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Female-biased sex ratio in moulting Black-necked Grebes *Podiceps nigricollis* in southern Spain

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We tested if Black-necked Grebe, a species in which both sexes undertake moult-migration, have an unbiased sex ratio at a moulting site in Europe, as previously found in North America and as was expected for a species with biparental care. For this we used a unique long-term dataset of 5821 grebes captured for ringing throughout the moulting seasons of 2006–2012 in the Odiel salt-marshes (SW Spain). The grebes were sexed and classified as adults (74%) or juveniles (26%). Birds ringed at Odiel were recovered over a wide area up to central Russia and south to the Canary Islands and Morocco. We report on a unique case of a strongly biased sex ratio in a moult-migrating bird species with biparental care, in which adult females were significantly more abundant than adult males in all 7 years (1.6–4.2 females per male). Biased sex ratios were not found among juveniles. Differences between North America and Europe in the sex ratios of adult Black-necked Grebes at moulting sites may be explained by the much larger American moulting sites, which would facilitate an unbiased sex ratio in North America, but not in Europe. Moulting sites in Europe may reach carrying capacity because of their smaller size, forcing the late migrating individuals (adult females and juveniles) to move longer distances to sites farther from breeding areas, such us the Odiel salt-marshes.

Key words: hypersaline habitats, plumage moult, Podicipedidae, sexual segregation, waterbirds

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Because breeding and moulting are energetically expensive processes they are usually separated in time (Payne 1972), and the sex with a smaller participation in breeding activities moults earlier than the sex contributing more to breeding activities (e.g. Siimaki *et al.* 1994, Svensson & Nilsson 1997). After breeding, many waterbird species (mainly Podicipedidae, Phoenicopteridae, Anatidae, Rallidae, Gruidaea and Alcidae) move to specific sites for moulting, where all flight feathers are shed simultaneously. This type of displacement is known as moult migration (Salomonsen 1968, Jehl 1990, Kjellén 1994). Age and sex differences in moult migration have been reported in several species. In general, the sex that does not provide parental care is the one that performs moult migration, whereas the sex that undertakes parental care moults at the breeding site. For instance, male ducks are more numerous than females at moult-migration sites (Salomonsen 1968, Hohman *et al.* 1992), and when female ducks undertake moult migrations, they are usually failed breeders (Salomonsen 1968, Amat *et al.* 1987, Hohman *et al.* 1992). In Wilson's Phalaropes *Phalaropus tricolor*, in which males remain in breeding areas attending broods, it is the females that undertake moult migration (Jehl 1988).

One of the main ecological conditions that allows the undertaking of moult migration by both sexes in biparental species is probably abundant food, whose availability extends well into the autumn, thus giving both parents the time necessary to complete moult in sites far from breeding areas (Jehl 1988, Cooper *et al.* 1984, Varo *et al.* 2011). Because in grebes both parents attend the chicks (Fjeldså 2004), an unbiased sex ratio should be expected in the moulting localities. Indeed, this has been reported for the Black-necked Grebe *Podiceps nigricollis* in North America (Jehl 1988, Cuéllar Brito 2007, Jehl & Henry 2010). Similarly, no biased sex ratio has been found in moult-migrant Little Terns *Sternula albifrons*, another species with biparental care, at a moulting site in Italy (Cherubini *et al.* 1996).

Perhaps the Black-necked Grebe is the avian species that forms the largest concentrations during moult migration. Up to one million birds may congregate to moult in a single lake in North America (Storer & Jehl 1985, Jehl 1988). The moulting concentrations of this grebe in Europe are much smaller than in North America: up to 10,700 individuals at our study site in the Odiel salt-marshes in SW Spain (Varo *et al.* 2011), 5700 in SE Romania (Van Impe 1969), 3900 in the Balearic Islands (Mayol 1984), and 3000 in both SE Spain (García-Jiménez & Calvo-Sendín 1987) and SE France (Iborra *et al.* 1991). Although up to 186,000 Black-necked Grebes were recorded in 1970 in Burdur Lake in Turkey (Cramp & Simmons 1977), nowadays the lake does not support so many grebes due to severe hydrological changes that may have affected food supplies (Green *et al.* 1996, Gülle *et al.* 2010). Indeed, a census in September 2006 reported 10,300 birds (www.birdforum.net/archive/index.php?t-237529.html).

