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Migratory protogyny and condition-dependent arrival in Icelandic Red-necked Phalaropes

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In many migratory birds, arrival at breeding grounds is sexually asynchronous. This pattern is often explained by the idea that early arrival benefits the sex under stronger sexual selection by improving access to mates through territoriality. However, in species where females arrive first and are non-territorial, this explanation falls short. One alternative is that early-arriving females are simply in better condition. Here we report, for the first time, evidence of migratory protogyny in the Icelandic population of Red-necked Phalaropes (*Phalaropus lobatus*), a shorebird with reversed sexual dimorphism. We also present the first direct test of the condition-dependent hypothesis in a protogynous species, using arrival data, morphometric measurements, and leukocyte profiles. Although females arrived significantly earlier than males, we found no evidence that early arrival was linked to superior body condition. Leukocyte profiles did not suggest marked sex differences either, although we had insufficient statistical power to test this. Our results point instead to the role of sex-specific migratory strategies and intrasexual competition in shaping arrival timing. With its unique life history, *P. lobatus* offers a powerful model for studying the evolution of sex-biased migration. We

encourage further research integrating fine-scale tracking, reproductive monitoring, and physiological data to better understand the ecological and evolutionary drivers of migratory protogyny.

1. Introduction

Ever since Gätke's observations in 1895, which showed that males of numerous passerines and waders consistently preceded females in Heligoland, migratory protandry (male-first arrival) has been regarded as the prevailing pattern in migratory birds (Coppack & Pulido 2009). This pattern has traditionally been explained by the mate-opportunity hypothesis, which posits that early arrival benefits males by allowing them to establish territories and increase their chances of obtaining mates, particularly in polygynous species (Morbey *et al.* 2012). Territorial acquisition has therefore been regarded as a key driver of sex-biased arrival schedules.

However, this explanation does not apply to species in which the competing sex does not defend territories to gain access to mates. In such systems, early arrival cannot be interpreted through the lens of territorial advantage, and other selective pressures must be considered. A striking example occurs in species that show migratory protogyny, where females arrive earlier than males, a pattern that is exceptionally rare among birds. The Red-necked Phalarope (*Phalaropus lobatus*) is one of the few known examples. This shorebird exhibits reversed sex roles and sexual dimorphism, with females being more ornamented, engaging in aggressive courtship, and leaving all parental care to males. Earlier arrival by females has been documented in the North American breeding populations (Jehl 1986, Reynolds *et al.* 1986), suggesting that migratory protogyny is a consistent element of its phenology.

Although the Red-necked Phalarope is non-territorial, migratory protogyny in this species has still been interpreted through the mate-opportunity hypothesis. In this context, earlier arrival may enhance female access to mates through direct competition, rather than through territorial defense. This interpretation is supported by several characteristics of the species' reproductive system: females compete vigorously for mates, and the majority of pair bonds remain intact throughout nesting (Reynolds *et al.* 1986). Further, extra-pair paternity appears to be rare in its sister species, Grey Phalarope (*P. fulicarius*) (Krietsch *et al.* 2022), suggesting that low levels of extra-pair paternity may be a shared trait across phalaropes. Together, these traits suggest that the mate-limitation model may explain why early arrival could be advantageous for females.

An alternative, and not mutually exclusive, explanation is the condition-dependent hypothesis. Also known as the body size hypothesis, this model proposes that the larger sex may be better able to cope with harsh environmental conditions and may complete migration more efficiently. As a result, the more resilient sex would tend to arrive earlier (Kissner *et al.* 2003). In the case of phalaropes, females are larger and may be physiologically better equipped to tolerate early-season challenges or even to skip stopovers during migration (Morbey *et al.* 2012).

Whereas previous studies have considered sexual size dimorphism in relation to migratory timing (Kissner *et al.* 2003), no research to date has evaluated whether individual-level variation in energy stores (*i.e.* body condition) influences the order of arrival in phalaropes. Moreover, hematological parameters, such as leukocyte profiles and heterophil-to-lymphocyte ratios, are increasingly used as non-invasive indicators of physiological state (Davis *et al.* 2008, Hatch *et al.* 2010), yet these measures have not been applied to the topic of migratory protogyny. While these indices do not provide a direct measure of immune competence, they can offer insight into the variation in stress physiology at arrival. Measuring both energetic and stress-related hematological indices may help to clarify whether early-arriving individuals are in superior health, and whether this could help explain the emergence of migratory protogyny in sex-role reversed systems.

