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Fluctuating asymmetry and autumn migration in Willow Warbler *Phylloscopus trochilus* L.

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Fluctuating asymmetry (FA) reflects the ability of animals to cope with environmental and genetic stress. Studies made so far have not yet focused and discussed FA´s possible effects on migrating birds. In migrating passerines, FA may reflect an individual's overall condition and dominance during the moulting and pre-migratory period. We studied how FA correlates with the timing of migration in one common migratory species, the Willow Warbler (*Phylloscopus trochilus* L.). In our study, adult females that migrated earlier have more asymmetrical outermost tail feathers than those migrating later. In males, there was no significant correlation between FA and timing of migration. Adult females moult later than males and thus may suffer from time constraints in their moult before migration. Competition for food resources in contemporary migrating females may explain why more asymmetrical, probably low quality females, may have to migrate first.

1. Introduction

Fluctuating asymmetry has been widely studied and discussed in recent years (e.g. Møller & Höglund 1991, Møller 1992, 1993, 1994, Manning & Chamberlain 1994, Swaddle & Cuthill 1994, Witter & Swaddle 1994). In an ideal case bilateral organisms are considered to be symmetrical, i.e., organs on both sides are the same size. Fluctuating asymmetry occurs when a normally symmetrical trait is larger on one side of the body (left/right) than on the other side and there is no tendency that the larger character would be more valuable (Palmer & Strobeck 1986). Asymmetry in morphological traits has been suggested to be a sign of an individual's inability to cope with environmental stress (developmental stability, e.g. Palmer & Strobeck 1986, Manning & Chamberlain 1994), and may also reflect problems in genetical control of the same genome (Parsons 1990).

So far studies have mainly concentrated on the importance of FA when studying sexual selection processes (Watson & Thornhill 1994, but see also Møller & Eriksson 1994). Such studies consider that symmetry differences exist in sexually selected traits, for example in ornaments. Effects can be also important in non-ornamented traits (Rintamäki et al., submitted) or in traits that are important in flight (e.g. tail feathers, Balmford et al. 1993, Evans et al. 1994). After all, if symmetry is a valuable indicator of an individual´s quality and, therefore, important for females to assess males, it might be significant also in other respects. For example, among migrating passerines symmetry may be important.

Most of the passerine species in Northern Fennoscandia migrate from breeding areas to wintering regions. In Finland approximately 2/3 (63%) of passerines are clear migrants and, in addition, 29% of species are facultative dispersals. Thus, over 90% of passerines are potential migrants (this study). A common migrating behaviour in passerines is that different age- and sex classes migrate, at least partly, at different times (Moreau 1972, Curry-Lindahl 1981, Berthold 1993).

Possible differences between symmetrical and asymmetrical individuals in migratory birds arise if an early arrival provides benefits (Cuervo & Møller, pers. comm.). The idea is that more symmetrical individuals are potentially better flyers and represent better quality, and thus are better competitors. Cuervo´s and Møller´s data imply that migratory birds are under directional selection, so that migratory populations (Sweden) in some species are more asymmetrical compared to the non-migratory populations (United Kingdom). This result, even if breeding conditions are remarkably different, reflects that there may be differences among non-migratory and migratory populations of birds.

To study a possible relation between FA and the timing of migration, we measured tail asymmetry in a long-distance migratory bird, the Willow Warbler, during the autumn migration. We compared whether individuals captured at different times during the migration differed also in their symmetry. The Willow Warbler was chosen because it is a common breeding species in Finland, and because it is easy to distinguish in sex and in age in autumn. We chose to measure the tail instead of the wing because repeatability of measurements and thus measurement errors seem to be easier to avoid by measuring tail feathers. Furthermore, the tail is considered to be important in flight and manoeuvrability (Møller 1991, Balmford et al. 1993, Thomas 1993, Evans et al. 1994).

