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

Kim Jaatinen, Aleksi Lehikoinen & David B. Lank

[illegible]

[illegible]

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 ok6416n164.6(rul)4.9(at)4.9(584.9(U9(hward)m)13.8(i)hward)-2394rmilihwardig9(hwa

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 [illegible]. 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-

. 2001, Karlionova . 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 . 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 . 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 . 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 (= 593; Meissner & Zięcik 2005), 40.2% at Münster, Germany (= 644; Münster 1990), 34.7% in the Wash, U.K. (= 248; Gill . 1995) and about one-third in Finland (= 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, 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 mi-

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 -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

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 2003, D.B. Lank, unpubl. data) although compositional differences are possible. A recent study in the Greater Sage Grouse (), 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 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 hnhng51uindiechality]T50.04.6(e.u)hg31g.-13.3064 -1ro11 produce proportionally more females when in poor body condition (Thuman . 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 . 2004).

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 [illegible] koiraiden [illegible] [illegible] [illegible] suokukoilla

Vinoutunut sukupuolijakauma voi vaikuttaa populaation elinvoimaisuuteen. Vinouman syitä voivat olla esimerkiksi vinoutunut primäärinen sukupuolijakauma tai sukupuolten väliset erot poikas- tai aikuiskuolleisuudessa. Suokukon maailmanlaajuisen populaation on oletettu olevan voimakkaasti naarasvoittoinen. Selvitimme tässä työssä naarasvoittoisuuden syntymisen ajankohtaa tu.7(o)a8 -1.173.173.1ot1a.18been5(l).4.6(aa)-234.rt4.6(l)4.6(e3.2(a59(i)4.6(s)1.1(koje3.2(a59(i))1.(iti

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 during the nestling stage. — Ibis 134: 237–244.

Hogan-Warburg, A. J. 1966: Social behavior of the ruff (L.). — Ardea 54: 109–229.

Höglund, J. & Lundberg, A. 1989: Plumage color correlates with body size in the Ruff ( ). — 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 ( ). — Behavioral Ecology 8: 218–225.

Jukema, J. & Piersma, T. 2004: Small male Ruffs 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 during northward migration in The Netherlands. — Limosa 74: 17–26.

Karlionova, N., Pinchuk, P., Meissner, W. & Verkuil, Y. 2007: Biometrics of Ruffs 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 ( ). — 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, . — Nature 378: 59–62.

Lank, D.B., Coupe, M. & Wynne-Edwards, K.E. 1999: Testosterone-induced male traits in female ruffs ( ): autosomal inheritance and gender differentiation. — Proceedings of the Royal Society of London Ser. B 266: 2323–2330.

Lehikoinen, A., Christersen, 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., Hollmèn, 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 ( ) 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 . — 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 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 in both migration periods. — Vogelwelt 111: 2–18. (In German with English summary)

Münster, O. A. G. 1991: The moult of the ruff ( ) 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 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 demontration 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., Kumpula, 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.

Røskaft, 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., Yezerinac, 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