments used in mate choice by Lapwing females.

2. Material and methods

2.1. Study site and species

The fieldwork was carried out from mid March to mid May 2002 at Gimra, Jæren, SW Norway (58°47'N, 05°37'E) in a field dominated by moist, spring-sown grassland. In spring 2002, a density of 1.7 Lapwing nests per ha and 1.3 territories per ha were found in the study area (Lislevand 2003).

Male Lapwings are highly territorial during breeding, in our study area holding all-purpose territories within which nesting, chick-rearing and virtually all feeding took place. In spring Lapwing females usually arrive to the breeding area a few days later than males, but occasional delays of up to three weeks have been recorded (Kooiker & Buckow 1997). Upon arrival females may visit several territories before settling (Byrkjedal *et al.* 2013). During this period, male aggressiveness increases towards other males and they perform spectacular flight displays. In territorial ground disputes they expose the crest in an “erect attitude” while confronting a rival (Glutz von Blotzheim *et al.* 1975).

2.2. Field methods

The study area was visited daily from 18 March to 30 April 2002. Individual identifications of males and females were done using individually recognizable plumage patterns on the head, breast and shoulders (Byrkjedal *et al.* 1997); only two of the males included in this study had been individually colour-ringed. Plumage patterns for individual recognition were obtained as we carefully studied the individual birds through spottingscopes at the beginning of the field work and made drawings pointing out individual marks. These drawings

were later carried for reference, and with the subsequent frequent observation of the individuals we soon familiarized ourselves with the individual birds. We plotted positions of individual males and flight display routes with few days' intervals in order to map territory borders.

We used laying date of first egg on each territory as a phenological proxy, instead of the date of female settlement, which we were unable to record for the present study. We have previously found a strong correlation between female settling date and start of egg-laying (Byrkjedal *et al.* 1997). If nests were found with more than one egg we calculated the date of first egg within a clutch by assuming a laying interval of one day between first and second, as well as third and fourth eggs, but two days between second and third eggs (Grønstøl 2001, Larsen *et al.* 2003). In the following egg laying dates are expressed as number of days from 26 March 2002 which was the date we located the first egg of the season (day 1).

We assigned mating status to males by recording the number of females nesting on each male's territory and found that 17 males ended up as monogamous, nine as bigamous, four as trigamous and one as tetragamous. Since male Lapwings are difficult to trap, we filmed them with a digital Sony Handycam video camera mounted on a 30 × telescope (Kite SP-ED 80) and from the footage sampled still pictures for subsequent analyses of plumage characteristics. An advantage from use of film footage was that pictures could be sampled when birds took positions that best displayed the plumage parts (face and back laterally, breast frontally). In order to get best possible pictures of the birds' crests and other plumage traits, periods with high winds, bright light and heavy rain were avoided. Filming took place from a car or a hide at the perimeter of the fields and distance to the focal bird was approx. 50–150 m.

2.3. Measurements of plumage characteristics

The characters examined are indicated in Fig. 1. In order to eliminate the variability inherent in photographic images due to positions, distances, etc., standardized head and breast outlines with the general facial patterns indicated with dotted lines were prepared and duplicated, and these sheets were used to draw the actual black and white facial

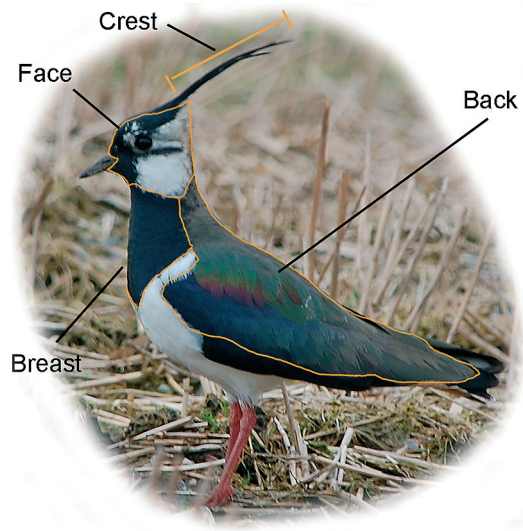


Fig. 1. Delimitation of the plumage areas examined for black portion (face, breast) and light brownish feather edges (dorsal area). The fourth trait, crest, is also evident.

patterns for each individual from the still pictures. To enhance standardization the drawing was performed by the same person (BS) each time. For most of the males both sides of the head could be drawn. The standardized drawings of face and breast patterns were digitally scanned and white and black areas measured in mm² using the computer program Image-pro-plus (Media Cybernetics). Since the software works to a high precision, only one measurement was performed per individual. In our analyses we used percentage of black areas in each individual drawing. When both the left and right sides were measured we used the mean percentage per individual.

