

Sex-Specific Arrival Times on the Breeding Grounds: Hybridizing Migratory Skuas Provide Empirical Support for the Role of Sex Ratios

Simeon Lisovski,^{1,2,*} Anne Fröhlich,² Matthew von Tersch,³ Marcel Klaassen,¹ Hans-Ulrich Peter,² and Markus S. Ritz^{2,4}

1. Deakin University, School of Life and Environmental Sciences, Centre for Integrative Ecology, Victoria, 3220 Geelong, Australia; 2. Polar and Bird Ecology Group, Institute of Ecology, Friedrich Schiller University Jena, 07743 Jena, Germany; 3. British Antarctic Survey, Natural Environment Research Council, Cambridge CB3 0ET, United Kingdom; and Department of Archaeology, University of York, York YO10 5DD, United Kingdom; 4. Senckenberg Museum of Natural History Görlitz, 02826 Görlitz, Germany

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ABSTRACT: In migratory animals, protandry (earlier arrival of males on the breeding grounds) prevails over protogyny (females preceding males). In theory, sex differences in timing of arrival should be driven by the operational sex ratio, shifting toward protogyny in female-biased populations. However, empirical support for this hypothesis is, to date, lacking. To test this hypothesis, we analyzed arrival data from three populations of the long-distance migratory south polar skua (*Catharacta maccormicki*). These populations differed in their operational sex ratio caused by the unidirectional hybridization of male south polar skuas with female brown skuas (*Catharacta antarctica lonnbergi*). We found that arrival times were protandrous in allopatry, shifting toward protogyny in female-biased populations when breeding in sympatry. This unique observation is consistent with theoretical predictions that sex-specific arrival times should be influenced by sex ratio and that protogyny should be observed in populations with female-biased operational sex ratio.

Keywords: migration, arrival dates, *Catharacta*, population sex ratio, sex role reversal, spring migration.

Introduction

The timing of arrival on the breeding grounds is considered to be a crucial element in the fitness of migratory birds (e.g., Both and Visser 2001). While there are obvious benefits for an early arrival, such as early nesting start and, consequently, more and fitter offspring (Smith and Moore 2005), there might also be costs, such as adverse weather conditions during the early season (e.g., Møller 1994; Brown and Brown 2000). Depending on differences in selection pres-

ures between the sexes, their migration schedules (e.g., timing of arrival at the breeding grounds) may differ. The prevailing mode in migrating birds is protandry, where males arrive on the breeding grounds ahead of females. In the case of protogyny, the female is the first to arrive, a phenomenon observed in a few sex-role-reversed bird species only (Oring and Lank 1982; Reynolds et al. 1986). At least seven non-mutually-exclusive hypotheses have been proposed to explain sex-specific arrival times (Morbey and Ydenberg 2001). In avian systems, five of these hypotheses are either irrelevant or lacking empirical support (Morbey and Ydenberg 2001; Morbey et al. 2012). Of the remaining two, the rank-advantage hypothesis (Ketterson and Nolan 1976) has received wide acceptance, assuming that early arrival leads to the occupation of high-quality territories. The alternative, the mate-opportunity hypothesis (Scott 1977), has also been considered in the avian literature, suggesting that early-arriving animals may gain a fitness increase through extrapair matings. However, a simulation study by Kokko et al. (2006) showed that the rank-advantage hypothesis alone failed to produce sex-specific differences in timing of arrival, which was achieved only by differences in population sex ratio and sperm competition. Kokko et al.'s (2006) study predicted that protandry would prevail in male-biased populations, whereas protogyny would prevail in populations with a female surplus. Additionally, extrapair young produced selection pressure toward protandry. However, mainly since field manipulations of sex ratios over a time period long enough to influence migration patterns are nearly impossible, Kokko et al.'s (2006) straightforward prediction for the crucial effect of biased sex ratios remains unchallenged.

