

Female-biased sex ratios and the proportion of cryptic male morphs of migrant juvenile Ruffs (*Philomachus pugnax*) in Finland

Kim Jaatinen, Aleksi Lehikoinen & David B. Lank

K. Jaatinen, ARONIA Coastal Zone Research Team, Åbo Akademi University and Novia University of Applied Sciences, Raseborgsvägen 9, FI-10600 Ekenäs, Finland. E-mail kim.jaatinen@gmail.com

A. Lehikoinen, Finnish Museum of Natural History, PO Box 17, FI-00014 University of Helsinki, Finland. E-mail aleksi.lehikoinen@helsinki.fi

D.B. Lank, Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6. E-mail dlank@sfu.ca

Received 16 November 2009, accepted 5 August 2010

Biases in sex ratio may affect the viability of populations, and may arise for different reasons, such as biased primary ratio and differential juvenile or adult mortality of sexes. Global populations of Ruffs are thought to be strongly female biased. To determine the demographic origin of this sex bias, we report the sex ratios among juvenile Ruffs on their southward migration in Finland during 1985–2006. We also quantify the proportion of cryptic, female-like ‘faeder’ males at this demographic stage, and examine migration timing by sex. We found a strong female bias in juvenile populations; across the study years, 34% of individuals were males. Female juveniles migrated earlier than male juveniles. Faeder males made up ca. 1% of juvenile populations, similar to estimates from mixed-age populations elsewhere. These results, combined with previous studies, confirm the strong female bias and the low frequency of ‘faeders’ at the juvenile stage of the Ruff. The sex bias might thus demographically originate from sex-allocation strategies by females at the egg stage. Given the genetic determination of the status of faeders, their proportion among juveniles provides the first estimate of the morphs’ proportional reproductive success.



1. Introduction

The Ruff (*Philomachus pugnax*) is a sexually size-dimorphic, lekking wader. Males average ca. 1.7 times the mass of females and are ca. 1.1–1.2 times larger in linear dimensions (Münster 1990, Meissner & Zięcik 2005). Ruffs breed across subarctic northern Eurasia, and make extensive migrations

to wintering grounds, primarily in Africa. Their population appears to have a female-biased sex ratio (Cramp & Simmons 1983, Delany *et al.* 2009, Zwartz *et al.* 2009). This is unusual among birds, but may be the rule for lekking species (Donald 2007) and, theoretically, for strongly sexually-selected species in general (Shuster & Wade 2003). Ruffs are also of particular interest with respect to

ratios of male morphs, being unique among birds in having three genetically distinct male morphs, which differ in mating behaviour, nuptial plumage, and body size (Hogan-Warburg 1966, van Rhijn 1973, 1991, Höglund & Lundberg 1989, Jukema & Piersma 2004, 2006, Lank *et al.* 1995, 1999, D.B. Lank, S.B. McRae & L.L. Farrell, unpubl. data). At leks, three morphs can be distinguished. Territorial ‘independent’ males and non-territorial ‘satellite’ males are both ornamented, but differ from each other in the colouration of breeding plumage, displaying behaviour and (slightly) body size. The ratio of independent and satellite males follows directly from the relative success of the morphs in reproductive competition (Hugie & Lank 1987, Widemo *et al.* 1998, Thuman 2003). The actual social or ecological factors determining the equilibrium morph ratio remain undocumented. Males of the third morph, ‘faeders’, are small, unornamented and female-like (Jukema & Piersma 2004, 2006). Faeders can be distinguished from females, and from the other male morphs, based on their intermediate wing length, and they may constitute 0.35–1.3% of individuals in populations (Jukema & Piersma 2006, Karlionova *et al.* 2007, Verkuil *et al.* 2008). The demographic patterns and social or ecological mechanisms determining the proportion of faeder males in populations are completely unknown.

Assessments of sex and male-morph ratios in populations during the breeding season are difficult due to sex- and morph-dependent differences in local movement patterns (e.g., Lank & Smith 1987). The best estimates of sex ratio come from studies done in the non-breeding season, but drawing conclusions from these about the global sex ratio is complicated because of strong geographical clines (Cramp & Simmons 1983, Delany *et al.* 2009, Zwartz *et al.* 2009). In western Europe, for example, over-wintering Ruff populations constitute almost completely males, but these population sizes are small, representing perhaps 1–2% of the global population of Ruffs. In western Africa, where the bulk of the species spends the non-breeding season, the ratio appears moderately female biased, and 30–40% of individuals are males. More extremely, in southern and eastern Africa, only 10% of individuals may be males. It has been suggested that many “missing” males occur at the southern boundary of the Sahara Desert, partially

offsetting the apparent overall female bias (Münster 1996). The global sex ratio appears to be on the order of up to 40% males. – In the present paper, sex ratio refers to the percentage of males in a population or a sample.