We were unable to measure crest length or the amount of dorsal fringes directly from the video footage. Instead we obtained scores of these variables independently from six observers who had prior field experience with Lapwings but without knowing the males' mating status. For each individual male we printed a set of still pictures from the digital video footage showing the crest and the back of each individual. These pictures showed the head laterally, and thus the bill would serve as a scale against which the crest length could be judged. Bill length is a useful scale by varying far less than crest length (data from 10 breeding season males in SW Norway: mean bill length = 24.4

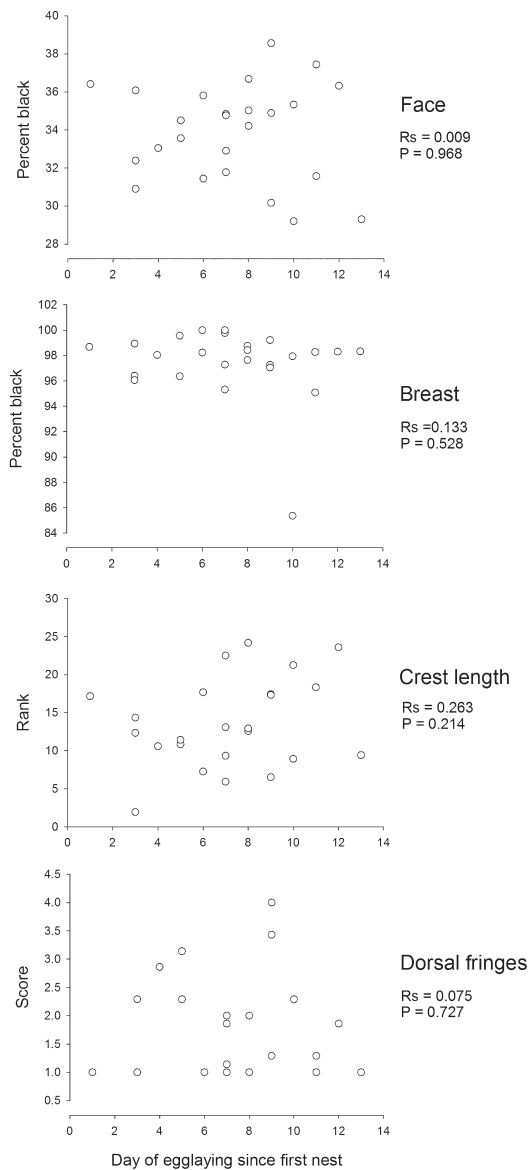


Fig. 2 Character states and egg-laying phenology of first nest on territory, expressed by number of days since first egg was laid in earliest territory. Spearman correlations of character states on date are given.

mm, range 22.2–26.0 mm, CV = 4.2; mean crest length = 90.7 mm, range 79–110 mm, CV = 10.9). From the same set of photos each observer was asked to rank crest length of each male as smaller, equal to or larger than the other males in the sample, and the rank scores averaged for the six observers.

The amount of fringes on wings and back was scored according to the following four categories: 1) no fringes visible, 2) a few unevenly distributed fringes visible, 3) many fringes visible but without covering the whole wings, and 4) both wings and parts of the back extensively covered by fringes. Scores of the six observers were averaged for each individual Lapwing. Kendall Coefficients of Concordance (W_c ; Siegel & Castellan 1988, Zar 2010) showed a significant agreement between reviewers both for scores of crest length and buff fringes on wings/back ($W_c = 0.62$ and 0.96 for crest length and amount of buff fringes, respectively, $p < 0.005$ in both cases when correcting for ties; Zar 2010).

2.4. Statistical analysis

We used the software IBM SPSS Statistics Version 19 for statistical analyses. Non-parametric tests were used throughout. In the analyses we grouped the birds in monogamously and polygynously mated males, the latter including bigamous, trigamous and tetragamous individuals. We compared trait rank orders of monogamous and polygynous males by using Mann–Whitney U -tests. We also tested for such relationships using a multivariate approach; a logistic regression with logit link and backward model selection. This procedure was used on a reduced data set from which all birds with missing data were removed. We treated male mating status as response variable and crest length, dorsal fringes and head and breast blackness as explanatory variables. As the latter two variables were positively correlated (see results), and because of the limited sample sizes, we included only one of these simultaneously in the model. The conclusions from these multivariate models did not differ from the univariate tests based on the maximum data set and we therefore only report the latter. Correlations between the traits, and with egg-laying phenology, were computed by Spearman rank correlations.