2. Material and methods

2.1. General aspects

The study was done during the autumn of 1994 at the Tauvo bird observatory (64°48′N, 24°38′E) in Siikajoki commune, Finland. The observatory is located along the coast of the Bay of Bothnia where passing migrants are relatively easy to catch in mist nets. Data were collected during migration from mid-July to mid-September. Sampling for measurements was made as evenly as possible during the day and througout the migration season. Because weather conditions affect the migration of Willow Warblers, we were not able to collect equal sample sizes during the whole migration season. In autumn it is also difficult to collect sufficient data from adult birds. The data schedule is summarised in Table 1 and in Figures 1a and 1b.

Juvenile and adult Willow Warblers can be differentiated by comparing the moulting stage and plumage colour (Svensson 1992). Sexes can be separated by using wing length as a criterion (unpublished data in this work, see also Svensson 1992). In this study individuals were sexed so that *adult* males have wing length greater than 69 mm and females less than 69 mm. Juveniles have 1 mm shorter wings, so juvenile males were those with a wing length greater than 68 mm and, similarly, females less than 68 mm (Tynjälä et al., unpubl.

Table 1. Data collected from tail feather measurements.

Period	Sample days	Number of cases
8.–31.7.	22	203
1.– 31.8.	28	242
1.–19.9.	14	40

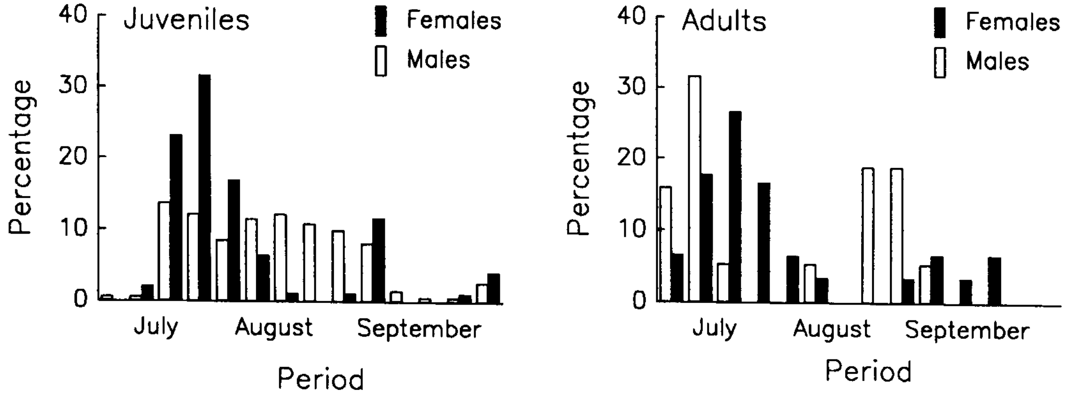

Fig. 1. Distribution of juvenile and adult Willow Warblers collected during 4-day-periods from the middle of July to the early September, 1994.

data). Overlapping cases were left out from the analyses. The values given above were confirmed by cloacal inspection made during spring migration and in breeding season (Tynjälä et al., unpubl. data). All captured birds belong, in practice, to the same subspecies (*P. trochilus acredula*) and belong most likely to the same population that breeds in Northern Fennoscandia and Western Russia. Only a minority of Willow Warblers belongs to the other races or colour types (< 5%, Tynjälä et al., unpubl. data).

2.2. FA measurements

To study fluctuating asymmetry during migration, two to three persons measured both of the outermost tail feathers. In addition, tail length was measured from the base of the tail to the longest central tail feather tip. Tail feathers were studied as an asymmetry trait because it is easier to standardise the measuring technique of different persons for comparable results. Measurements were done with a ruler provided with a pin at zero point. The spike was gently pushed to the base of the feather and the length was read at an accuracy of 0.5 mm. Measurements are more reliable and repeatable when taken with a ruler with the pin than without it (Jenni & Winkler 1989). After capture, birds were carried to the bird station for ringing and measuring (max. some few hundred meters) in special carrying bags designed so that birds cannot damage their feathers. Only undamaged and full-grown feathers were measured.

