SHORT NOTE

Body size, assortative mating and divorce rates in a little-known skua taxon, the Falkland Skua *Stercorarius antarcticus antarcticus*

Claudia Pich[1] · **Paulo Catry[2]**

Abstract

Several studies have attempted to identify the selective pressures leading to reversed size dimorphism (RSD), a characteristic of skuas and of a wide range of bird species with a raptorial lifestyle. One of the prevailing hypotheses posits that females in species of aggressive and well-armed males should select males that are smaller than themselves, to avoid injuries during pair formation and mating. This hypothesis predicts assortative mating by size in such species, and in previous research, this was confirmed to occur in two skua species. This study presents, for the first time, biometric data for Falkland Skuas *Stercorarius antarcticus antarcticus* based on large sample sizes. Despite the clear RSD, we found no assortative mating by size, which could be related to the low divorce rates and few opportunities for mate selection in this population. Our results highlight the need for further work to find an explanatory hypothesis for the evolution and maintenance of reversed size dimorphism in skuas.

Keywords Falkland Skua · Body size · Reversed size dimorphism · Assortative mating

Introduction

Reversed sexual size dimorphism (RSD) has evolved in various bird families or subfamilies, such as falcons (Falconidae), hawks (Accipitridae), frigatebirds (Frigatidae) and skuas (Stercorariidae) with a raptorial lifestyle. Despite this common link between several of the otherwise disparate and unrelated groups exhibiting RSD, there has been surprisingly little consensus on the probable mechanisms leading to its evolution (Phillips et al. 2002). In fact, numerous hypotheses have been proposed for the evolution of RSD, mainly concerned with sexual selection, trophic niche divergence, or specialization in reproductive roles (Andersson and Norberg 1981; Mueller 1990; Hakkarainen and Korpimäki 1991), but much uncertainty remains regarding their acceptance or rejection.

Catry et al. (1999) found evidence for assortative mating by size in two species of skuas. This might be due to females avoiding large males that, in this well-armed and aggressive species, could inflict injuries during pair formation (see Smith 1982). This mechanism might provide a selective pressure for RSD in skuas (Catry et al. 1999). However, one further study on another skua, the Brown Skuas (*Stercorarius antarcticus lonnbergi*), failed to find evidence for assortative mating by size (Phillips et al. 2002). The Falkland Skua (*Stercorarius antarcticus antarcticus*) is a seabird nearly endemic to the Falklands Islands and a scarcely studied subspecies compared with other taxa of the Stercorariidae family. Additionally, the only existing demographic data reported a significant population decline on New Island, one of the major strongholds of this seabird (Catry et al. 2011).

Body size is a fundamental trait of species and populations, and information on body size is critical for the study of a wide range of pure and applied ecological and evolutionary questions (e.g. Barth 1967; Barrett et al. 1985; Fairbairn and Shine 1993; Mancini et al. 2014; Heswall et al. 2021). Published data on biometrics of Falkland Skuas are based on very small sample sizes (only 13 males and 20 females, Hamilton 1934).

✉ Claudia Pich
pich.claudia@gmail.com

1 Consorci per a la Recuperació de Fauna de les Illes Balears (COFIB), Ctra Sineu km 15.4, 07142 Santa Eugènia, Balearic Islands, Spain

2 MARE – Marine and Environmental Sciences Centre, ISPA – Instituto Universitário, Rua Jardim do Tabaco 34, 1149-041 Lisbon, Portugal

Most seabirds, including skuas, have high survival and low divorce rates, and a high incidence of non-breeding after mate loss (Catry et al. 1997; Mercier et al. 2021). This suggests that there may be limited opportunities for mate choice, which may potentially constrain the possibility of development of assortative mating by size. Hence, when assessing assortative mating by size, it is relevant to also assess divorce rates of the study populations.

Our objective in this study is to report for the first time robust morphometric data of Falkland Skuas and assess whether assortative mating by size occurs in this population. We also analyse divorce rates as supporting information to discuss our results.