3. Results

The distributions of the traits in relation to breeding phenology are shown in Fig. 2. None of the characters showed any correlation with laying date of the first egg on the territory (Spearman rank correlations, $p = 0.214$ – 0.968). We found no signifi-

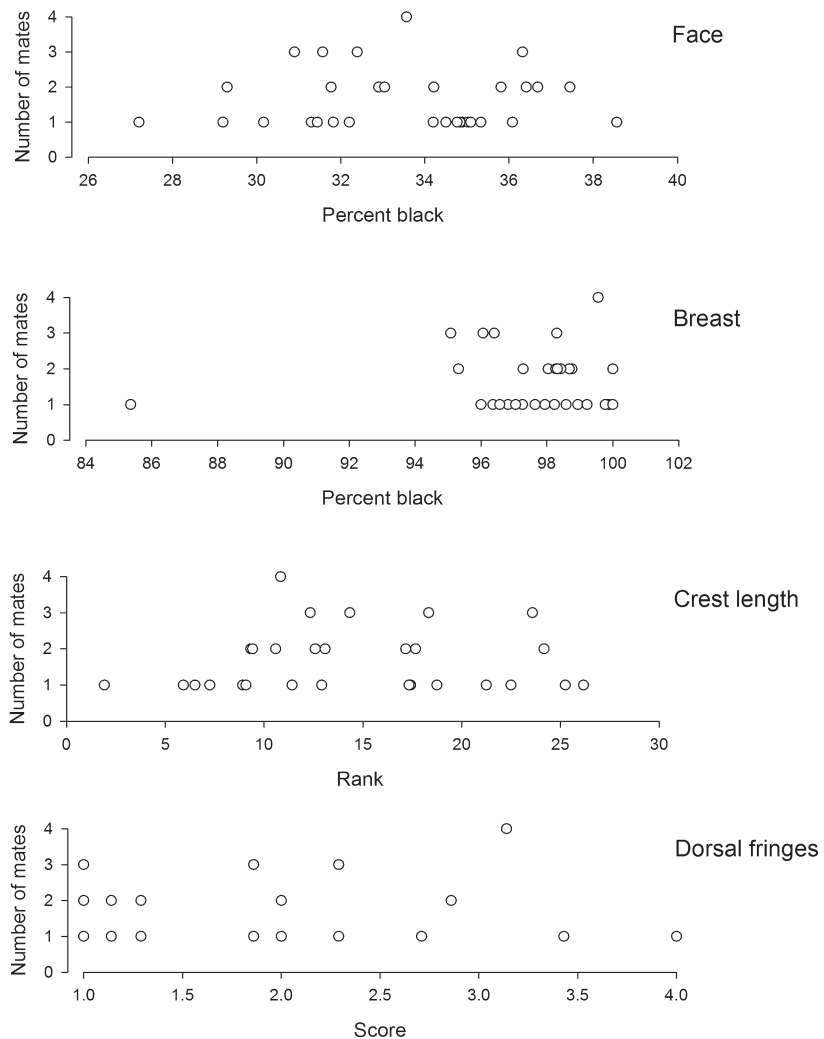


Fig. 3. Distribution of the states of four ornamental traits in male Lapwings, in relation to their mating status. Dorsal fringe score rank from no fringes (score 1) to extensive occurrence of fringes (score 4).

cant differences between monogamous and polygynous males in the state of either of the characters analysed (Fig. 3, Table 1, Mann–Whitney *U*-tests, $p = 0.09–0.9$). The character states of breast and face showed a statistically significant correlation, but no interrelationship between the other characters were found (Table 2).

4. Discussion

The present results do not confirm that differences in male crest length, black areas of face and breast, or light fringes of dorsal feathers in male Lapwings play a role in females' choice of mate, as neither mating success in terms of breeding phenology nor number of social mates correlate with or-

namental expression of the examined characters. This seems surprising, as facial contrasts and lack of light fringes both in breast and back might signal males' completeness of moult, and possibly age, and thus be correlates of the males' condition and suitability as mates. The amount of dorsal fringes shows some variation in the predicted direction, but failing to show statistical significance in spite of the number of birds examined (30 males), this relationship, if any, cannot be strong. Being an extravagant feather structure the crest length should also be affected by moult energetics and thereby male quality (cf. Møller 1988, Møller & Höglund 1991, Turner 2006).

It is increasingly evident that females in many species may compete for mates and that female-

Table 1. Comparison of ranked character states of monogamous and polygynous males. We report the average ranks, number of cases, Mann–Whitney U -statistics and corresponding P -values, the null hypothesis being that monogamous and polygynous males have the same medians.