2.3. Data quality

There was no systematic difference between males' and females' outermost tail feather dimensions (Table 2). Furthermore, we checked differences between sides among individuals and also possible measuring errors by taking 18 repeated measurements from four specimens (ANOVA $F = 590$, $df = 3$, $P < 0.001$). Thus, variance between Willow Warbler individuals was much higher than variance between repeated measurements. All repeated measurements were done so that the measurerer was not able to recognise birds individually and thus could not remember previous measurements. Repeated measurements of a certain individual by two persons gave the same results: P-values for two-sample variances (F-test) between measurerers were 0.41 and 0.41 for both tail feathers ($F = 2.05$, $N = 23$ in both cases). Also, differences between repeated measuring of the same tail feathers in two-sample variances were non-significant ($F = 1.35$, $P = 0.24$, $N = 23$). Furthermore, we checked that the *difference* between repeated left-right side meas-

Table 2. Descriptive statistics for male and female Willow Warblers left and right outermost tail feather lengths.

	Right side			Left side		
	Mean	SD	N	Mean	SD	N
Males	50.3	18.7	341	50.4	17.4	341
Females	46.2	20.4	125	46.2	20.1	125

urements were repeatable (Pearson correlation: $r = 0.89, N = 23, P < 0.001$).

In our analyses (Spearman two-tailed correlation analysis) we transformed original values to describe relative asymmetry (absolute difference divided by mean value of outermost tail feather's length). This was done to avoid errors that may arise if an individual's size is not standardised. Data were sufficiently normally distributed (Wilk-Shapiro-test) and mean differences of right-left - values were near zero (see Table 3). We used the term "juvenile" for individuals born during the study year and "adult" for those born earlier.

2.4. Fat deposits

Fat reserves for each bird were recorded during the autumn migration following the method of Busse and Kania (1970). This was done because we thought that symmetry, timing of migration and fat level, which probably indicates the condition of a bird, may correlate with each other. Body mass was measured with a Pesola spring balance.

3. Results

3.1 General aspects of sex and age

Comparative analyses between age and sex class, body mass, and tail length have been summarised in Table 4. Males were heavier and had longer tails than females. Also, adults were heavier and tended to have longer tails than juveniles. Adult and juvenile males did not differ in their body mass, while in females there was a difference between age classes. In tail length females also differed, and juvenile and adult males have slightly different sized tails.

3.2. Aspects of asymmetry

Mean values of relative tail asymmetries in both Willow Warbler sexes were similar (Table 3). Absolute asymmetries vs. tail length coefficients were near zero or positive (juvenile males –0.28 and females 0.01, adult males 0.40 and females –0.04). Both results coincide with earlier findings by Møller and Höglund (1991) for non-ornamented species. There was no correlation between absolute asymmetry and tail length, if we compared only sex (males: $r_s = -0.05$, ns, $N = 339$ and females: $r_s = 0.03$, ns, $N = 123$). We also checked if symmetry correlated with body mass, but it did not.

3.3. Asymmetry and timing

The female tail asymmetry score was negatively correlated with capture date. Both adult and juvenile females were significantly more symmetrical later in the autumn, even if in the juveniles correlation was not particularly high (Fig. 2a juveniles and Fig. 2b adults). In males, there was no relation between asymmetry and capture date.

The median capture date of adult males was significantly earlier than that of juveniles (Mann-Whitney U-test: $z = 2.46, P = 0.014, N = 340$), but

Table 3. Descriptive statistics summarized for each sex and age classes. I = number of individuals, II = signed mean of left-right value for outermost tail feathers (mm), III = SD for II, IV = skewness, V = kurtosis, VI = relative asymmetry for outermost tail feathers, VII = SD for VI, VIII = Wilk-Shapiro normality test-value for mean signed left-right outermost tail feather values and IX = Spearman rank order correlation coefficients for left and right sides of tail (two-tailed significancies: P < 0.05 = *, P < 0.001 = **, P < 0.001 = ***).