In our unique study system, we were able to take advantage of naturally occurring variation in the operational sex

* Corresponding author; e-mail: simeon.lisovski@gmail.com.

ratio between populations. The south polar skua (*Catharacta maccormicki*) and the brown skua (*Catharacta antarctica lonnbergi*) are two closely related species. Despite a multitude of mutual ecological features, the south polar skua is a long-distance migrant that spends the nonbreeding season in high northern latitudes (Kopp et al. 2011), whereas the brown skua remains in the Southern Hemisphere, relatively close to their breeding sites (Phillips et al. 2007). Except for a hybridization zone on the Antarctic Peninsula and adjacent islands, the two species have largely separate breeding distributions (Bennett 1920; Ritz et al. 2006). Mixed pairs within sympatric populations always consist of male south polar skuas and female brown skuas (Parmelee 1988; Ritz et al. 2006). Therefore, sympatry alters the operational sex ratio for south polar skuas to be female biased, since a proportion of the males are mated with brown skua females. Conversely, brown skua populations in sympatry will be male biased. However, due to their relatively short migration distance (~1,000 km compared with >10,000 km for south polar skuas), we do not expect any sex-specific arrival dates for brown skuas.

Here, we aim to investigate the consistency of the theoretical predictions after modifying the original model to better reflect the skua system. In accordance with Kokko et al.'s (2006) findings, we predict that the spring arrival dates of south polar skuas shift toward protogyny under sympatric breeding conditions.

Material and Methods

Individual-Based Model

We used the model described by Kokko et al. (2006) as a basis and tailored the biological processes observed in the skua system. The appendix (available online) provides a detailed description of the model. The R code for the individual-based model is deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.6v5g3> (Lisovski et al. 2016). At a glance, the model assumes that variation in individual arrival is induced by a sex-specific allele determining the target arrival date. Major modifications to the original model were that females could also occupy and defend breeding territories. In addition, south polar skua males were able to choose a mate among conspecifics or brown skuas. The mating behavior of south polar skua males was modeled as the probability that a south polar skua male mates with a brown skua female. This behavior was conditional to the number of initially available conspecific females (f_1) and the number of initially available brown skua females (f_2) and equals

$$P(f_1, f_2) = \{(\alpha/2)^{\log_{0.5}(f_2/(f_1+f_2))}\}.$$

The parameter α in the expression specifies the mating behavior; for example, $\alpha = 1$ means that south polar skua males do not discriminate either way, $\alpha < 1$ means that they discriminate, and $\alpha > 1$ means that they favor brown skua females. South polar skua offspring inherit the allelic value randomly from either parent. Unfortunately, little is known about the relative gene introgression from the two species into their hybrid offspring, notably when it comes to genes determining their migratory behavior. To exclude the potential confounding effect of hybrids, we investigated model scenarios where either 100%, 50%, or 0% of the hybrids inherit the migratory allelic value of the respective south polar skua father. All simulations were run for at least 50 years and until the difference between female and male arrival times remained stable.

Field Sites

Spring arrival was investigated in an allopatric south polar skua population and in a population where the south polar skua occurred sympatrically with brown skuas. The allopatric population (14 breeding pairs) at Adelaide Island (Rothera Point, Antarctica; 67°34'S, 68°08'W), ~330 km south of the hybrid zone, was surveyed during the austral summer season 2010/2011. The sympatric population at King George Island (Fildes Peninsula, King George Island, South Shetland Islands, Antarctica; 62°12'S, 58°56'W) was surveyed during the summer seasons 2006/2007 and 2008/2009. It consisted of 255 south polar skua pairs, 89 brown skua pairs, and 29 mixed pairs. Previously published information on arrival in 1975/1976 in a south polar skua population under nearly allopatric conditions at Anvers Island (64°36'S, 63°30'W; Neilson 1983), on the southern edge of the hybrid zone, was included in our analysis. The relative numbers of mixed pairs during the study period was ~2% (with ~250 south polar, 12 brown skua, and 5 mixed pairs) and was recorded as being equally low (<1%) in 2004 (Ritz et al. 2006). Operational sex ratio in south polar skuas was calculated for each study island by dividing the numbers of south polar skua pairs by the sum of the numbers of south polar skua pairs and mixed pairs.