Demographic sources for the putative female-biased sex ratio are unclear. No sex-specific estimates of the annual survivorship of adults other than Boyd’s (1962) are available. Boyd (1962) calculated annual survivorship rates of 50% for males and 40% for females, based on 42 and 13 recoveries of each sex, respectively. An apparent male bias in return rates to local breeding areas (Andersen 1948), suggesting higher adult survivorship for males, was based on only 11 females, and a bias towards marking successful breeding males, which have higher return rates than less successful males (Andersen 1951, Widemo 1997). Annual breeding densities vary more in females than in males (Andersen 1948), suggesting substantial between-year movements by females, which could lower the return rates and mark-recapture estimates of apparent survival. To sum up, sex bias in adult survivorship appears poorly documented.

Additionally or alternatively, a bias could originate from females’ manipulation of the primary (start of development) or secondary (hatching) sex ratio, which occurs in some species of birds (Donald 2007), possibly including Ruffs. Thuman *et al.* (2003) found that the annual body condition of female Ruffs was associated with the annual sex ratio of their chicks. In one year, when nesting females were leaner, the hatching sex ratio was around 40%, whereas in two years, when nesting females were fatter, no significant bias in sex ratio was found. Although the samples by Thuman *et al.* (2003) were not large, these data suggest condition-dependent sex allocation resulting in a bias towards the production of females, the substantially smaller sex.

The sex and morph data of Ruffs, collected by ringers at migratory stopover sites, provides a potentially rich source of information but, as with non-breeding season estimates, these data must be interpreted with respect to temporal, geographical, and local variation in capture rates. The timing of migration of adult males and females differs markedly during both northward and southward migration. In spring, males arrive at migratory stopover sites earlier than females (Münster 1989a, Jukema

et al. 2001, Karlionova *et al.* 2007), enabling them to occupy leks prior to the arrival of females. Subsequent to the mating season, males initiate migration while females stay to provide parental care, resulting in earlier southward migration and wing moult by males (Koopman 1986, Münster 1991), although the differences in migration timing may be less than commonly assumed (Münster 1989a). Migration routes also differ, as males and females share their breeding areas but over-winter in partly separate areas. Females seem to generally migrate further east than males do (Karlionova *et al.* 2007). Finally, different habitat usage (Verkuil & de Goeij 2003), stopover times, or the probability of capture in walk-in traps or mist nets (Münster 1989b) could affect observed sex ratios based on census or capture data.

A potentially useful source of information to narrow down the source of the female bias is the sex ratio of juveniles. Biases at this stage cannot derive from differences in adult mortality rates, but can include primary sex ratios plus any differences in survivorship during egg development, juvenile growth, and post-fledging (e.g., Clutton-Brock *et al.* 1985, Røskaft & Slagsvold 1985, Griffiths 1992). Thus, sex ratios observed during juvenile migration will likely be intermediate between primary and adult sex ratios (e.g., Lehikoinen *et al.* 2008a, b). Large numbers of juveniles have been caught on their first southward migration at several sites in Europe. The timing of migration should not markedly differ between male and female juveniles, as both sexes are similarly constrained by ontogenetic development. However, geographical biases may remain, assuming that juvenile sex ratios at non-breeding sites are similar to those reported for the overall population. All four publications of autumn-migrant juvenile Ruffs report a female bias: 35.5% of individuals were males in the Gulf of Gdańsk ($n = 593$; Meissner & Zięcik 2005), 40.2% at Münster, Germany ($n = 644$; Münster 1990), 34.7% in the Wash, U.K. ($n = 248$; Gill *et al.* 1995) and about one-third in Finland ($n = 562$; Saurola 1977).

If sex biases consistent with those reported for the total population occur at the juvenile stage, differential adult mortality may be of minor importance in determining sex ratio. Similarly, if the frequencies of male faeder morph among juveniles match those reported for mixed-age populations,

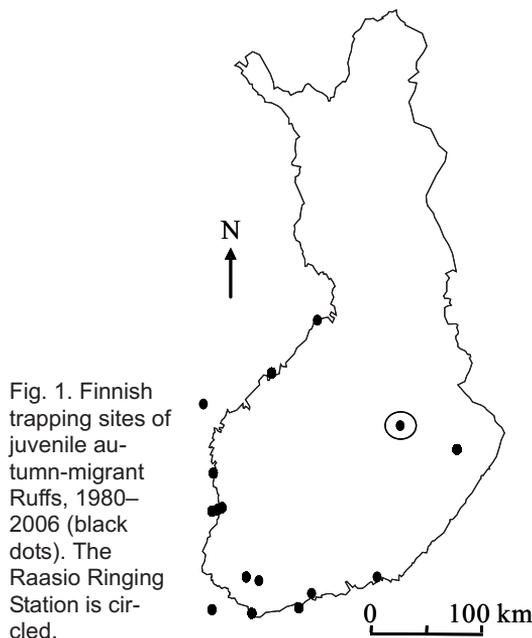


Fig. 1. Finnish trapping sites of juvenile autumn-migrant Ruffs, 1980–2006 (black dots). The Raasio Ringing Station is circled.

the likelihood that differential adult mortality among male morphs in influencing the faeder proportion appears small. However, strongly divergent findings would indicate a greater importance of differential mortality among adults in terms of sex ratio and/or proportion of faeders. We therefore examined the sex ratio and faeder proportion of juvenile migrant Ruffs, captured during their first southward migration through Finland, using a large data set collected during 1980–2006. For methodological reasons, we compare the timing of migration between juvenile males and females, and investigate variation in body size through the migration season. We interpret our results in comparison with those found for juveniles at other migration sites, and compare the observed sex and morph ratios at this demographic stage with results from studies done in mixed-age populations.