	I	II	III	IV	V	VI	VII	VIII	IX
Males									
Juvenile	320	0.72	7.6	0.77	2.48	0.0106	0.0109	0.92	0.89***
Adult	19	0.88	8.7	–0.37	0.01	0.0128	0.0111	0.96	0.95***
Females									
Juvenile	93	1.34	6.1	0.93	2.48	0.008	0.0107	0.87	0.87***
Adult	29	0.69	9.4	0.16	1.61	0.0140	0.0137	0.91	0.95***

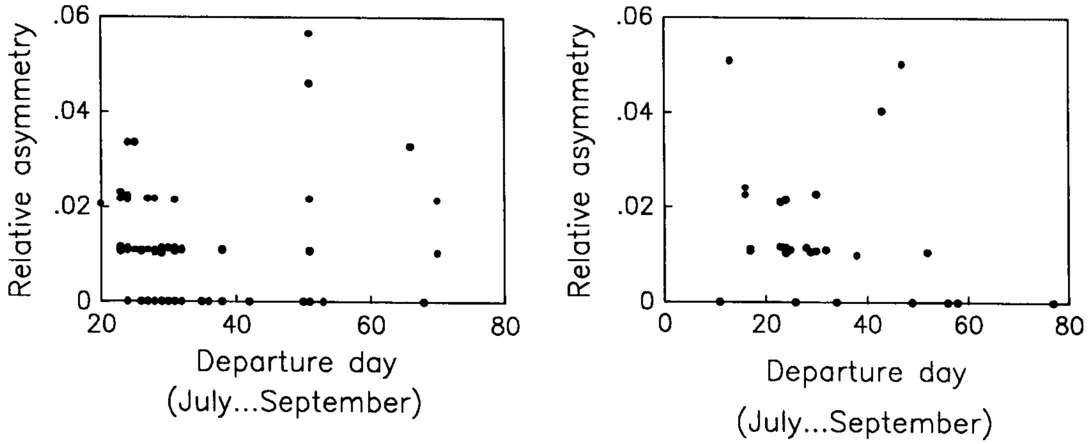

Fig. 2. Timing of migration of juvenile (a) and adult (b) Willow Warbler females in relation to outermost tail feather relative asymmetry. Sampling days include whole migrating period from July to September. (day 0 = 10th July in adults and day 20 = 20th July in juveniles). Correlations are shown in table 6.

not in females (z = 1.61, P = 0.11, N = 125, Table 5). Females were significantly earlier than males (z = 5.53, P < 0.001, N = 465). This result might be partly due to skewness of our data: most measured individuals (69%) were juvenile males. Spearman correlations are presented in Table 6. In data where sexes and ages were pooled within 4-day-periods (N = 14), individuals became, on an average, more symmetrical during the migrating season (Fig. 3).

Table 4. Male and female mean body mass (g) and tail length (mm) between and within sexes and age groups (juvenile or older) tested by using two-tailed rank sum test (Mann-Whitney U-test).

Group	body mass	tail	N
Adult males	9.3	52.8	18
Juvenile males	9.2	52.0	320
Adult females	8.4	48.6	29
Juvenile females	8.2	47.7	95
Body mass	z	N	P-value
Male vs. female	14.6	463	< 0.001
Juvenile vs. adult	2.3	480	0.02
Juv. male vs. adult	1.0	338	0.30
Juv. female vs. adult	2.2	124	0.03
Tail length			
Male vs. female	14.9	463	< 0.001
Juvenile vs. adult	1.8	480	0.08
Juv. male vs. adult	1.9	338	0.06
Juv. female vs. adult	2.5	123	0.01

3.4. Fat deposits and timing

Fat-score coefficients were not particularly high but both juvenile males and females tended to have less fat later in the migration season, while in adults correlations were not significant (Table 6). In pooled 4-day-period data, individuals were fatter later in the season (Fig. 4). Data pooling may overestimate some groups that are presented over the others (juvenile males), therefore we looked for differences between fat index and age or sex groups. Fat, in individuals and was the same even in different age groups (Mann-Whitney U-test z = 0.52, P = 0.61, N = 483) or sex groups (z = 1.48, P = 0.14, N = 465). Furthermore, standard deviation values were significantly larger in late migrants ($r_s = 0.71$, $P < 0.01$, N = 14) possibly reflecting that later in the migrating season individuals' fat reserves differ more.