Arrival Dates

At King George Island, two specific areas, holding ~35% of the local skua population at the Fildes Peninsula, were visited every second to third day from the 25th of October to the 20th of December in both summer seasons. Areas were chosen on the basis of their accessibility and high percentage (~90%) of individually marked birds. During visits, marked birds were noted, and the site was registered as a territory. If birds were first sighted in a so-called nonbreeder club (consistent locations of social gatherings at freshwater lakes), the

corresponding date was taken for the individual's arrival date. In 2010/2011, observations at Adelaide Island followed the same schedule but surveys could not be done due to logistic constraints in six periods spanning 2 to 10 days (median, 4 days). In addition, the density of banded individuals was lower in this area. Arrival dates of individuals first seen at the visit following a period of absence were set at the mean date of the absence period. In two cases, the arrival dates of unbanded birds were set to the arrival date of the banded mate because the unbanded bird was already present during the first observation of its ringed mate (and possibly already earlier). Arrival time data for King George Island and Adelaide Island has been deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.6v5g3> (Lisovski et al. 2016).

Morphometrics

The first principal component of wing, tarsus, and culmen measurements explained 83% of the total variance and was used to distinguish between the two species (Peter et al. 1990). Individuals not clearly classified to either one of the two species were additionally analyzed using a discriminate function analyses with the same measurements and weight (Ritz 2009). On the basis of these results and due to their unknown migratory destination, individuals with a higher than 70% probability to be a hybrid were excluded and not considered in statistical analyses. This eliminated 11 individuals in 2006/2007 (7 south polar skuas from pure pairs, 1 brown skua and 1 south polar skua from mixed pairs) and 12 individuals in 2008/2009 (10 south polar skuas from pure pairs, 2 brown skuas and 2 south polar skuas from mixed pairs). Adults were caught with a baited snare and banded with a metal ring and a uniquely coded black-and-white plastic ring, allowing identification from a distance of ~50 m. Birds were sexed on the basis of DNA from 50- μ L blood samples by amplifying the W chromosome-linked CHD gene (Griffiths et al. 1996; Fridolfsson and Ellegren 1999).

Results

Individual-Based Model

Consistent with the original model developed by Kokko et al. (2006), our adjusted model simulations resulted in increasing protogyny when the proportions of south polar skua males decreased (fig. 1a). Furthermore, mating preference of south polar skua males for conspecifics decreased the degree of protogyny. If males did not discriminate species or even prefer heterospecifics, protogyny occurred with even moderate numbers of available brown skuas. The effect of extrapair young on sex specific arrival time was also consistent with the original model; extrapair paternity shifted the arrival time

difference toward protandry (fig. 1b). The degree of protogyny was also sensitive to the proportion of hybrids inheriting the south polar skua arrival gene (fig. 1c). At the extremes, protogyny was amplified if all hybrids inherited the arrival gene of the south polar skua father and shifted toward less pronounced protogyny at the other extreme, where all hybrids inherited the brown skua allelic value.

Arrival Dates in Allopatry

Average arrival date of south polar skua males on Adelaide Island was the 22nd of November in 2010, 2 days before the mean arrival of females. This difference was, however, not significant (fig. 2; table 1), which may be attributed to the small sample size associated with a low post hoc power (Faul et al. 2007) of only 0.14. At Anvers Island, on the southern edge of the hybrid zone under near-allopatric conditions, males preceded females by 6 days in 1975/1976 (table 1; data from Neilson 1983).