The sex ratio of Black-necked Grebes during moulting has not been previously investigated in any European locality. In this paper we report a biased adult sex ratio among grebes moulting in SW Spain, and advance a hypothesis aimed at explaining the observed difference between the sex ratios of moulting grebes at sites in North America and the present study site in southern Spain. In particular, we will propose that continental differences in the size of wetlands where the grebes moult may determine that the carrying capacity of sites in Europe is reached after the arrival of a given number of birds, leading late moulting individuals to migrate to more distant sites from breeding areas. This would not occur in North America because of the larger size of wetlands where the grebes moult.

METHODS

The study was conducted during 2006–2012 at the Odiel salt-marshes in south-western Spain (7185 ha; 37°14'N, 6°57'W; see description in Sánchez *et al.* 2006), in which 1174 ha were transformed into a saltpan complex. The evaporation ponds of the saltpan are used as moulting sites by Black-necked Grebes, mainly during late July to early December (Varo *et al.* 2011, Fox *et al.* 2013). Water levels in the ponds used by grebes are usually < 1 m. A team of 15–30 persons drew moulting flocks of grebes into corrals, in which they were captured for ringing 9–19 times each season. The birds were sexed visually by an experienced ringer, without recording any body measurement. Sex was determined by head-bill length, males being larger than females (Jehl *et al.* 1998). The grebes were aged according to eye coloration (Storer & Jehl 1985), juveniles having a paler iris than adults.

To test the robustness of the sexing procedure we collected blood samples from a tarsus vein of 309 grebes, for which sex was determined using molecular methods (Griffiths *et al.* 1998). Using a 2 × 2 contingency table we then compared sexes visually assigned by the ringer with sexes determined using the molecular method.

During our study we captured 5821 individual grebes, of which 78.1–96.2% were sexed in a given year (see Table 2). Depending on the state of the remiges, birds were assigned to one of three categories: unmoulted, moulting and moulted. For the analysis of sex ratios, adults and juveniles were separated. Many birds were recaptured on several occasions throughout the season ($n = 12{,}107$, including recaptures), but when considering yearly variation only one captured individual per year was used. Data were analysed using χ^2-tests assuming an expected 1:1 sex ratio. Because we used multiple tests (one for each year), we adjusted probability values by using the Bonferroni correction (Rice 1989, Beal & Khamis 1991), which set significant values at $P < 0.007$.

Table 1. Comparison of differences between sexes assigned visually (based on head-bill length) and sex determined using the molecular method. Comparisons were made for 309 birds.

	Visual		**Molecular**			
	♀	♂	♀	♂	χ^2_1	P
Juveniles	13	8	14	7	0.10	0.747
Adults	222	66	211	77	1.13	0.288
Total	235	74	225	84	0.85	0.356

Skewed sex ratios at Odiel could potentially be due to one sex staying for shorter periods at the moulting site than the other. To test this, we compared the number of days elapsed between the first and the last capture of individual adult grebes between sexes, for birds captured multiple times within a season. Sexual differences in this estimate of staying times were analysed using Mann–Whitney U-tests.

RESULTS

There were no statistically significant differences between sex ratios established visually and when sex was determined using the molecular method (Table 1). The ringer sexed 85% of the birds correctly. There were significant deviations from a 1:1 sex ratio in adults, females being significantly more abundant in all seven years (Table 2). The sex ratios of adults also remained female-biased in the three established categories: unmoulted (1.28 females/male, $n = 468$), moulting (2.03 females/male, $n = 747$), and moulted (1.68 females/male, $n = 2608$). However, there was no deviation from a 1:1 sex ratio in juveniles (Table 2).

There were no differences between adult males and females in the estimated staying time, i.e. mean number of days elapsed between first and last capture in a given season (Table 3), indicating that both sexes used the Odiel saltpan for similar periods.

Black-necked Grebes ringed during moult in the Odiel salt-marshes have been recovered across a large geographical area, spanning from south-central Russia to Morocco and the Canary Islands (Figure 1).