Table 5. Timing of migration recorded from the middle of July (i.e. day 1 = 15th July) in different willow warbler sex and age classes. Values are percentiles (fractiles) 25, 50 (median) and 75.

	25	50	75	N
Adult male	15	23	47	19
Juvenile male	30	40	49	321
Adult female	22	27	39	30
Juvenile female	26	29	36	95

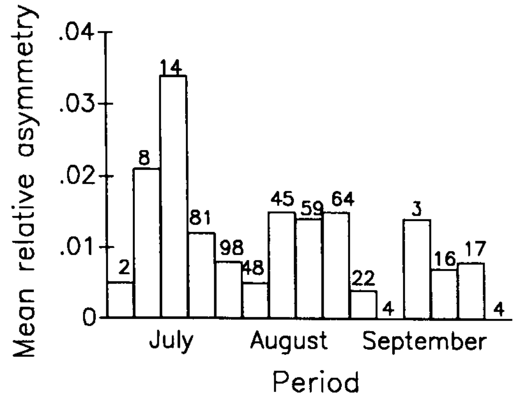

Fig. 3. Relative outermost tail feather asymmetry during the course of migration. Pooled data with all sexes and age classes where each column represents mean value for 4-day-periods and values above column are sample sizes ($r_s = -0.63$, $P < 0.01$, $N = 14$).

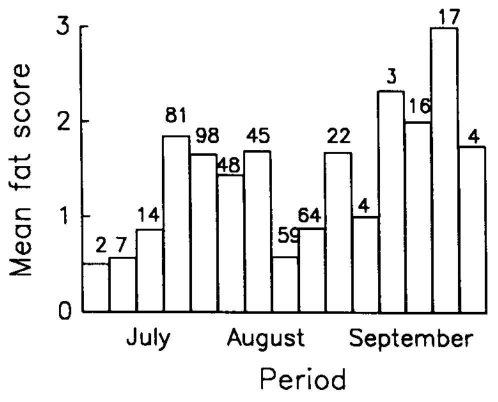

Fig. 4. Mean fat-score index compared with timing of migration. Data is pooled, consisting of both sexes and all age classes. Each column represents mean value for 4-day-periods and values above column are sample sizes ($r_s = 0.61$, $P < 0.01$, $N = 14$).

3.5. Fat-score and asymmetry

Data representing individuals' fat reserves and correlation with tail asymmetry are summarised in Table 6. None of the correlations in sex and age groups were significant. Pooled data showed correlation between relative asymmetry and fat-index. Relative asymmetry tended to be lower in birds with higher fat-score (Fig 5). The method we used to describe fat reserves is very robust. Therefore, the negative trend between fat-score and asymmetry is notable. This result may indicate that individuals having more fat are also less asymmetrical.

4. Discussion

Fluctuating asymmetry seems to be more expressed in sexually selected traits than in nonsexual traits (Møller and Höglund 1991). Studies published so far have not addressed the possible importance of fluctuating asymmetry in migrating birds. We found that in the autumn adult Willow Warbler females had more symmetrical outermost tail feathers later in the migration season, while in males there was no dependence between timing of migration and FA.