Arrival Dates in Sympatry

At King George Island, south polar skua females from pure pairs preceded conspecific males by 3 days in both seasons (fig. 2; table 1). Male south polar skuas from mixed pairs were 5 (in 2006/2007) to 6 (in 2008/2009) days earlier than their conspecific males from pure pairs. Sympatric breeding brown skuas arrived at King George Island 6 and 5 days before south polar skuas in 2006/2007 and 2008/2009, respectively (ANOVA; 2006/2007 species: $F_{1,122} = 18.01, P < .001$; sex, $F_{1,122} = 1.00, P = .32$; sex \times species, $F_{1,122} = 0.94, P < .33$; 2008/2009 species: $F_{1,106} = 19.96, P < .001$; sex, $F_{1,106} = 0.01, P = .90$; sex \times species, $F_{1,106} = 4.07, P = .046$). The significant interaction term between sex and species in 2008/2009 indicated intersexual differences in arrival times between the two species. In contrast to south polar skuas, arrival in brown skuas did not differ between sexes or pair types (2006/2007: sex, $F_{1,44} = 2.00, P = .16$; pair type, $F_{1,44} = 1.01, P = .32$; 2008/2009: sex, $F_{1,37} = 0.98, P = .33$; pair type: $F_{1,32} = 0.10, P = .74$). Within pairs, female south polar skuas arrived at least one day before their mates at the breeding ground in 17 (51%) of 30 and 17 (73%) of 23 pairs in the seasons 2006/2007 and 2008/2009, respectively, whereas female brown skuas arrived earlier in only 4 (25%) of 16 and 2 (14%) of 14 pure pairs and in 6 (46%) of 13 and 3 (30%) of 10 mixed pairs, respectively. Arrival dates of mates were correlated in all mating combinations (Spearman rank correlation; south polar skua: $r_{52} = 0.34, P = .012$; brown skua: $r_{29} = 0.39, P = .035$; mixed pairs: $r_{22} = 0.50, P = .013$). Individual arrival times of south polar skuas and brown skuas of mixed pairs appeared to be correlated across the seasons 2006/2007 and 2008/2009 (partial correlation controlled for sex; south polar skua pairs: $r_{25} = 0.58, P = .003$; mixed