In this study, we offer a preliminary test of the condition-dependent hypothesis in a population of Red-necked Phalaropes breeding in northern Iceland. We first describe the sex-specific arrival patterns of adults at the breeding grounds. We then compare body condition estimates between early and late arriving individuals. Finally, we present a descriptive analysis of hematological parameters, to explore potential sex differences in physiological stress upon arrival.

2. Methods and Materials

We studied the arrival phenology of Red-necked Phalaropes at the Rif Field Station in Raufarhöfn (66°27′15″N, 15°57′00″W; Fig. S1), a village approximately 12.5 km south of the Arctic Circle on the eastern side of the Melrakkaslétta peninsula, Iceland. Although the peninsula had not been previously confirmed as a breeding site for this species, we documented breeding activity on 26 June 2023 by capturing a male with a chick (66°29'20"N, 16°14'49.6"W). This late-June confirmation prompted us to focus our census on the period from late May to early June, which we expected would capture the pre-breeding settlement phase of Red-necked Phalaropes in the area.

We conducted an 18-day field census from 23 May to 10 June 2022. On Monday, Wednesday, and Friday mornings, we counted all visible males and females at six fixed observation points along a 24-km road covering the eastern and northern sections of the peninsula (Fig. S1). Each observation at each site lasted 4 to 6 minutes, adjusted to the number of birds present, to standardize the survey effort across days. Sexing was based on pronounced sexual dichromatism: females have a dark gray cap and a bright rusty-red neck, while males exhibit a browner cap and a duller rust-colored neck (Rubega *et al.* 2020).

To assess whether the proportion of males among sexed individuals changed over time, we fitted a binomial generalized linear model (GLM) using daily counts of males and females as the response variable and day of the year as the predictor. To account for potential temporal non-independence (*e.g.*, repeated observations of the same individuals), we examined residuals for autocorrelation. No significant autocorrelation was detected (Fig. S2), supporting the assumption of independence.

From 2021 to 2023, we captured 18 adults (9 males and 9 females) at feeding ponds using 12×1 m mist nets to obtain standard morphometric measurements. Sex differences in morphometric traits were evaluated using one-tailed t-tests. Body condition was estimated using the scaled mass index (SMI) with wing length as a body size proxy (Peig & Green 2009). Finally, we tested the relationship between arrival timing and body condition using a linear model, with ln-transformed SMI as the response variable and days since first arrival as the predictor.

During May and June 2022, blood smears were collected from 6 males and 5 females by puncturing the brachial vein, following standard procedures (Bennett 1970). Time from capture to blood collection did not exceed 7 minutes. Leukocyte profiles were obtained by examining randomly selected microscope fields until 50 leukocytes per smear were counted. We calculated the heterophil-to-lymphocyte (H/L) ratio, a common proxy of stress in avian studies (Davis *et al.* 2008). Due to the limited sample size, we did not perform statistical analyses on hematological variables.

3. Results and Discussion

We recorded pronounced migratory protogyny in the Icelandic population of Red-necked Phalaropes, with the proportion of males increasing significantly over the 18-day census period (GLM: $\beta = 0.180 \pm 0.037$, $z = 4.8$, $p < 0.001$, $n = 197$; Fig. 1A). This pattern supports the view that migratory protogyny is a consistent feature of this species' migratory strategy.

Morphometric analyses showed that females were significantly larger and heavier than males (Table 1). But interestingly, despite this marked difference in body mass, the sexes had comparable body condition, as measured by the scaled mass index ($p = 0.815$). Individual body condition showed no relationship between arrival timing (linear model: $\beta = –0.00027$, $p = 0.944$, $n = 18$). Leukocyte profiles from a subset of individuals (6 males, 5 females) also revealed