2. Material and methods

Between 1980 and 2006, altogether 1,526 first-year Ruffs were captured for ringing in Finland, mainly using walk-in traps ($n = 1,462$) and to a lesser degree using mist netting ($n = 68$; Busse 2000; Fig. 1). Fifty-five percent ($n = 847$) of all ringed individuals were caught at the Raasio

Table 1. Proportion of male juvenile migrants, and of faeder males, captured in mist nets and walk-in traps at the Raasio Ringing Station versus a pooled sample from other stations in Finland. n = total juvenile ruffs captured.

Area	Mist nets		Walk-in traps		Both methods	
	n	Proportion males	n	Proportion males	n	Proportion faeders
Raasio, Siilinjärvi	0	–	843	0.367	843	0.006
Other Finnish stations	68	0.338	615	0.318	683	0.015
Total	68	0.338	1,458	0.345	1,526	0.01

Wader Ringing Station (63° 9' N, 27° 43' E) during 1987–2006 (Fig. 1). The trapping at Raasio started in early July and continued until the end of September each year (see, e.g., Ukkonen 2002, 2007) in order to cover the main migration season of the young Ruffs (Lehikoinen & Vähätalo 2000). First-year Ruffs can be distinguished from adults at this time of year by their distinctive rusty plumage (Cramp & Simmons 1983). At all Finnish stations, captured Ruffs were weighed and wing length was measured by experienced ornithologists using the maximum chord method (e.g., Bairlein 1995, Busse 2000). To narrow down populations of origin, and to look for potential differences between populations in passage times within each sex, we computed mean wing lengths and examined patterns with respect to capture date. We examined the possible departure in sex ratio from

the predicted 1:1 by using t -test, and possible trends in sex ratio along with the progress of the season using Spearman rank correlation analyses.

We classified birds into three gender groups based on wing length, which is the best discriminating metric (Karlionova *et al.* 2007): females (wing length < 170 mm), displaying males (wing length > 180 mm) and faeder males (169 mm < wing length < 181 mm), as confirmed by molecular markers (Jukema & Piersma 2004, 2006, Karlionova *et al.* 2007). These thresholds were determined primarily from adult birds captured in the Netherlands with newly-moulted feathers, rather than from young birds. However, autumn measurements taken from young birds differ from spring measurements taken from older ones by only ca. 0.2 mm (Münster 1990), so these thresholds appear applicable to our sample. We restricted

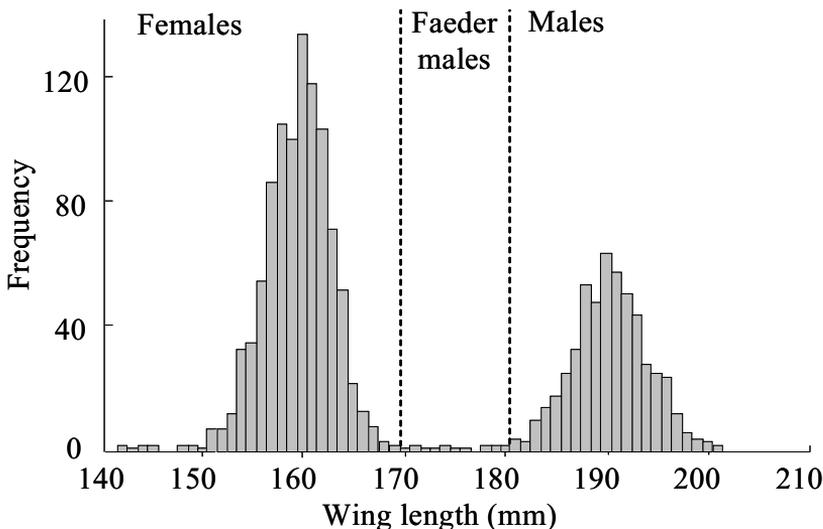


Fig. 2. Wing-length distributions of autumn-migrant juvenile Ruffs captured in Finland, 1980–2006. Gender and faeder classifications follow Jukema & Piersma (2006).

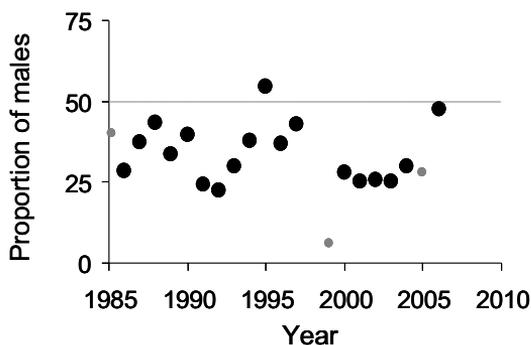


Fig. 3. Annual percentage of males among young Ruffs caught in Finland during autumn migration, 1985–2006. The large black dots indicate years with a sample size of at least 20 individuals, and the small grey dots indicate sample sizes of fewer than 20.

the analyses of annual sex ratios of young birds to years when more than 20 individuals were caught (18 out of 27 years). We compared the migration phenology of the females and ornamented males caught in Raasio and calculated cumulative dates for migration, i.e., dates when 5%, 50% and 95% of the birds of each sex ringed over the whole season were ringed. We tested the similarity in migration time between sexes using *t*-test, and the effect of time on wing length using linear regression analysis.