Character	Mean rank monog.	Mean rank polygyn.	No. monog.	No. polygyn.	U	P
Face blackness	15.4	16.8	17	14	108.0	0.662
Breast blackness	15.9	16.3	17	14	115.0	0.889
Crest length	13.8	15.3	15	13	87.0	0.629
Dorsal fringes	18.0	12.6	16	14	72.0	0.090

Table 2. Spearman correlations between the traits.

	Face blackness		Crest length		Dorsal fringes	
	R_s	P	R_s	P	R_s	P
Breast blackness	0.48	0.007	−0.09	0.641	0.06	0.750
Face blackness			0.09	0.643	−0.14	0.471
Crest length					−0.29	0.150

female aggression may impact on mating outcomes in animals (Slagsvold & Lifjeld 1994, Grønstøl *et al.* 2003) causing female settlement not to follow an ideal free distribution. In such cases, if females of high-quality males are able to efficiently deter all competitors, and lower quality males attract fewer females, males of both high and low quality may be mated monogamously, and males of intermediate quality would be the ones to become polygynous. This can apparently occur in Lapwings (Grønstøl *et al.* 2003). A less perfect match between number of social mates and male ornament expression would then ensue, as monogamous males would be likely to be over-represented in either end of the ornament expression spectre.

A Moses extreme reaction test performed post-hoc, however, did not find a different spread in ornamental expression of monogamous and polygynous males ($p = 0.383$ – 1.0 , 1 outlier trimmed from each end).

The most attractive males are nevertheless expected to be chosen first by prospecting females, and even if these males should remain monogamous, the pair could gain reproductive advantages by both mates being strong, high-quality individuals, apart from benefitting from an early breeding, which generally is considered advantageous in

birds (Drent & Daan 1980, Daan *et al.* 1989). High-quality males could also be the more attractive partners for extra-pair copulations and thus obtain higher mating success than indicated from their social pair bond.

From a correlative study like this one, a function of investigated characters as ornaments for female mate choice cannot be ruled out even though the predicted relationships were not confirmed. The predictions might be weakened by at least three aspects related to the species' biology, viz. (a) mate faithfulness between different breeding seasons, (b) decision rules for female choice, and (c) mate selection according to mate compatibility and not to male qualities from a population perspective.

The degree of mate faithfulness between years is not known for Lapwing, but considering their longevity with prospects of numerous breeding seasons for individual birds (Peach *et al.* 1994, Thompson *et al.* 1994), the pairing-up by at least some of the females with a male from a previous season cannot be ruled out. The rank of ornaments among the males in an area depends on which males are present, presumably varying from year to year, and if faithfulness to a male chosen a previous year overrides the attractiveness of males with stronger developed ornaments, observed re-

relationships between mating and ornaments in one single season may be obscured.

In general, decision rules in female choice can follow two main alternative courses: a female may compare a large number of the males available in an area before making her choice or, she may make her mating decision once she encounters a male who exceeds her own acceptance threshold of male attractiveness (Janetos 1980, Parker 1983). In the latter case, a less clear relationship between ornamental expression and mating can be expected, as each female judges only a small fraction of the available males.

Mate selection based on compatible-genes benefits predicts individual mate preferences instead of the same preferences among females for a population highest quality males leading to good-genes benefits (Puurtinen *et al.* 2009). Avoid mating with close kin might be a plausible compatible-genes selection in Lapwing. A limited natal dispersal in some individuals not infrequently brings Lapwings to breed in fields where they were hatched (Thompson *et al.* 1994, Lislevand *et al.* 2009). If they mate disassortatively in relation to close kin, their choice might affect the observed pattern of ornament expression versus matings.

We were unable to control for these aspects in the present study. However, after nest loss Lapwing males perform much courtship display to retain their mate for renesting (Lislevand & Byrkjedal 2004) indicating that the strength of pair bonds may vary according to the situation. Also, in our study area males would perform courtship display to any new female entering their territories (own observations), and prospecting females can examine many males and territories in a short time (Byrkjedal *et al.* 2013). These observations indicate that females seem liable to readily judge the attractiveness and/or quality of males, and this would strengthen the predictions examined in this study.

We also point out two methodological limitations: (a) crest length was ranked instead of measured, and (b) phenology was analysed from egg-laying dates instead of dates of mating. While measuring crest length would have been preferred to ranking, there was an almost perfect agreement in ranking among the persons who independently performed this task, and a previous study showed a high correlation between date of first egg and fe-

male settling on territories (see Methods section).