Methods

Fieldwork was conducted on New Island (51° 43′ S, 61° 18′ W), one of the westernmost islands of the Falklands archipelago. Biometrical data were collected from 2008 to 2019 during the breeding season. Nesting generally starts in November with territory formation and egg laying and ends in February–March with the fledging of the chicks. Birds from different territories were captured by hand or with a hand-net while attending the nest. Five body measurements were taken: bill length (from the tip of the bill to the start of the feathering at the base of the culmen), gonys (bill height at the gonys), tarsus length, wing length (maximum flattened cord) and mass during incubation.

Egg dimensions (length and breadth) were recorded to the nearest 0.1 mm from 2008 to 2011. Indices of egg volume were calculated as $length \times breadth^2$ (Furness 1987). The vast majority of first clutches in skuas are composed of two eggs (Furness 1987, 1996).

These measurements were taken by different observers throughout the years, but all fieldworkers had previously jointly measured birds with Paulo Catry to ensure the consistency of methods. It is likely that measurement error differed slightly between observers, but it does not seem plausible that after joint training measurement error would be so large as to mask natural variation. Wing length was measured with a ruler to the nearest mm, mass was determined with a 2-kg Pesola spring-balance to the nearest 10 g and bill length, gonys, tarsus length and egg length and breadth were obtained with callipers, to the nearest 0.1 mm. For body mass, we only present data from birds weighed during incubation.

All measured birds were ringed with a metal ring and a coded Darvic ring to allow easy identification from a distance without the need for recapture. Breeding pairs were recorded during long-term monitoring on New Island (2008–2019) through regular visits to the nesting territories during laying and incubation.

To determine the sex of the birds, we used blood samples, and observations of copulation or of courtship feeding. For sex determination by molecular methods, a small blood sample was obtained from the interdigital capillaries and stored in 98% ethanol. DNA was extracted from blood samples, and PCR amplification carried out with primers 2550F and 2718R (Fridolfsson and Ellegren 1999).

To evaluate the degree of dimorphism between sexes, the dimorphism index (DI) used was [(female size-male size)/ (female size + male size)] $\times$ 100 (Marti 1990; Catry et al. 1999; Phillips et al. 2002).

A principal components analysis for all measured individuals was carried out incorporating the morphometric variables bill length, gonys, tarsus length and wing length to produce single-factor scores (PC1 scores) representing body size (Rising and Somers 1989). Body mass was not used as a measure of size because it also reflects body condition.

Male and female morphometric and composite body size indices (PC1) were compared within pairs to test for evidence of assortative mating with respect to size.

Divorce rates were obtained from the number of divorced pairs as a proportion of the total number of breeding pairs per year. A divorce is said to have occurred when two birds that bred together in year A are alive in year A + 1 but no longer breeding together (Catry et al. 1997). Power calculations for correlation test were conducted using pwr package in R (https://cran.r-project.org/web/packages/pwr/pwr.pdf). Based by the rule of thumb suggested by Cohen (1992) r values of 0.1, 0.3 and 0.5 represent small, medium and large effects sizes, respectively. For this dataset, the population correlation coefficients are the effect size.

Results

Measurements of male and female Falkland Skuas are presented in Table 1. Although there was considerable overlap in the five characters analysed, females were significantly larger than males ($p < 0.001$ ANOVA test) in tarsus length, wing length and body mass during incubation.

Egg measurements from first clutches for which laying order is known are presented in Table 2. Eggs laid first were larger than second eggs in all measurements.

A dimorphism index was calculated at the population level and within each pair for all body size measurements and body mass (Table 3).

The percentage of variance explained by PC1 was 44%. Correlations between all body measurements, body mass and PC1 score were calculated (Table 4). There were no significant correlations within-pairs ($n = 81$) in any univariate measurements or in PC1 (Table 5). The power analysis for a medium effect size ($r = 0.3$) indicates a power varying between 0.70 and 0.77 for the different variables assessed,

Table 1 Morphometrics of male and female Falkland Skuas (*Stercorarius antarcticus antarcticus*) and comparison between sexes