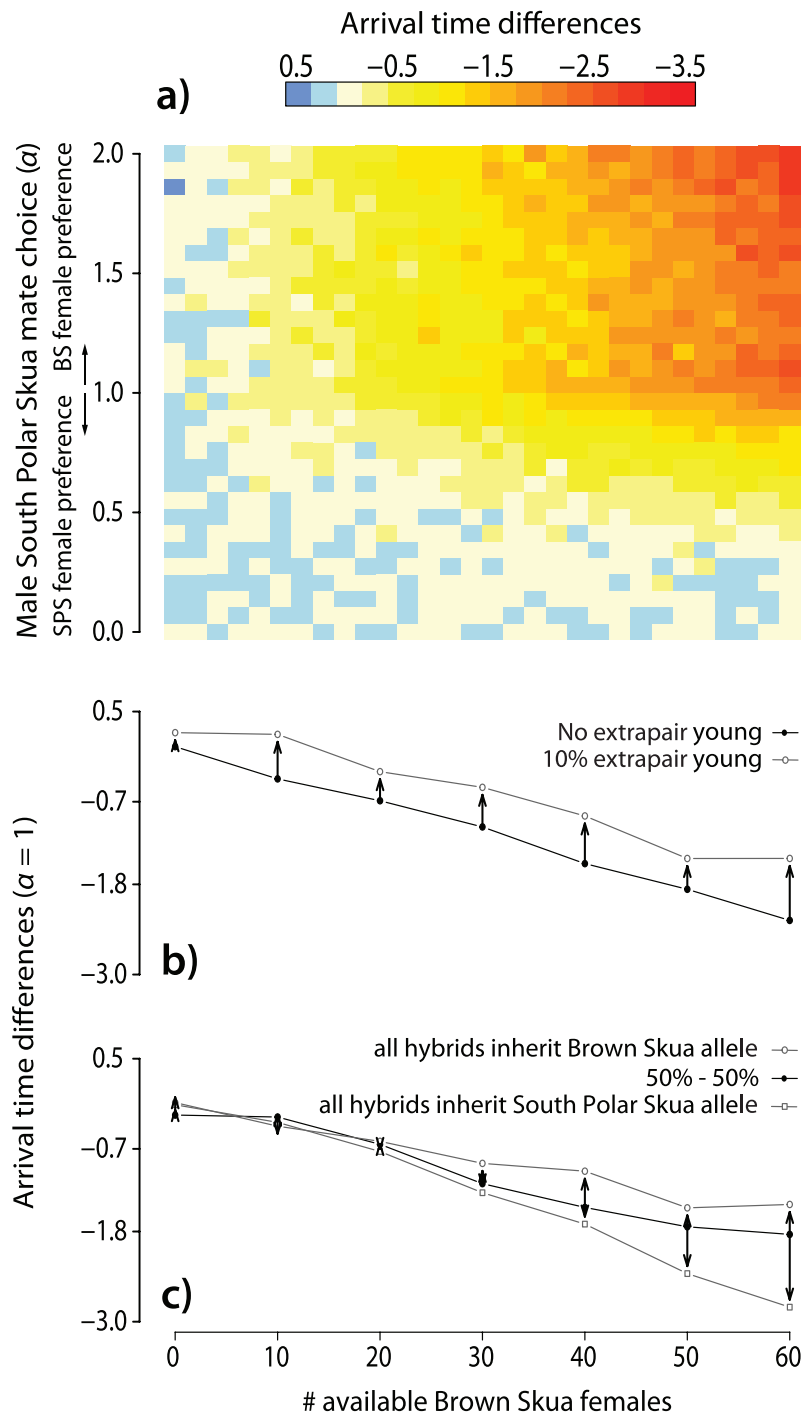


Figure 1: Results of the individual-based model developed to investigate the sex-specific arrival time difference (female-male arrival time) in a population with unidirectional hybridization: males of one species (south polar skua) can choose between conspecifics or another species (brown skua) if females of the latter are available (mating preferences are defined by α). Simulations were run with a south polar skua population of 200 females and 200 males. The number of available brown skua females varied between 0 and 60. Each cell in *a* is the mean arrival time difference of 50 independent simulations, *b* shows the mean arrival time differences for two different extrapair young probabilities (0%, 10%) and different numbers of available brown skua females, and *c* demonstrates the effect of hybrids going into the pool of south polar skuas or brown skuas or of being equally divided between the two species. Each value in *b* and *c* is the result of 50 independent simulations with no mating preference for females of either species ($\alpha = 1$). Other model parameters for simulations *a* and *b* were as follows: $\beta = 0.4$, $\mu = 0.01$, $D = 40$, $NrT = 200$. BS = brown skua; SPS = south polar skua.