In Central Europe (Belgium, Switzerland, Germany, Czech Republic, Poland, Hungary, Rumania, Belarus and Ukraine) and Russia, most of the grebes (77% of 35) were recovered during the breeding season (March–July). However, in Mediterranean countries (France, Italy, Portugal, Spain and Morocco), more grebes (64% of 53) were recovered outside the breeding season ($\chi^2_1 = 14.4$, $P < 0.001$). This indicates that Black-necked Grebes breeding in Central Europe and Russia use the Odiel salt-marshes as a moulting site, whereas those recovered around the western Mediterranean were mainly moulting/wintering birds.

Table 2. Number of adult and juvenile male and female Black-necked Grebes captured at Odiel salt-marshes during 2006–2012. Differences in the abundance of males and females were tested using χ^2-tests. Because of multiple testing, probability-values were adjusted with a Bonferroni correction.

	Adults			Juveniles			Total individuals	Percentage sexed
	♀	♂	♀/♂	♀	♂	♀/♂		
2006	682	431	1.58*	114	130	0.88^{ns}	1489	91.1
2007	657	362	1.81*	168	151	1.11^{ns}	1713	78.1
2008	568	139	4.09*	34	17	2.00^{ns}	788	96.2
2009	703	424	1.66*	156	134	1.16^{ns}	1719	82.4
2010	337	190	1.77*	63	96	0.66^{ns}	834	82.3
2011	427	101	4.23*	36	19	1.89^{ns}	672	86.8
2012	533	313	1.70*	105	119	0.88^{ns}	1352	79.1
2006–2012	2420	1432	1.69*	660	659	1.00^{ns}	5821	88.8

^{ns}not significant ($P > 0.007$); $^*P < 0.001$.

Table 3. Dates at which Black-necked Grebes were captured and average number of days elapsed between the first and the last captures of individual male or female adult grebes in a given year. Differences between sexes were tested with Mann–Whitney U-tests.

First and last day of captures	♀ Mean ± SD (*n*)	♂ Mean ± SD (*n*)	U	*P*
03/08/2006 – 15/12/2006	43.97 ± 32.55 (299)	41.97 ± 33.82 (173)	24,427	0.31
06/08/2007 – 23/11/2007	25.97 ± 17.65 (144)	28.50 ± 20.33 (66)	4378	0.36
13/08/2008 – 06/12/2008	32.76 ± 25.20 (123)	26.94 ± 22.85 (16)	807	0.24
11/08/2009 – 11/12/2009	37.94 ± 27.65 (275)	32.32 ± 22.61 (123)	15,460	0.17
03/09/2010 – 26/11/2010	32.03 ± 18.96 (89)	25.21 ± 14.85 (39)	1376	0.06
11/08/2011 – 05/12/2011	24.73 ± 21.43 (158)	28.70 ± 21.52 (27)	1804	0.19
31/08/2012 – 30/11/2012	27.06 ± 14.15 (127)	25.67 ± 11.86 (66)	4080	0.75