	Males (n=67)			Females (n=66)			p
	Mean±SD	Sample size	Range	Mean±SD	Sample size	Range	
Bill length	47.7±2.3	64	43.7–51.9	48.2±1.9	63	43.7–53	0.15
Gonys	18.5±0.8	66	15.9–20.2	18.7±0.7	65	17.1–20.7	0.094
Tarsus length	68.9±2.4	66	61.0–74.7	70.6±1.9	65	66.6–74.6	<0.001
Wing length	389±7	66	370.0–412.0	397.4±8	65	374.0–414.0	<0.001
Body mass	1175±97.5	64	1025–1575	1340±133	59	1000–1675	<0.001

Linear measurements in mm and mass in grams

Table 2 Egg measurements of Falkland Skuas nesting on New Island

	First egg (n=104)		Second egg (n=91)		Total (n=195)		
	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	p
Length (mm)	72.7±2.8	66–80.3	70.9±2.6	65.4–78.8	71.8±2.9	65.4–80.3	<0.001
Breadth (mm)	50.4±1.3	46.6–53.2	49.9±1.4	47–53.8	50.2±1.4	46.6–53.8	0.019
Volume Index (cm^3)	184.6±11.7	155.6–216	176.8±12.4	154.4–207.6	181±12.6	154.4–216	<0.001

No eggs from replacement clutches are included here

Table 3 Measurements of dimorphism index for all birds and for each pair (mean±SD)

	Population (n=133)	Pairs (n=81)
Bill length	0.6	0.9±2.9
Gonys	0.6	0.6±2.8
Tarsus length	1.2	1.3±2.2
Wing length	1.1	1.3±1.5
Body mass	6.6	6.9±6.1

Table 5 Results of the Pearson correlation between male and female measurements within breeding pairs of Falkland Skuas

	n	Correlation	p
Bill length	70	r=0.20	0.079
Gonys	79	r=−0.15	0.198
Tarsus length	79	r=−0.19	0.091
Wing length	77	r=−0.09	0.461
Body mass	67	r=0.03	0.820
PC1	70	r=0.05	0.690

Table 4 Pearson correlation amongst PC1, morphometrics and body mass for Falkland Skuas

	1	2	3	4	5
1. PC1	–				
2. Bill length	0.631**	–			
3. Gonys	0.639**	0.250**	–		
4. Tarsus length	0.741**	0.258**	0.321**	–	
5. Wing length	0.646**	0.228*	0.17	0.359**	–
6. Body mass	0.380**	-0.028	0.270**	0.336**	0.418**

*$p<0.05$; **$p<0.01$

Table 6 Dimorphism index for non-divorced pairs and divorced pairs of Falkland Skuas

	Non-divorced (n=40)	Divorced (n=13)	t	p
Bill length	1.4±2.6	−1.1±2.6	2.89	0.005
Gonys	0.1±3.4	0.01±2.5	0.93	0.355
Tarsus length	1.4±2.3	0.8±2.3	0.83	0.409
Wing length	1.1±1.4	0.1±0.8	0.22	0.829
Body mass	5.7±6.5	6.5±5.3	−0.37	0.713
PC1	−1.5±4.1	−0.5±1.7	−0.10	0.921

while for a large effect size ($r=0.5$), the power is above 0.99 for all attempted correlations.

Between 2009 and 2017, the overall divorce rate was 8.1% ($n=223$ occasions when both members of a partnership survived the winter and were resighted again). No pairs reunified in subsequent breeding seasons after they had divorced. Of the partnerships that ended during the study,

72% did so as a result of the disappearance of one of the partners, and only 28% finished as a result of a divorce.

Table 6 presents comparisons of dimorphism indices of various measurements between pairs that remained united throughout the study and pairs for which divorce was recorded. Pairs which divorced during this study had males

with relatively larger bills, compared to females, but there were no differences in other measured variables.

Discussion

The current study found that females of Falkland Skuas are larger in body size than males, confirming a reversed sexual dimorphism (RSD) in this taxon (Furness 1996). Comparison of our measurements with published data on other large skuas (formerly classified as *Catharacta*, and including also *Stercorarius antarcticus lonnbergi*, *S. a. hamiltoni*, *S. skua*, *S. maccormicki*, *S. chilensis*) reveals that the Falkland Skuas is the smallest taxon (Online Resources in Tables 1–4) (Furness 1987; Catry et al. 1999). We note that body mass measurements may vary from one season to another, as well as within a breeding season, and hence, the results from this variable need to be taken cautiously. On the other hand, there are inevitable differences between measurements of different fieldworkers in different studies and even within our study. We do not believe, however, that these are likely to significantly affect our conclusions. The mean egg volume was the third smallest after eggs from South Polar Skuas and Great Skuas (Online Resources in Table 5) (Furness 1987; Catry and Furness 1997).