Tail feathers are moulted rapidly during moult (Svensson 1992), but still it is not clear whether rapid or slow development of a feather is connected to FA. An experiment made in Starlings (*Sturnus vulgaris,* Swaddle & Witter 1994, see also Parsons 1964, Sciulli et al. 1979) suggests that nutritional and energetic stress causes developmental asymmetries. Achieving enough food (fat reserves) can be an important factor for individuals to complete moult successfully before migration. Unfortunately

Table 6. Spearman rank correlation coefficients for aspects of asymmetry, fat-index and timing of migration. Two-tailed significancies: P < 0.05 = *, P < 0.01 = **, P < 0.001 = ***.

	Timing vs. fat-score	Timing vs. asymmetry	Asymmetry vs. fat-score	N
Juvenile males	– 0.16**	– 0.09	– 0.09	321
Adult males	+ 0.25	– 0.12	+ 0.29	18
Juvenile females	- 0.20*	– 0.23**	+ 0.05	95
Adult females	+ 0.25	– 0.42**	– 0.27	30

our data were too scanty to show if females with greater fat reserves were more symmetrical. Symmetry differences may arise if tail feathers are more fully grown later in the migration season. This possibility is unlikely because measurements were standardised to take into account individuals' size (relative asymmetry), feathers were seemingly fullgrown and because the outermost tail feathers are generally moulted simultaneously (Svensson 1992).

The Willow Warbler has an extremely exceptional moulting system (Stresemann 1927–44). Adult individuals moult completely twice a year: partly during and mainly after the breeding season in late summer, and during the wintering season in Africa. Adult males and females also differ in their moulting strategy: females begin their postnuptial primary feathers moult 1.5 weeks later than males (Tiainen 1981). Moult of rectrices occurs usually rapidly and begins after three to five primaries are moulted (Svensson 1992). Why do females moult later and show greater symmetry in later migrants? Tiainen (1981) suggests that differences in moulting time between sexes may be due to male sexual activity in autumn when adults may have to defend their positions against juvenile males. Another, not mutually exclusive explanation, is that females guarantee better maternal care to their offspring by beginning their moult later than males (Tiainen 1981). However, these suggestions do not explain differences between sexes in relation to FA and timing of migration.

In birds the larger sex and older individuals are *in sensu lato* often dominant over the smaller ones (e.g., Greenwood & Wheeler 1985, Höglund & Alatalo 1995). In Willow Warblers males are significantly larger than females. Since females are more likely to be at a lower rank in the dominance hierarchy than males, they should also be more susceptible to environmental stress and thus show more variation in FA. Males migrate separately, while females seem to leave more or less simultaneously. Thus females may have to compete for resources during the pre-migratory period.

There are several suggestions that might explain why later migrants are more symmetrical. Early migrants may represent different subpopulations than later ones, and thus different breeding conditions during that year. Furthermore, if breeding conditions have changed during the season, early breeders may have suffered from poor weather conditions. There might exist more variation in juvenile females' FA early in the migration season, since many low rank individuals may die soon after their independence from maternal care. However, this does not explain why adult females show higher symmetry late in the season. Therefore, considering adult birds, it is possible that low rank individuals may have to leave first, since dominant birds exclude them from important resources.

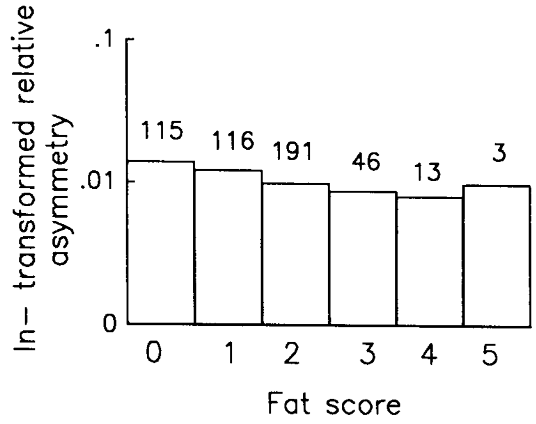

Fig. 5. Fat-score index in proportion to relative outermost tail feather asymmetry. Values above column are sample sizes ($r_s = -0.83$, $P < 0.10$, $N = 6$).