3. Results

Approximately two thirds of the juvenile Ruffs caught were females (Table 1, Fig. 2). The mean annual female proportion was 0.66 ± 0.091 SD. Annual sex ratios were significantly female biased relative to an expected 1:1 ratio (*t*-test; $t_{17} = -7.53$, $P < 0.001$; Fig. 3). More males than females were captured in only one of the 18 years included in the data. There was no significant trend in the annual sex ratio of juvenile birds during 1986–2006 ($r_s = -0.16$, $P = 0.52$, $df = 17$; Fig. 3). The samples from Raasio did not significantly differ from the pooled sample of the other Finnish locations (Table 1). No site was consistently male biased. The sex ratio did not significantly differ between different capture techniques (mist nets vs. walk-in traps; $\chi^2_1 = 0.00$, $P = 0.98$). Faeder males, as identified by wing length, comprised ca. 1% of all birds caught (0.6–1.5%; Table 1, Fig. 2).

In Raasio, females were captured on average 1–2 days earlier than males (*t*-test for males: 17 Aug ± 0.7 (SE); for females: 15 Aug ± 0.6 , $t_{840} = 2.00$, $P = 0.04$; Table 2). The mean (\pm SD) wing lengths were 190.5 ± 3.55 for ornamented males, 174.6 ± 4.04 for putative faeders and 159.7 ± 3.24 for females. Within sexes, wing length did not significantly change over time (females: $F_{1,530} = 2.22$, $b = -0.015$, $P = 0.13$; males: $F_{1,308} = 1.71$, $b = 0.022$, $P = 0.19$).

4. Discussion

The sex and faeder ratios of juvenile migrant Ruffs obtained in Finland are comparable to those estimated from mixed-age populations elsewhere (see above). Hence, the strongest demographic factors responsible for determining both ratios occur early in life, at the egg, fledgling, or post-fledgling stage, and are thus unlikely to result from remarkable differences in survivorship later on in life.

4.1. Sex ratio

The sex ratios of first-year migrant Ruffs, measured in Finland over a twenty-year period, were consistently female biased: males made up on average about 34% of all individuals, as previously reported from a sample gathered during 1974–1976 (Saurola 1977). The number of females caught exceeded that of males in 17 out of 18 years (Fig. 3).

We believe that our results represent true values for populations of post-fledgling migrants and are unlikely to be severely biased. Females were captured about two days earlier than males, pre-

Table 2. Timing of autumn migration in young male and female ruffs (capture dates for the cumulative percentage of birds caught within each sex) at the Raasio Ringing Station between 1987 and 2006.

Sex	Migration phase		
	5%	50%	95%
Females	23 July	16 August	9 September
Males	27 July	17 August	8 September

sumably reflecting slightly earlier migratory passage. Earlier female than male juvenile passage has previously been documented in central Germany (Münster 1989b) and in Britain (Gill *et al.* 1995). Females fledge about two days earlier than males (D.B. Lank, personal observations on captive birds), which could account for the difference in migratory timing. Because our sampling spanned the full autumn-migration period between July and the end of September (particularly at the Raasio Ringing Station, which contributed the majority of the data), biases in temporal sampling may not explain for the observed sex differences in numbers or timing. Another pitfall is that male and female Ruffs differ in habitat usage (Verkuil & de Goeij 2003). The diversity of capture sites in the present data, however, makes habitat use an unlikely source of bias. Sex ratios were similar in Raasio and in the pooled sample from other, primarily coastal, sites (Fig. 1). No site was consistently male biased. Also trapping biases appear minor, as the proportion of males was consistent between sampling techniques (Table 1), supporting a previous study between observed and mist-netted sex ratios of the Ruff (Münster 1989b).

One truly potential bias is geography. As males and females have different non-breeding distributions, with males remaining further north (Cramp & Simmons 1983, Münster 1996, Delany *et al.* 2009, Zwarts *et al.* 2009), males might take more northerly migratory routes from northern Russia, where at least 90% of Ruffs breed, whereas females might use more southerly routes (Cramp and Simmons 1983, Delany *et al.* 2009). Ruffs passing through Finland primarily originate in northern Finland and Russia (Saurola 1977, unpublished data of the Ringing Centre of the Finnish Museum of Natural History). The wing lengths reported here are consistent with a “western” origin, suggesting that the measured individuals did not come from eastern Siberia (Karlinova *et al.* 2007), and we found no changes in wing-length measures over time. The lack of a size trend in the Finnish ringing data indicates that the birds sampled are representative of a single population, and our results for sex and morph ratios apply within that population.