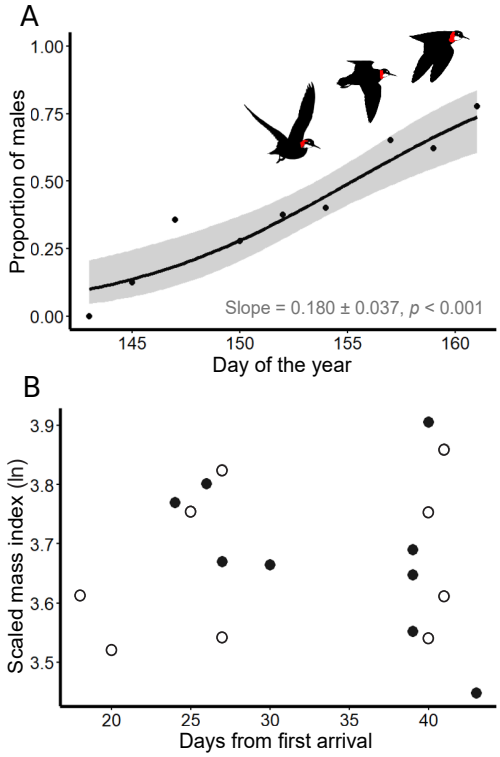

Fig. 1. A) Variation in the proportion of male Red-necked Phalaropes (*Phalaropus lobatus*) during the 2022 breeding season in the Melrakkaslétta peninsula, Iceland (n = 197). Values close to 0 indicate a female bias, close to 1 indicate a male bias, and 0.5 represents an equal proportion of males to females. The solid black line shows the regression line from a binomial generalized linear model, and the gray ribbon represents the 95% confidence interval around the fitted trend, indicating an increasing number of males relative to the day. B) Variation in body condition in female (white) and male (black) phalaropes captured between 18 and 43 days after spotting the arrival of the first individual in the breeding area in the Melrakkaslétta peninsula (linear model: β = –0.00027 ± 0.00386, p = 0.944, n = 18).

similar heterophil-to-lymphocyte (H/L) ratios, with no consistent sex-specific patterns. Overall, these findings provide no support for the condition-dependent hypothesis, which predicts that early-arriving individuals should be in a superior condition.

Although we found no evidence that early-arriving females were in better condition, they did have longer wings and greater body mass than males (Table 1). These traits may enhance migratory efficiency by enabling faster and more stable flight (Sullivan *et al.* 2019, Harvey *et al.* 2022) or by reducing the need for extended stopovers. Direct evidence for this idea is scarce; however, one case study by van Bemmelen *et al.* (2019) tracked a single female Red-necked Phalarope breeding in Iceland that completed spring migration faster than most conspecific males. Although she stopped at all four known staging sites, her stay at each was shorter than two days, suggesting a more rapid migratory pace than that of males. Because this observation is limited to one individual and could reflect chance or stochastic environmental conditions (Lindström 2020), it cannot be taken as representative. In the same study, van Bemmelen *et al.* (2019) also analyzed a Swedish population (5 females, 7 males) and found no significant sex differences in departure from non-breeding grounds or in overall migration speed (all p > 0.1). Although this lack of differences may not be generalizable across populations, together these findings suggest that migratory protogyny in phalaropes is unlikely to stem from superior body condition at departure, but may instead involve subtle, sex-specific differences in migration pace or time-allocation strategies.

Theoretical models by Morbey and Hedenström (2020) suggest that faster migration, achieved either through increased flight efficiency or reduced stopover time, can facilitate earlier arrival when earlier breeding confers fitness benefits. Moreover, although based on passerines with conventional sex roles, Deakin *et al.* (2023) found that earlier arrival was associated with larger body and wing size in males and energetically efficient wing morphology, pointing to a broader association between flight morphology and migratory timing. In our study, females had wings 7% longer than males, which matches the species with the greatest wing sexual dimorphism in Deakin *et al.* (2023). Wing shape and size are critical for flight efficiency (Sullivan *et al.* 2019); therefore, wings 7% larger in females might make considerable performance differences over migrations of ~10 000 km. However, further research is needed to determine the relevance of wing size in shaping phalaropes' migratory protogyny.

Hypothetically, if female Red-necked

Phalaropes are able to complete spring migration faster than males, potentially by spending less time at stopover sites, this could have physiological consequences. Stopovers are important for the recovery of immune function in migratory birds (Eikenaar *et al.* 2023), and longer or more intense migratory bouts are expected to suppress certain immune parameters (Nebel *et al.* 2012). In our study, males and females seem to have comparable leukocyte profiles, but this cannot be confirmed due to the low sample size. Assuming both sexes begin spring migration with a similar immune baseline, one possibility is that females possess a greater ability to restore immune balance shortly after arrival. This is supported by evidence that some immune traits can recover rapidly once physical exertion ceases (Eikenaar *et al.* 2020, 2023). Nevertheless, more fine-scale temporal sampling, especially immediately upon arrival, would be required to test this hypothesis directly.