According to Bergmann's rule, taxa living in colder regions have larger body sizes than those in warm regions. In this sense, the small size of the *antarcticus* subspecies of Brown Skuas fits well with the theory, when compared with *lonnbergi* (who lives mostly south of the Antarctic convergence). However, this does neither explain the difference between *hamiltoni* and *antarcticus* nor the fact that South Polar Skuas, one of the smallest species of the large skuas, lives in colder environments (Antarctica) than the other skuas.

In Falkland Skuas, the first egg is on average larger than second egg, a trait commonly found amongst seabird species, that could be explained as a mechanism to facilitate brood reduction or to reduce hatching asynchrony (Slagsvold et al. 1984; Catry and Furness 1997).

We found no evidence for assortative mating by size in Falkland Skuas, which goes against the current hypothesis linking sexual selection to the evolution of RSD. Similarly, Phillips et al. (2002) were unable to demonstrate assortative mating by size in Brown Skuas in South Georgia (correlation between PC1 score, representing body size, within pairs was $r = -0.02$, $n = 101$, ns). Hence, the positive correlations between PC1 scores within pairs for Arctic Skuas *S. parasiticus* ($r = 0.28$, $n = 67$, $p = 0.027$) and Great Skuas ($r = 0.22$, $n = 61$, $p = 0.085$) described by Catry et al. (1999) do not seem to apply to skuas in general.

Dimorphism indices for wing length in Falkland Skuas have similar values to other skuas and jaegers, and the small differences found do not seem to reflect different foraging modes (see Catry et al. 1999). However, Falkland Skuas have a dimorphism index for body mass greater than the other large skua taxa (5.3 on average). This is analogous to the degree of dimorphism observed in jaegers (6.6 on average) that are generally more aerial foragers (e.g. Reinhardt et al. 2000). These interspecific comparisons make it difficult to support the hypothesis that small male size has evolved for efficient foraging during breeding (Andersson and Norberg 1981; Mueller 1990; Hakkarainen and Korpimäki 1991).

Divorce rates in Falkland Skuas (8.1%) were higher but similar compared to other skuas. For Arctic Skuas a 7% divorce rate was reported (Phillips 1995), 6.4% in Great Skuas (Catry et al. 1997), and in South Polar Skuas divorce rates ranged from 1.5% (Wood 1971) to 0.0% (Mercier et al. 2021). Birds that seldom divorce in populations with high survival rates (as is typical of skuas) may have few opportunities for being selective when there are limited options amongst widowed or new recruits. This may constrain the possibility for assortative mating to appear. Except for one measurement (bill length) pairs that divorced during this study were not more or less dimorphic than pairs that remained united, indicating that dimorphism may have little or no role in pair formation and maintenance.

In conclusion, our study shows that the smallest of all large skua taxa does not display assortative mating by size, questioning the generality of the findings by Catry et al. (1999), and leaving the evolution of RSD in skuas without an explanatory hypothesis that is well supported from the currently existing data.

Declarations

Conflict of interest All authors declare that they have no conflict of interest.

Ethical approval The authors adhered to all relevant laws, regulations, and protocols in conducting this research.

Consent to participate Not applicable.

References

Andersson M, Norberg RÅ (1981) Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. Biol J Linn Soc 15:105–130. https://doi.org/10.1111/j.1095-8312.1981.tb00752.x

Barrett RT, Fieler R, Anker-Nilssen T, Rikardsen F (1985) Measurements and weight changes of Norwegian adult puffins *Fratercula arctica* and kittiwakes *Rissa tridactyla* during the breeding season. Ringing Migr 6:102–112. https://doi.org/10.1080/03078698.1985.9673865

Barth EK (1967) Standard body measurements in *Larus argentatus*, *L. fuscus*, *L. canus*, and *L. marinus*. Nytt Mag Zool 14:7–83