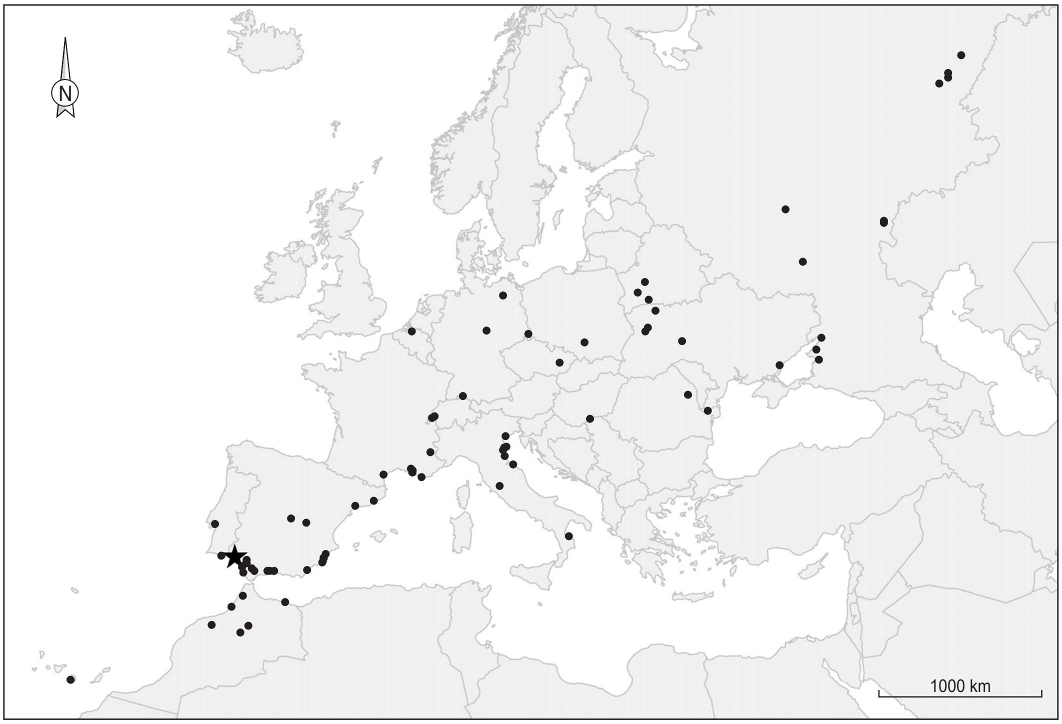

Figure 1. Geographical distribution of recoveries (dots) of Black-necked Grebes ringed during the moulting period at Odiel saltmarshes in SW Spain (star). Only sites located at >50 km from the ringing site are shown.

DISCUSSION

Our study shows that the sex ratio of adult Black-necked Grebes at a moulting locality in southern Europe is female-biased, and that this is not due to shorter staying periods of males than females. To our knowledge, this is the first time such a strongly biased sex ratio has been reported in any bird species with biparental care performing moult-migration. Furthermore, sex ratios also remained female-biased in grebes caught before starting wing moult and during and after completing wing moult. Our results suggest that adult males are likely to be more numerous than females at some other Palearctic localities during moulting, but to our knowledge ours is the only study on sex ratios of moulting Black-necked Grebes in Europe. This contrasts with what has been found in North America, where no biased sex ratios have been reported at several moulting sites (Jehl 1988, Cuéllar Brito 2007, Jehl & Henry 2010).

A sexual spatial segregation is common in many duck species during winter, with males wintering further north than females and juveniles (Bellrose *et al.* 1961, Campredon 1983). It has been suggested that male behavioural dominance is the mechanism behind this latitudinal segregation (Hepp & Hair 1984). However, no intraspecific agonistic interactions are observed among grebes in the moulting sites (Jehl 1988, Varo *et al.* 2011), hence sexual spatial segregation in the Black-necked Grebe in Europe is not likely to be related to behavioural dominance of males. In the case of the Black-necked Grebe in particular, we propose that the spatial distribution of moulting birds would conform to the ideal free distribution model (Fretwell & Lucas 1970), according to which individuals occur in direct proportion to the availability of resources among habitats. This has been shown for another grebe species during breeding (Sebastián-González *et al.* 2010).

In the Black-necked Grebe, males finish parental care earlier than females (Cullen *et al.* 1999). This may allow males to reach the moulting sites in advance of females and juveniles. Depending on the size of wetlands, the carrying capacity of sites could be reached after the arrival of thousands of moult migrating birds. Because the wetlands where the Black-necked Grebes moult in North America are very large, it is unlikely that they reach their carrying capacity.

However, this may not be the case in Europe, where the size of wetlands used by Black-necked Grebes to moult is much smaller, which may lead to late moult-migrating adult females and juveniles in Europe having to travel longer distances to moulting sites in which the carrying capacity has not yet been reached.