Geographical biases might be a priori expected to occur toward capturing proportionally more males than females. If this was true, the ratios re-

ported here would be more male biased than are the global population ratios. However, our observed sex ratio of 34% males, consistent with Saurola (1977) and data for juveniles measured at the Wash, U.K. (34.7%), in northern Poland (35.5%), and in Münster, Germany (40.2%; see Introduction). An even wider range of sites will be needed to further test for potential geographic biases. However, only a few locations might theoretically produce more male-biased migrant populations (e.g., Northern Norway), but values obtained from the U.K., which can also be considered a “northern extreme”, make it unlikely.

4.1.2. Theoretical and mechanistic considerations

The body condition of females, related to sex allocation in Ruff (Thuman *et al.* 2003), could be responsible for the female bias seen at the juvenile stage. If this were true, females would consider their body condition poor for most years, since the juvenile sex ratios were consistently female biased (Fig. 3). In other words, assuming fairly stable environmental conditions, selection may have favored a sex allocation strategy that results in a substantial female bias. Skewed sex ratios within populations, and sex-allocation strategies favouring such biases, can be evolutionarily stable despite the constant negative-frequency-dependent forces favouring equal parental investment in reproduction through male and female offspring in diploids (Fisher 1930, Charnov 1982). In birds, female-biased sex ratios of adults are less common than are male-biased ratios, except for many lekking species (Donald 2007). Shuster & Wade (2003) have argued that the benefits in net fitness from producing more females under poor conditions is greater than that of producing more males under better conditions, and consequently sexual selection should more often lead to female-biased sex-allocation strategies.

In several species of birds, females in better phenotypic condition produce a higher proportion of the larger and presumably more competitive sex, while there is a surplus of the smaller sex in the offspring of females of poorer condition (Nilsson & Svensson 1996, Nager *et al.* 1999, Badyaev *et al.* 2002, Roed *et al.* 2007, Servanty *et al.*

2007). These studies examine species in which parents significantly care for growing young. It is less clear which allocation rules occur in species with precocial young, such as the Ruff. In such species the differential costs of rearing males and females may be small. We might expect these costs to manifest themselves more strongly at the egg-production stage. In Ruffs, eggs with male and female chicks are similar in mass and size (Thuman *et al.* 2003, D.B. Lank, unpubl. data) although compositional differences are possible. A recent study in the Greater Sage Grouse (*Centrocercus urophasianus*), a strongly sexually dimorphic and sexually selected species, did not find evidence for sex-allocation strategies among females (Atamian & Sedinger 2010).

At a mechanistic level, female-biased sex ratios have been attributed to the expression of deleterious alleles in males, the heterogametic sex in mammals (Clutton-Brock *et al.* 1985, Donald 2007). In birds, however, females are the heterogametic sex, and thus this mechanism does not apply. Biases in post-hatching mortality could occur if male Ruffs have a greater sensitivity to environmental perturbations due to, for example, greater energetic stress during growth which in turn leads to higher mortality (e.g., Clutton-Brock *et al.* 1985, Røskaft & Slagsvold 1985, Griffiths 1992; see Cooch *et al.* 1997 and Lehikoinen *et al.* 2008b for examples from precocial birds). The only study we know of this topic measured sex-specific mortality in a species with little sexual dimorphism. That study actually reported the opposite effect: broods of the Kentish Plover (*Charadrius alexandrinus*) became increasingly male biased over time, implying higher mortality among the slower-growing female chicks (Székely *et al.* 2004).

4.3. Faeder ratio

We classified 0.6–1.5% of the juvenile Ruffs as faeders, i.e., permanent female-mimicking males, using criteria established by previous studies (Jukema & Piersma 2004, 2006, Karlinova *et al.* 2007). This frequency is similar to those reported for mixed-age samples from the Netherlands, Germany, the U.K., Senegal and Belarus (Karlinova *et al.* 2007, Verkuil *et al.* 2008). Since we did not

confirm sexual identity using molecular markers, some misclassification of extremely large females or extremely small faeders may have occurred. However, the probability of misclassification should be the same as in the other studies assuming identical assignment conditions. While the absolute percentages may be slightly erroneous, the comparison is valid.

The similarity between the faeder ratio reported here and those from mixed-age samples suggests that the processes determining the frequency of the faeder morph within populations are not strongly affected by post-juvenile survivorship differences. Because breeding studies indicate that faeders are a third genetic morph with straightforward Mendelian genetics (D.B. Lank, S.B. McRae & L.L. Farrell, unpubl. data), their initial proportion in fertilized eggs should follow directly from the relative reproductive success of the morph. As differential mortality at the egg or chick stage can theoretically occur, either favouring or disfavouring faeder offspring, the frequency observed among juveniles provides only a first approximation of faeder success. Assuming an autosomal genetic mechanism (D.B. Lank, S.B. McRae & L.L. Farrell, unpubl. data) and a population with 40% of individuals being males, however, faeders obtain a sufficient number of matings to produce at least 2% of offspring that survive to the juvenile stage, including unrecognized female offspring. These figures translate into producing around 2.5% of males.