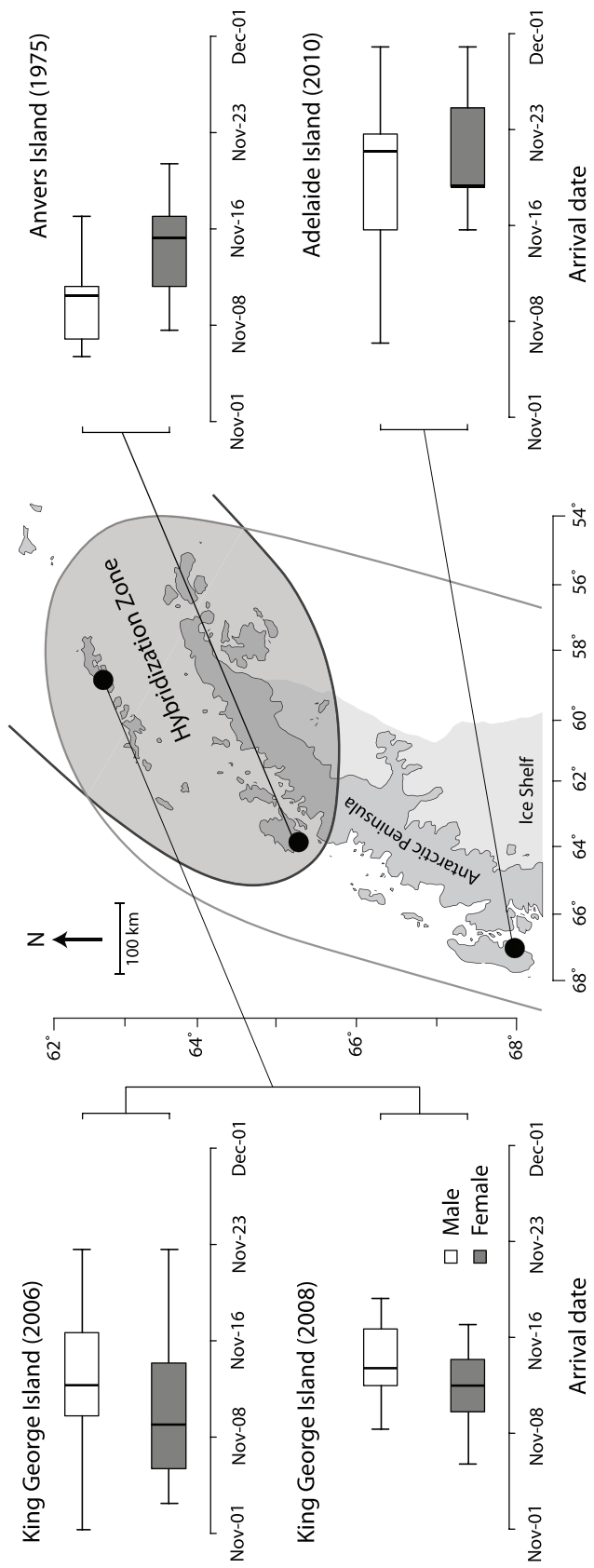


Figure 2: Sex-specific arrival dates of south polar skuas from three different populations in the Antarctic Peninsula region. The left graphs show arrival dates at King George Island, located in the south polar \times brown skua hybridization zone, during two different breeding seasons. White and gray boxplots (2.5 percentile, first quartile, median, third quartile, 97.5 percentile) indicate males and females, respectively. The upper right graph shows arrival times at Anvers Island, adopted from Neilson (1983). The lower right graph shows sex-specific arrival dates from an allopatric south polar skua population at Adelaide Island.

Table 1: South polar skua sex ratios, sample sizes (*N*), and mean arrival dates for the breeding populations under study

Location	Season	Relative sex ratio	<i>N</i>		Mean arrival		Pair type		Sex	
			Female	Male	Female	Male	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
King George Island	2006/2007	.86	29	25	10.11	13.11	3.61	.061	4.40	.039
King George Island	2008/2009	.86	32	27	9.11	12.11	6.39	.014	6.45	.013
Anvers Island	1975/1976	~1	16	17	13.11	7.11	13.74	.001
Adelaide Island	2010/2011	1	11	13	24.11	22.1173	.402

Note: *F* and *P* values correspond to ANOVAs of arrival date with sex and pair type (for the sympatric population at King George Island) as independent variables. South polar skua sex ratios are after Ritz et al. (2006).

pairs: $r_{10} = 0.61$, $P = .045$). In contrast, no correlation could be found among individuals of brown skua pairs ($r_{12} = 0.45$, $P = .15$).

Discussion

Our observations on arrival times in south polar skuas are in agreement with the theoretical predictions of Kokko et al. (2006). In the sympatric south polar skua population, where hybridization occurred and a significant proportion (11%) of south polar skua males were paired with brown skua females, leading to a female-biased sex ratio, females arrived before their conspecific mates. In contrast, protandry prevailed in the two allopatric south polar skua populations.

The original model from Kokko et al. (2006) and our modified model, which better reflects the skua breeding system, indicate that the observed operational sex ratio of 0.89 (11% more females) is sufficient to result in protogyny. This prediction was independent of the relative proportion of the species-specific arrival genes in hybrids (fig. 1c). Both models also predict that the involvement of extrapair young shifts the sex-specific arrival times toward protandry. However, that protogyny is the prevailing observation in the sympatric population supports current knowledge that extrapair young is either zero or negligible in south polar skuas (Catry and Furness 1997; Millar et al. 1997).