Catry P, Furness RW (1997) Egg volume and within-clutch asymmetry in great skuas: are they related to adult quality? Colon Waterbird 20:399–405. https://doi.org/10.2307/1521589

Catry P, Ratcliffe N, Furness RW (1997) Partnerships and mechanisms of divorce in the Great Skua. Anim Behav 54:1475–1482. https://doi.org/10.1006/anbe.1997.0552

Catry P, Phillips RA, Furness RW (1999) Evolution of reversed sexual size dimorphism in skuas and jaegers. Auk 116:158–168. https://doi.org/10.2307/4089462

Catry P, Almeida A, Lecoq M, Granadeiro JP, Matias R (2011) Low breeding success and sharp population decline at the largest known Falkland Skua colony. Polar Biol 34:1239–1241. https://doi.org/10.1007/s00300-011-0978-1

Cohen J (1992) Statistical power analysis. Curr Dir Psychol Sci 1:98–101. https://doi.org/10.1111/1467-8721.ep10768783

Fairbairn J, Shine R (1993) Patterns of sexual size dimorphism in seabirds of the Southern Hemisphere. Oikos 68:139–145. https://doi.org/10.2307/3545319

Fridolfsson AK, Ellegren H (1999) A simple and universal method for molecular sexing of non-ratite birds. J Avian Biol 30:116–121. https://doi.org/10.2307/3677252

Furness RW (1987) The skuas. T & AD Poyser, Calton

Furness RW (1996) The Stercorariidae. In: Handbook of the birds of the world 3. Lynx Edicions, Barcelona, pp 556–571

Hakkarainen H, Korpimäki E (1991) Reversed sexual size dimorphism in Tengmalm's owl: is small male size adaptive? Oikos 61:337–346. https://doi.org/10.2307/3545241

Hamilton JE (1934) The sub-antarctic forms of the Great Skua (*Catharacta skua skua*). Discov Rep 9:161–174

Heswall AM, Friesen MR, Martin AB, Gaskett AC (2021) Seabird bycatch risk correlates with body size, and relatively larger skulls, bills, wings and sensory structures. Mar Biol 168:1–13. https://doi.org/10.1007/s00227-021-03873-4

Mancini PL, Hobson KA, Bugoni L (2014) Role of body size in shaping the trophic structure of tropical seabird communities. Mar Ecol Prog Ser 497:243–257. https://doi.org/10.3354/meps10589

Marti CD (1990) Sex and age dimorphism in the Barn Owl and a test of mate choice. Auk 107:246–254. https://doi.org/10.2307/4087606

Mercier G, Yoccoz NG, Descamps S (2021) Influence of reproductive output on divorce rates in polar seabirds. Ecol Evol 11:12989–13000. https://doi.org/10.1002/ece3.7775

Mueller HC (1990) The evolution of reversed sexual dimorphism in size in monogamous species of birds. Biol Rev 65:553–585. https://doi.org/10.1111/j.1469-185X.1990.tb01238.x

Phillips RA (1995) Population ecology of Arctic skuas *Stercorarius parasiticus*, on Foula. PhD thesis, University of Glasgow

Phillips RA, Dawson DA, Ross DJ (2002) Mating patterns and reversed size dimorphism in Southern skuas (*Stercorarius skua lonnbergi*). Auk 119:858–863. https://doi.org/10.1093/auk/119.3.858

Reinhardt K, Hahn S, Peter HU, Wemhoff H (2000) A review of the diets of Southern Hemisphere skuas. Mar Ornithol 28:7–19

Rising JD, Somers KM (1989) The measurement of overall body size in birds. Auk 106:666–674. https://doi.org/10.1093/auk/106.4.666

Slagsvold T, Sandvik J, Rofstad G, Lorentsen Ö, Husby M (1984) On the adaptive value of intraclutch egg-size variation in birds. Auk 101:685–697. https://doi.org/10.2307/4086895

Smith SM (1982) Raptor "reverse" dimorphism revisited: a new hypothesis. Oikos 39:118–122. https://doi.org/10.2307/3544542

Wood RC (1971) Population dynamics of breeding South Polar Skuas of unknown age. Auk 88:805–814. https://doi.org/10.2307/4083839