4.4. Population implications

The Finnish Ruff population has declined to a third of its size since the early 1980s. This dramatic decline, being about 5% each year (Väisänen 2006), is occurring within the context of a flyway-wide decline (Cramp & Simmons 1983, Wetlands International 2006, Delany *et al.* 2009, Zwartz *et al.* 2009). The causes are not known and more detailed knowledge about Ruffs and their life histories is needed. Although there was no significant trend in the annual sex ratios among the studied individuals, the sex ratio has been strongly female biased since the 1970s, coinciding with a steep decline in the Ruff population (Saurola 1977, Väisänen *et al.* 1998, Väisänen 2006). If female Ruffs

produce proportionally more females when in poor body condition (Thuman *et al.* 2003), the present results may indicate relatively poor average condition of breeding females over a very large geographic area. Alternatively, the observed sex ratio may be at an adaptive equilibrium (Shuster & Wade 2003, Donald 2007; see also above). One potential bright spot is that in a polygynous species, a female bias enhances the potential reproductive rate, thereby possibly facilitating population recovery if the unknown environmental factors responsible for the decline are ameliorated (Bessa-Gomes *et al.* 2004).

Acknowledgements. We thank all ornithologists involved in ringing for collecting the data. The Ringing Centre of Finnish Museum of Natural History has maintained the electronic ringing databases since the 1970s. The manuscript benefited from comments by Y. Verkuil and T. Székely. DBL's research has been consistently supported by the Natural Science and Engineering Research Council of Canada. AL was supported by grants from Jenny and Antti Wihuri Foundation, and KJ by grants from the Finnish Cultural Foundation, Waldemar von Frenkells stiftelse, and the Swedish Cultural Foundation.

Naarasvoittoinen sukupuolijakauma ja kryptisten koiraiden osuus nuorilla muuttavilla suokukoilla

Vinoutunut sukupuolijakauma voi vaikuttaa populaation elinvoimaisuuteen. Vinouman syitä voivat olla esimerkiksi vinoutunut primäärinen sukupuolijakauma tai sukupuolten väliset erot poikas- tai aikuiskuolleisuudessa. Suokukon *Philomachus pugnax* maailmanlaajuisen populaation on oletettu olevan voimakkaasti naarasvoittoinen. Selvitimme tässä työssä naarasvoittoisuuden syntymisen ajankohtaa tutkimalla nuorten suokukkojen sukupuolijakaumaa niiden ensimmäisen syysmuuton aikana Suomessa vuosina 1985–2006. Määritimme myös kryptisten, naarasta muistuttavien koiraiden (nk. ”faeder”) osuuden tässä ikäluokassa sekä eri sukupuolten muuton ajoittumisen.

Tuloksemme osoittavat, että huomattava osa nuorista suokukoista on naaraita (66 %). Naaraat muuttivat merkittävästi aiemmin kuin koiraat. Löysimme nuorista suokukoista n. 1% kryptisiä koiraita, mikä vastaa aikaisempia tuloksia eri-ikäisistä yksilöistä koostuvista populaatioista. Tulok-

semme vahvistavat käsitystä lajin voimakkaasta naarasvinoumasta ja alhaisesta ”faeder”-koiraiden osuudesta. Vinoutunut sukupuolijakauma saattaa siten johtua naaraiden munintavaiheessa tekemästä jälkeläistuotannon kohdentamisesta naarasjälkeläisiin. ”Faeder”-koiraiden geneettisen määräytymisen perusteella tulokset antavat myös ensimmäistä kertaa arvion tämän muodon suhteellisesta lisääntymismenestyksestä.

References

- Andersen, F.S. 1948: Contributions to the biology of the ruff (*Philomachus pugnax* (L.)) II. — Dansk Ornitologisk Forenings Tidsskrift 42: 125–148.
- Andersen, F. S. 1951: Contributions to the biology of the ruff (*Philomachus pugnax* (L.)) III. — Dansk Ornitologisk Forenings Tidsskrift 45: 145–173.
- Atamian, M.T. & Sedinger, J.S. 2010. Balanced sex ratio at hatch in a greater sage-grouse (*Centrocercus urophasianus*) population. — Auk 127: 16–22.
- Badyaev, A.V., Hill, G.E., Beck, M.L., Dervan, A.A., Duckworth, R.A., McGraw, K.J., Nolan, P.M. & Whittingham, L.A. 2002: Sex-biased hatching order and adaptive population divergence in a passerine bird. — Science 295: 316–318.
- Bairlein, F. 1995: Manual of field methods. — Wilhelmshaven, Germany.
- Bessa-Gomes, C., Legendre, S. & Clobert, J. 2004: Allee effects, mating systems and the extinction risk in populations with two sexes. — Ecology Letters 7: 802–812.
- Boyd, H. 1962: Mortality and fertility of European Charadrii. — Ibis 104: 368–388.
- Busse, P. 2000: Bird station manual. — SE European Bird Migration Network, University of Gdansk.
- Charnov, E.L. 1982: The theory of sex allocation. — Princeton University Press, Princeton.
- Clutton-Brock, T.H., Albon, S.T. & Guinness, F.E. 1985: Parental investment and sex differences in juvenile mortality in birds and mammals. — Nature 313: 131–133.
- Cooch, E.G., Lank, D.B., Robertson, R.J. & Cooke, F. 1997: Effects of parental age and environmental change on offspring sex-ratio in a precocial bird. — Journal of Animal Ecology 66: 189–202.
- Cramp, S. & Simmons, K.E.L. (eds.) 1983: The birds of the Western Palearctic, vol. III. — Oxford University Press, Oxford.
- Delany, S., Scott, D., Dodman, T. & Stroud, D. (eds.) 2009: An atlas of wader populations in Africa and Western Eurasia. — Wetlands International, Wageningen, The Netherlands.
- Donald, P.F. 2007: Adult sex ratios in wild bird populations. — Ibis 149: 671–692.