In our specific study system, mate preference in male south polar skuas may play an important role—obviously, if male south polar skuas prefer to mate with conspecifics, the arrival time difference would be less pronounced compared with a situation in which male south polar skuas prefer to hybridize with brown skuas. Unfortunately, we can only speculate on the mating preferences of male south polar skuas. However, since hybrids have no obvious reduction in viability or reproductive performance (Ritz et al. 2006), early-arriving south polar skua males could be indiscriminate with respect to species but still tend toward mating with brown skua females simply because of their earlier arrival compared with south polar skua females and the resulting chance to start breeding as soon as possible and profit from the already-established territory.

Conversely, however, one could also argue that protogyny in sympatrically breeding south polar skuas has arisen because early-arriving male south polar skuas are mainly paired with brown skua females. Mixed pairs could thus act as male sinks for south polar skuas and cause an apparent female surplus at the start of the season. While we can hardly test this possibility, general and species-specific aspects make it an unlikely alternative. Birds can use information gathered prior to their first breeding attempt for fitness-relevant decision making (Doligez et al. 2002). Skuas delay first breeding until they are ~7 years old but often return during their third or fourth summer to their natal breeding sites (Spellerberg 1971; Wood 1971). Since skuas are long-lived and usually faithful to their partner (Wood 1971), we expect a rather stable system, allowing immature birds to reliably assess the population sex ratio in the years prior to their first breeding attempts. Therefore, it appears more likely that an active decision-making process by surplus female south polar skuas breeding in the hybrid zone switched spring arrival from protandry to protogyny rather than a passive process caused by unidirectional hybridization.

As a result of unidirectional hybridization, a male bias should occur in sympatric brown skua populations. Theory predicts protandry as a result of male bias, but we could not find this pattern in brown skuas. The difference in distance between breeding and wintering areas in both species could serve as an explanation. Whereas south polar skuas are long-distance migrants and overwinter in high northern latitudes (Kopp et al. 2011), brown skuas remain in the Southern Hemisphere relatively close to their breeding sites (Phillips et al. 2007). And although the broader timing of spring migration for short-distance migrants is likely endogenously controlled, specific departure timing is known to be triggered by local weather conditions (Rappole 2013). The lack of individual repeatability in the arrival times of brown skuas supports this hypothesis. Another argument relates to the difference in feeding biology between the two species in sympatry (Reinhardt et al. 2000). While offshore foraging south polar skuas are strongly affected by adverse weather frequently occurring during early spring, the terrestrially feeding brown skuas may be less susceptible to such

conditions, allowing them to arrive on average one week earlier. Furthermore, the availability of terrestrial resources (penguin eggs, carrion) differs between sexes since the larger females have a higher probability to dominate carcasses (Hahn and Bauer 2008). Thus, selection pressure against early arrival may act stronger on male than on female brown skuas and might therefore delay their arrival.

Our observations suggest that in skuas intersexual differences in arrival are not fixed but are adjusted in relation to operational sex ratio. The optimal timing of arrival and clutch initiation seems crucial and likely to be under strong selection pressure, notably in the Antarctic regions, since birds are faced with a short period of favorable weather conditions that allow successful reproduction (Jouventin and Weimerskirch 1994).

In light of our observations, we suggest that the sex ratio in migratory populations may indeed play a crucial role in determining intersexual differences in the timing of arrival at the breeding grounds. To our knowledge, this is also the first record of protandry and protogyny occurring within a single bird species and between distinct populations. Our observations show once again the high potential of hybrid zones to be natural laboratories for evolutionary science (Hewitt 1988).

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Left, working on skuas is not always easy. A south polar skua (*Catharacta maccormicki*) is attacking Simeon Lisovski while he is recording information on incubation success on Fildes Peninsula, King George Island, Antarctica. (Photo credit: M. Kopp.) *Right*, a mixed pair of south polar skua male and brown skua female (far right, *C. antarcticus lonnbergi*) on Fildes Peninsula. (Photo credit: M. S. Ritz.)