Our data is insufficient to come to any conclusions regarding these possible explanations. Also, studying symmetry is difficult since differences in FA between individuals seem to be small and may partly be due to measuring errors. To conclude, differences undoubtly exist and suggest that studying symmetry also in traits not connected to direct fitness benefits (e.g. breeding success), can bring some new perspectives.

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Selostus: **Pajulinnun pyrstösulkien symmetrisyyden vaikutus syysmuuton ajoittumiseen**

Vaihteleva epäsymmetrisyys (engl. fluctuating asymmetry) viittaa oikean ja vasemman puolen välisiin eroihin yksilön parillisten elinten mitoissa (esimerkiksi raajat). Poikkeamat symmetriasta normaalisti kaksikylkissymmetrisillä eliöillä on tulkittavissa häiriöiksi yksilönkehityksessä. Symmetrisyyteen vaikuttaa yksilön kyky sietää ympäristön aiheuttamaa ja geneettistä stressiä kasvun aikana. Epäsymmetrisyyden ilmenemistä ja sen merkitystä on enimmäkseen tutkittu seksuaalivalinnan kannalta, eli siis valitsevatko esimerkiksi haarapääskynaaraat koiraita, joilla on symmetrisemmät uloimmat pyrstösulat vai eivät? Viimeaikaisissa tutkimuksissa on havaittu, että symmetrisyys voi olla merkittävää myös muutenkin. Linnuilla pyrstö on tärkeä lennon hallintaan ja liikkeisiin vaikuttava elin. Sen vuoksi sen symmetrisyyden voi olettaa olevan merkityksellinen muuttolinnuille.

Tutkimme Tauvon lintuasemalla syksyllä 1994 Afrikkaan muuttavan hyönteissyöjälintumme, pajulinnun, uloimpien pyrstösulkien symmetrisyyttä. Koko muuton ajan (heinä-syyskuu) keräsimme pyrstösulkien mitta-aineistoa nuorilta ja vanhoilta pajulinnuilta. Havaitsimme, että sekä nuoret että vanhat naaraspajulinnut olivat symmetrisempiä muuttokauden loppupuolella. Koirailla tällaista eroa ei havaittu. Pajulinnulla on poikkeuksellinen sulkasato, sillä aikuiset linnut sulkivat kaikki ruumiinhöyhenesä ja sulat kahdesti vuodessa: talvella talvehtimisalueella ja kesällä pesimäkauden jälkeen. Mahdollinen syy havaittuun eroon sukupuolilla voi liittyä sulkasadon ajoittumiseen. Nimittäin koiraat aloittavat sulkasatonsa keskimäärin aikaisemmin heti pesinnän jälkeen kuin naaraat, jotka jatkavat jälkeläisten hoitoa pitempään. Naaraat joutuvat aloittamaan sulkasatonsa myöhemmin ja se voi aiheuttaa naaraiden välille kilpailutilanteen, esimerkiksi ravinnosta. Tässä kilpailussa huonosti pärjäävät yksilöt ovat mahdollisesti pakotetut aloittamaan muuttonsa aikaisemmin, mikä ilmenisi symmetrian lisääntymisenä muuton edetessä. Aineiston perusteella on kuitenkin vaikea sanoa yksiselitteisesti, miksi myöhemmmin muuttavilla naarailla on symmetrisemmät pyrstösulat. Eri aikaan Tauvossa esiintyvät linnut ovat voineet pesiä eri alueilla, joissa ravinnon määrä on ollut erilainen ja siten aiheuttaa eron symmetrisyydessä. Työmme vahvistaa käsitystä, että symmetrisyys voi olla yksilöille merkittävää myös muutenkin kuin puolisonvalintatilanteessa. Siten symmetrisyyden tutkiminen muuttavilla linnuilla tuo uutta tietoa siitä, miten ja miksi eliöt eroavat yksilöinä.

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