- Fisher, R.A. 1930: The genetical theory of natural selection. — Oxford University Press, Oxford.
- Gill, J.A., Clark, J., Clark, N. & Sutherland, W.J. 1995: Sex difference in the migration, moult and wintering areas of British-ringed Ruff. — *Ringing and Migration* 16: 159–167.
- Griffiths, R. 1992: Sex-biased mortality in the lesser black-backed gull *Larus fuscus* during the nestling stage. — *Ibis* 134: 237–244.
- Hogan-Warburg, A. J. 1966: Social behavior of the ruff *Philomachus pugnax* (L.). — *Ardea* 54: 109–229.
- Höglund, J. & Lundberg, A. 1989: Plumage color correlates with body size in the Ruff (*Philomachus pugnax*). — *Auk* 106: 336–338.
- Hugie, D. M. and Lank, D. B. 1997: The resident's dilemma: a female-choice model for the evolution of alternative male reproductive strategies in lekking male ruffs (*Philomachus pugnax*). — *Behavioral Ecology* 8: 218–225.
- Jukema, J. & Piersma, T. 2004: Small male Ruffs *Philomachus pugnax* with feminine plumages: evidence for a third reproductive strategy, the faeder? — *Limosa* 77: 1–10. (in Dutch with English summary).
- Jukema, J. & Piersma, T. 2006: Permanent female mimics in a lekking shorebird. — *Biology Letters* 2: 161–164.
- Jukema, J., Wymenga, E. & Piersma, T. 2001: Stopping over in SW Friesland: fattening and moulting in ruffs *Philomachus pugnax* during northward migration in The Netherlands. — *Limosa* 74: 17–26.
- Karlionova, N., Pinchuk, P., Meissner, W. & Verkuil, Y. 2007: Biometrics of Ruffs *Philomachus pugnax* migrating in spring through southern Belarus with species emphasis on the occurrence of 'faeders'. — *Ringing and Migration* 23: 134–140.
- Koopman, K. 1986: Primary moult and weight changes of ruffs in the Netherlands in relation to migration. — *Ardea* 74: 69–77.
- Lank, D.B. & Smith, C.M. 1987: Conditional lekking in ruff (*Philomachus pugnax*). — *Behavioral Ecology and Sociobiology* 20: 137–145.
- Lank, D.B., Smith, C.M., Hanotte, O., Burke, T.A. & Cooke, F. 1995: Genetic polymorphism for alternative mating behaviour in lekking male ruff, *Philomachus pugnax*. — *Nature* 378: 59–62.
- Lank, D.B., Coupe, M. & Wynne-Edwards, K.E. 1999: Testosterone-induced male traits in female ruffs (*Philomachus pugnax*): autosomal inheritance and gender differentiation. — *Proceedings of the Royal Society of London Ser. B* 266: 2323–2330.
- Lehikoinen, A., Christensen, T. K., Öst, M., Kilpi, M., Saurola, P. & Vattulainen, A. 2008a: Large-scale change in the sex ratio of a declining eider population. — *Wildlife Biology* 14: 288–301.
- Lehikoinen, A., Öst, M., Hollmén, T. & Kilpi, M. 2008b: Can duckling mortality explain male bias in ducks? — *Condor* 110: 574–578.
- Lehikoinen, A. & Vähätalo, A. 2000: Phenology of bird migration at Hanko Bird Observatory, Finland in 1979–1999. — *Tringa* 27: 150–227. (In Finnish with English summary)
- Meissner W., & Zięcik P. 2005: Biometrics of juvenile ruffs (*Philomachus pugnax*) migrating in autumn through the Puck Bay region (N Poland). — *Ring* 27: 189–196.
- Münster, O.A.G. 1989a: Observations on the spring migration of Ruffs *Philomachus pugnax*. — *Journal für Ornithologie* 130: 175–182. (In German with English summary)
- Münster, O.A.G. 1989b: Migration phenology and development of resting populations of the Ruff *Philomachus pugnax* in the sewage-farms of Münster/FRG based on field observations and ringing results. — *Die Voglewarte* 35: 132–155. (In German with English summary)
- Münster, O.A.G. 1990: Mensural data of the ruff *Philomachus pugnax* in both migration periods. — *Vogelwelt* 111: 2–18. (In German with English summary)
- Münster, O. A. G. 1991: The moult of the ruff (*Philomachus pugnax*) and the intra-individual variation of the primary moult patterns. — *Journal für Ornithologie* 132: 1–28. (In German with English summary)
- Münster, O. A. G. 1996: Do females really outnumber males in ruff *Philomachus pugnax* wintering in Africa. — *Journal für Ornithologie* 137: 91–100. (In German with English summary)
- Nager, R. G., Monaghan, P., Griffiths, R., Houston, D. C. & Dawson R. 1999: Experimental demonstration that offspring sex ratio varies with maternal condition. — *Proceedings of the National Academy of Sciences of the USA* 96: 570–573.
- Nilsson, J.-A. & Svensson, E. 1996: The cost of reproduction: a new link between current reproductive effort and future reproductive success. — *Proceedings of the Royal Society of London Ser. B* 263: 711–714.
- Roed, K. H., Holand, O., Mysterud, A., Tverdal, A., Kumpulainen, J. & Nieminen, M. 2007: Male phenotypic quality influences offspring sex ratio in a polygynous ungulate. — *Proceedings of the Royal Society of London Ser. B* 274: 727–733.
- Roskaft, E. & Slagsvold, T. 1985: Differential mortality of male and female offspring in experimentally manipulated broods of the Rook. — *Journal of Animal Ecology* 54: 261–266.
- Saurola, P. 1977: On the migration of the Ruff in the light of Finnish recoveries. — *Lintumies* 12: 14–22. (In Finnish)
- Servanty, S., Gaillard, J.M., Allaine, D., Brandt, S. & Baubet, E. 2007: Litter size and fetal sex ratio adjustment in a highly polytocous species: the wild boar. — *Behavioural Ecology* 18: 427–432.
- Shuster, S. M. & Wade, M. J. 2003: Mating systems and strategies. — Princeton University Press, Princeton.
- Székely, T., Cuthill, I. C., Yezzerinac, S., Griffiths, R. & Kis, J. 2004: Brood sex ratio in the Kentish plover. — *Behavioral Ecology* 15: 58–62.
- Svensson, E. & Nilsson, J.A. 1996: Mate quality affects