Perhaps in Europe the distance between the Odiel salt-marshes in SW Spain, one of the most important moulting sites for the Black-necked Grebe in southern Europe, and the main breeding localities of the species is longer than between other moulting and breeding sites of the species on this continent. Black-necked Grebes moulting at Odiel originated from breeding areas all over Europe (Figure 1). Given that the more important breeding populations of Black-necked Grebes in the Palearctic are in south-central Russia and Kazakhstan (Fjeldså 2004), and many moulting sites are in south and south-western Europe (see Introduction), birds moving from Russia/Kazakhstan to moult would first reach the eastern sites, and birds initiating the moult-migration later (i.e. females and juveniles) should have to move to localities located further southwest, such as the Odiel saltpans. Therefore, in Europe there may be an inverse relationship between the proportion of males in moulting sites and the distance between the main breeding areas and moulting sites.

In conclusion, differences in the size and carrying capacity of moulting sites may account for continental differences in the sexual distribution of moulting Black-necked Grebes between North America and Europe. To test our hypothesis it would be necessary to collect data on sex ratios at moulting sites of grebes across the south-western Palearctic, especially in Eastern Europe.

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SAMENVATTING

Het wetlandgebied rondom de monding van de Odielrivier in het zuidwesten van Spanje is een belangrijk ruigebied voor Geoorde Futen *Podiceps nigricollis*. Elk jaar, in de periode van eind juli tot begin december, verzamelen zich grote aantallen ruiende Geoorde Futen in de ondiepe zoutpannen in het gebied. Bij de Geoorde Fuut dragen beide ouders bij aan de broedzorg. Na afloop van de broedperiode vertonen beide geslachten een ruitrek. Daarom lijkt het aannemelijk dat mannetjes en vrouwtjes naar dezelfde ruigebieden trekken. Dit onderzoek toont aan dat de geslachtsverhouding van de ruiende Geoorde Futen in het Odielgebied sterk afwijkt van een 1:1 ratio. Er verblijven hier veel meer vrouwtjes dan mannetjes. Dit blijkt uit de vangstgegevens uit de jaren 2006–2012, waarin 5821 ruiende Geoorde Futen gevangen werden voor het ringonderzoek. Elk jaar werden het geslacht en de leeftijdsklasse (juveniel of adult) van een groot deel van de gevangen vogels op het oog vastgesteld (78,1–91,1% van de gevangen vogels in een gegeven jaar). Veel van deze vogels werden meermalen in het Odielgebied gevangen (aantal vangsten inclusief hervangsten, n = 12.107). Terugmeldingen van in het Odielgebied geringde Geoorde Futen kwamen uit een groot gebied, dat zich uitstrekt van Centraal-Rusland in het noordoosten tot aan Marokko en de Canarische Eilanden in het zuiden. Van 309 vogels werd een bloedmonster verzameld om het geslacht vast te kunnen stellen door middel van een DNA-analyse. Hieruit bleek dat de geslachtsbepaling op het oog in 85% van de gevallen correct was. Ook waren er geen significante verschillen tussen de berekende geslachtsverhouding op het oog en die gebaseerd op de DNA-analyses. In elk van de zeven onderzochte jaren bleken er significant meer adulte vrouwtjes dan adulte mannetjes te zijn (1,58–4,23 vrouwtjes per mannetje). Bij de juveniele vogels werd geen scheve verhouding tussen mannetjes en vrouwtjes gevonden. Een verschil in de verblijfstijd tussen mannetjes en vrouwtjes kan de afwijkende geslachtsverhouding bij de adulte vogels niet verklaren. Het tijdsinterval tussen de eerste en laatste vangst van individuele vogels in het gebied verschilde namelijk niet tussen beide geslachten. De afwijkende geslachtsverhouding van de ruiende Geoorde Futen in het Odielgebied staat in sterk contrast met de waargenomen geslachtsverhouding (1:1) in Noord-Amerikaanse ruigebieden. Een mogelijke verklaring voor dit verschil zou kunnen zijn dat de meren waarop de Amerikaanse vogels ruien, een veel grotere draagkracht hebben dan de Europese ruigebieden. Daardoor kan een groot deel van die populatie Geoorde Futen daar terecht, terwijl in Europa de kleinere ruigebieden eerder verzadigd raken. Individuen die wat later wegtrekken, vooral vrouwtjes en juveniele vogels, worden hierdoor mogelijk gedwongen om vanuit de broedgebieden verder zuidwaarts te reizen op zoek naar geschikte ruigebieden, bijvoorbeeld aan de monding van de Odielrivier. (PK)

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