Furthermore, our study did not include males that remained bachelors, as data for such males could not be obtained for this study. Including males of this category would potentially give a clearer picture in a correlative analysis if these males were to possess the least attractive ornaments.

In Lapwings, the males' first announcement of territory and their readiness for mating is done with flight displays drawing females to the territories (Grønstøl 1996). Once entered a male territory, prospecting females are exposed to vigorous male ground displays, which involve nest scraping in combination with tail and, to some extent, wing displays (Glutz von Blotzheim *et al.* 1975, Cramp & Simmons 1983, Shrubbs 2007, own obs.). In this position other parts of the male plumage than those studied by us might be more readily displayed to the females, i.e., exposure of legs (red) as well as rump (cinnamon under tail coverts, violet-purple upper tail coverts bordering white basis of tail). We cannot rule out a possible male quality signal value of these traits, more important than the traits in the present study. Also, the violet-purple scapulars forming a patch above the folded wing might hold a potential for signalling male quality. These characters might be worth studying, including their possible UV reflectance creating potentially more efficient signals (Hausmann *et al.* 2002).

So far, among male attributes used by female Lapwings in mate choice, only the flight display has been found to have significance, the males with most aerobatic displays gain highest mating success (Grønstøl 1996). The males' abilities in aerial displays may depend on the wing shape, peculiar to this species of lapwing (Piersma 1996).

In Pied Flycatcher *Ficedula hypoleuca* Alatalo *et al.* (1986) found territory quality to be more important to female choice than male ornamentation, and this cannot be ruled out in the case of the Lapwing. We may speculate that the traits we studied are more of direct importance as status signals among males in their aggressive interactions during territorial defence on the ground while standing face to face or performing parallel runs along territory borders (Glutz von Blotzheim *et al.* 1975, Shrubbs 2007, own observations). The individual variation in the studied traits might even have an importance in the individual recognition to reduce

conflict between neighbouring birds, as was found to be the case in the Ruddy Turnstone *Arenaria interpres* (Whitfield 1986), which, like the Lapwing, may breed at high densities. The lack of correlation between the characters, except face and breast, suggests that the characters we studied may not be affected by the same factors, and this may argue against a common moult energetic cost for crest, dorsal feathers, and face and breast. In their experimental study of Red-winged Blackbirds *Agelaius phoeniceus* Westneat (2006) concluded that not all elaborate traits have an ornamental function. While this might be the case also in the Lapwing, experimental studies would be needed to gain more firm conclusions on this hypothesis.

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Tofsvipehanars ornament i fjäderdräkten indikerar kanske inte framgång vid parbildning

Iögonfallande morfologiska karaktärer som signalerar individens fysiska tillstånd kan vara viktiga vid val av partner och därmed leda till sexuell selektion av dylika ornament. Hos fåglar omfattar sexuellt selekterade ornament både färgmönster och strukturella attribut. Hos tofsvipa (*Vanellus vanellus*) har hanarna under häckningstiden en lång karaktäristisk fjädertofs, kontrastrika svartvita teckningar i ansiktet, svart bröst och grönglänsande ovansida. Utanför häckningsperioden, i juvenil fjäderdräkt och hos honor är dessa karaktärer mindre framträdande. Då är tofsen är kortare, ansiktsteckningarna mindre kontrastrika och bröstet samt ovansidan har en varierande mängd ljusa fjäderbräm. Beroende på ruggningens energetik på senvintern/tidig vår, då hanarna byter till häckningsdräkt, kan alla dessa karaktärer tänkas signalera hanens kvalitet för honor som letar efter en make.

Vi undersökte om utformningen av de nämnda ornamenten korrelerade med hanens framgång vid parbildning, hos denna polygyna fågelart. Vi vän-

tade oss att hanarna med de mest välutvecklade ornamenten skulle (a) locka till sig en make tidigare och (b) få flera makar. Ornamentens tillstånd rangordnades för totalt 31 hanar med känt antal makar och känd häckningsfenologi.

Vi hittade ingen korrelation mellan ornamentens utformning och datum för äggläggning (revirets första ägg), eller antal makar på reviret. Därmed fann studien inte någon indikation på att tofsvipehonorna använder hanens tofslängd, mängden svart på bröstet, ansiktsfärg eller mängden fjäderbräm på ryggen som signaler vid val av make. Orsaken kan vara att dessa karaktärer faktiskt inte fungerar som betydelsefulla ornament i förbindelse med honans val av partner. För att testa denna hypotes mer grundligt behövs för frågan skraddarsydda experimentella studier.

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