In short, our study offers rare empirical evidence of migratory protogyny in the Icelandic population of Red-necked Phalaropes. We found no support for condition-dependent arrival, highlighting instead the likely importance of intrasexual competition and sex-specific migratory strategies in shaping arrival phenology. With its unusual combination of polyandry, reversed sexual dimorphism, and long-distance migration, the Red-necked Phalarope is an exceptional model for exploring the causes and consequences of sex-biased migration. We encourage future research to integrate fine-scale tracking, particularly at the departure of non-breeding areas, and physiological assessment to uncover the mechanisms driving this pattern. Understanding how sex shapes migration in this species will broaden our understanding of the evolution of movement, mating, and adaptation.

Muutoltapaluun protogynia ja paluuajan riippuvuus kunnosta islantilaisilla vesipääskyillä

Monien muuttolintujen naaraat ja koiraat palaavat pesimäalueille eri aikaan. Tätä ilmiötä on usein selitetty siten, että varhainen saapuminen hyödyttää sukupuolta, johon kohdistuu vahvempi sukupuolivalinta, koska se parantaa mahdollisuutta vallata reviiri ja siten löytää lisääntymiskumppani. Tämä selitys on kuitenkin riittämätön niiden lajien osalta, joilla naaraat saapuvat ensin eivätkä valtaa reviiriä. Yksi vaihtoehto on, että aikaisin saapuvat naaraat ovat

Table 1. Morphometric measurements and leukocyte profiles of Red-necked Phalaropes (*Phalaropus lobatus*) from northern Iceland. Values represent means ± standard deviations; sample sizes are reported in separate columns. Sexual differences in morphometric traits were tested using one-tailed t-tests. Leukocyte data are expressed as proportions of the total leukocyte count; statistical comparisons were not conducted for leukocyte parameters due to limited sample sizes. H = heterophils, L = lymphocytes.

	Male		Female		*p*
	N	Mean ± SD	N	Mean ± SD	
Wing (mm)	9	109.8 ± 3.7	9	117.4 ± 2.7	<0.001
Body mass (g)	9	35.4 ± 3.7	9	44.2 ± 4.9	<0.001
Scaled mass index (g)	9	40.1 ± 5.4	9	39.5 ± 5.2	0.81
Heterophils	6	0.342 ± 0.217	5	0.275 ± 0.188	-
Lymphocytes	6	0.641 ± 0.213	5	0.699 ± 0.21	-
H/L ratio	6	0.761 ± 0.859	5	0.478 ± 0.361	-
Total leukocyte count	6	15.87 ± 5.50	5	15.18 ± 5.35	-

paremmassa kunnossa. Tässä artikkelissa esitämme ensimmäisiä todisteita muutoltapaluun protogyniasta vesipääskypopulaatiossa (*Phalaropus lobatus*) Islannissa. Vesipääsky on kahlaaja, jolla naaraat ovat koiraita kookkaampia eli sukupuolidimorfismi on käänteistä. Testaamme myös ensimmäistä kertaa hypoteesia paluuajan kuntoriippuvuudesta protogynisellä lajilla käyttämällä saapumisaikoja, morfometrisiä mittauksia ja leukosyyttiprofiileja. Vaikka naaraat palasivat muutolta merkittävästi koiraita aiemmin, emme havainneet, että varhainen saapuminen olisi yhteydessä parempaan kuntoon. Leukosyyttiprofiilit eivät myöskään viitanneet merkittäviin eroihin sukupuolten välillä, vaikka aineisto ei sallinut tilastollista testaamista. Tuloksemme viittaavat pikemminkin sukupuolikohtaisten muuttostrategioiden ja sukupuolen sisäisen kilpailun rooliin saapumisajan määräytymisessä. Ainutlaatuisen elämänkaarensa ansiosta vesipääsky on erinomainen kohdelaji tutkittaessa sukupuolen osalta vinoutuneen muuton evoluutiota. Jotta ymmärrettäisiin paremmin muuton protogynian ekologisia ja evolutiivisia ajureita, tarvitaan lisää tutkimuksia, joissa yhdistetään yksityiskohtaista paikannusta, lisääntymisen seurantaa ja fysiologista aineistoa.

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Author contributions. OGM and JOV conceived the study and formulated the research questions. OGM, JOV and RS conducted the fieldwork and developed the methodology. OGM performed the data validation and formal analysis, with contributions from JOV. JOV prepared the initial draft of the figures; OGM finalized them. OGM wrote the first draft of the manuscript. JOV and PR contributed to reviewing and editing the manuscript. PR and TS supervised the research. TS and JOV secured funding for the study. All authors contributed to the final version of the manuscript.

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Online supplementary material

Supplementary materials available in the online version of the article include Figures S1–S2 and a PDF containing the R code.