- offspring sex ratio in blue tits. — Proceedings of the Royal Society B: Biological Sciences 263: 357–361.
- Thuman, K. A. 2003: Female reproductive strategies in the ruff (*Philomachus pugnax*). — Acta Universitatis Upsaliensis, Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology 830, Uppsala. 24 pp.
- Thuman, K.A., Widemo, F. & Griffiths, S.C. 2003: Condition-dependent sex allocation in a lek-breeding wader, the ruff (*Philomachus pugnax*). — Molecular Ecology 12: 213–218.
- Ukkonen, M. 2002: Raasio. — In Suomen lintuasemien toiminta 2001 (ed. Ojanen, M.): 73–74. Linnut-vuosikirja 2001. (In Finnish)
- Ukkonen, M. 2007: Raasio. — In: Nikkinen, L. (ed.): Suomen lintuasemien toiminta 2006. — Linnut-vuosikirja 2006: 116. (In Finnish)
- van Rhijn, J.G. 1973: Behavioural dimorphism in male Ruffs, *Philomachus pugnax* (L.). — Behaviour 47: 153–229.
- van Rhijn, J.G. 1991: The ruff. — T & AD Poyser, London.
- Väisänen, R.A. 2006: Monitoring population changes of 86 land bird species breeding in Finland in 1983–2005. — Linnut-vuosikirja 2005: 83–98. (In Finnish with English summary)
- Väisänen, R.A., Lammi, E. & Koskimies, P. 1998: Muuttuva pesimälinnusto. — Otava, Helsinki. (In Finnish with English summary)
- Verkuil, Y. I. & de Goeij P. 2003: Do reeves make different choices? Meadow selection by spring staging ruffs *Philomachus pugnax* in Southwest Friesland. — Limosa 76: 157–168. (In Dutch with English summary)
- Verkuil, Y.I., Jukema, J., Gill, J.A., Karlionova, N., Meltner, J., Hooijmeijer, J.C.E.W. & Piersma, T. 2008: Non-breeding faeder ruffs *Philomachus pugnax* associate according to sex, not morphology. — Bird Study 55: 241–246.
- Wetlands International 2006: Waterbird population estimates. Fourth edition. — Wetlands International, Wageningen, The Netherlands.
- Widemo, F. 1997: The social implications of traditional use of lek sites in the ruff *Philomachus pugnax*. — Behavioral Ecology 8: 211–217.
- Widemo, F. 1998: Alternative reproductive strategies in the ruff, *Philomachus pugnax*: a mixed ESS? — Animal Behaviour 56: 329–336.
- Zwartz, L., Bijlsma, R. G., van der Kamp, J. & Wymenga E. 2009: Living on the edge: wetlands and birds in a changing Sahel. — KNNV Publishing, Zeist, NL.