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Hybridisation between South polar skua (*Catharacta maccormicki*) and Brown skua (*C. antarctica lonnbergi*) in the Antarctic Peninsula region

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Abstract Hybridisation between South polar skua (*C. maccormicki*) and Brown skua (*C. antarctica lonnbergi*) in the area of the Antarctic Peninsula is known at least since the beginning of the last century but no survey has been done so far. This paper reviews information on the species composition of skua colonies of more than 10 pairs in the Antarctic Peninsula region, and the incidence of mixed pairs. Morphometrics, population size and breeding success were examined in detail at King George Island. The northward distribution of South polar skuas extended to King George Island (62°11′ S 59°00′ W), with a small outlying population on Signy Island (60°45′ S 45°36′ W), whereas Brown skuas did not breed further south than Anvers Island archipelago (64°46′ S 64°03′ W). The proportion of mixed pairs was highest at the northern end of the ~500-km-wide hybrid zone. Body size distribution of sympatric skuas from King George Island is clearly bimodal but overlaps considerably and hybrids cannot be identified. Skua population sizes at Potter Peninsula/King George Island remained stable between 1994 and 2004. Numbers of mixed breeding pairs fluctuated more strongly than those of pure species pairs. Breeding success of Brown skuas varied the least.

Introduction

The hybrid zone between South polar skua (*Catharacta maccormicki*) and Brown skua (*C. antarctica lonnbergi*) in the Antarctic Peninsula is especially suited to study hybridisation between recently emerged taxa with moving ranges. Both species are closely related (Blechschmidt et al. 1993; Cohen et al. 1997) and are suspected to have been separated into two species during the last big glaciation events. The hybrid zone exists at least since the beginning of the last century (Bennet 1920; Watson 1975). While the range of the Brown skua has remained stable, the South polar skua increased in population size at King George Island (Woehler et al. 2001; Hahn et al. 2003) and enlarged its range to the north in the late 1970s (Hemmings 1984) resulting in a broader hybrid zone.

The South polar skua is well-adapted to the extreme Antarctic environment and breeds all around Antarctica. The species feeds opportunistically on other seabirds and marine resources. South polar skuas are able to reproduce in complete dependency on marine food (Young 1963; Mund and Miller 1995; Baker and Barbraud 2001). Brown skuas breed mainly on sub-Antarctic islands around Antarctica and depend on terrestrial resources (e.g. penguins, carrion, station garbage) to reproduce successfully (Pietz 1987; Peter et al. 1990; Reinhardt 1997; Phillips et al. 2004). Both species occur sympatrically in the area of the Antarctic Peninsula, where they produce viable and fertile hybrids (Pietz 1987; Parmelee 1988).

The aim of this paper is to give an overview of the hybrid zone between South polar skua and Brown skua based on published and new information. Furthermore, we provide morphometric data on both species from a King George Island population, where the frequency of mixed pairs is especially high. Additionally, we present data on breeding pair numbers and reproductive success between 1994 and 2004 from the Potter Peninsula population at King George Island.

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Materials and methods

Species composition of breeding populations

Data on population size of both species at various localities in the area of the Antarctic Peninsula were reviewed from the literature. We only included colonies if the total skua population exceeded 10 breeding pairs and the species were distinguished. The used data are, therefore, only a fraction of the actual skua breeding populations in the area of the Antarctic Peninsula (Croxall et al. 1984; unpublished SCAR review). Data from Fildes and Potter Peninsula, King George Island, were collected by the authors.

Morphometrics

Wing, tarsus and culmen measurements were identified in an earlier study as useful measurements to distinguish between the sympatric skua species (Peter et al. 1990). For an inter-species comparison of body size in two study periods, we used data from 1984, 1985 and 2004 (2004 = austral summer 2003/04). Wing length was measured with a ruler as the distance from the tip to the bow of the wing when it was in a relaxed position beside the bird's body (± 1 mm). Tarsus length was measured as the maximum distance from the lower to the upper frontal end of the tarsus when it was in an angled position. Culmen length was the maximum distance from the tip of the bill to the beginning of feathering at the upper beak. Wing, tarsus and culmen measurements were standardised for each study period and reduced to a single index of body size using principle component analysis (Rising and Somers 1989). The first principal component (PC1) explained 75% and 82% of total variance in the first and second study period, respectively. Measurements were taken from December to March from non-breeders (1/3 of data) and breeding adults (2/3). Birds were sexed on the basis of DNA from blood samples of 50 µl by amplifying the W-chromosome linked CHD gene (Griffiths et al. 1996; Fridolfsson and Ellegren 1999) or if they bred together with a known sex adult. Sex was not known for birds measured in 1984 and 1985 and only in a fraction of birds from 2004. Therefore, measurements are given for sexes combined. Species assignment was done on the basis of plumage colouration (Peter et al. 1990; golden hackles in South polar skua, white spots at the back of Brown skua) and general appearance (small and gracile in South polar skua and bulky and heavy in Brown skua). The procedure cannot completely assure against false assignment of doubtful individuals and fails to identify hybrids. A stepwise discriminant analyses based on these visual species assignments was performed with wing, culmen, tarsus and mass measurements to reveal the usefulness of these measurements to distinguish between the two species.

Breeding population at Potter Peninsula

The skua breeding population at Potter Peninsula, King George Island, was monitored every austral summer since 1994 (except 1997). Breeding success data were only analysed if the visits lasted from December until the end of February. All nests were checked at least weekly and chick survival until fledging was recorded. Measures of variability of breeding success in the three pair assemblages were obtained by calculating the unstandardised residuals from a regression of breeding success over time. The absolute values from the residuals were then used to calculate the percentage of the absolute deviation. Due to between species differences in mean population size variability of breeding pair numbers was compared using co-efficient of variation.

Results

Species composition of breeding populations

Sympatric populations of South polar skua and Brown skua occur in an ~500-km-wide zone in the area of the Antarctic Peninsula (Fig. 1, Table 1). The incidence of mixed pairs was highest in the north of the hybrid zone, at King George Island, where more than 10% of all breeding pairs are mixed pairs. In the hybrid zone the proportion of South polar skua pairs increased with latitude from north to south. The most southerly record of breeding Brown skuas originated from Anvers Island (near the US Palmer station). The 12 breeding pairs nest in close association with small penguin colonies (Pietz 1984). Mixed pairings with males from the immense population of South polar skuas (ca. 700 breeding pairs) resulted in fertile hybrid offspring (Pietz 1987; Parmelee 1988). In the North, the South polar skua has extended its range to Signy Island/ South Orkneys, where a small number of pairs (1–3) still breed in most years (Hemmings 1984; British Antarctic Survey unpublished data). However, this colony is something of an outlier from the main range of South polar skuas on the Antarctic Peninsula, where they do not reach as far north as Elephant Island (M.Sanders, pers. com.).

Morphometrics

Combined measurements of wing, culmen, tarsus and mass from skuas at Potter and Fildes Peninsula during the two study periods are shown in Table 2. Both species have a broad range and no single measurement can be used to determine the species. The frequency distribution of the body size index (Fig. 2) is clearly bimodal but overlaps considerably. About 31% (1983–1984) and 24% (2004) of the measured individuals fall inside this overlap. However, stepwise discriminant analysis revealed that a combination of three measurements correctly assigned 553 of 566 individuals (97.7%) to species. The measurements are (ordered by size of correlation within discriminant function): tarsus, mass and culmen.

Breeding population at Potter Peninsula

We found no significant linear trends in the population size over the investigated decade for South polar skua

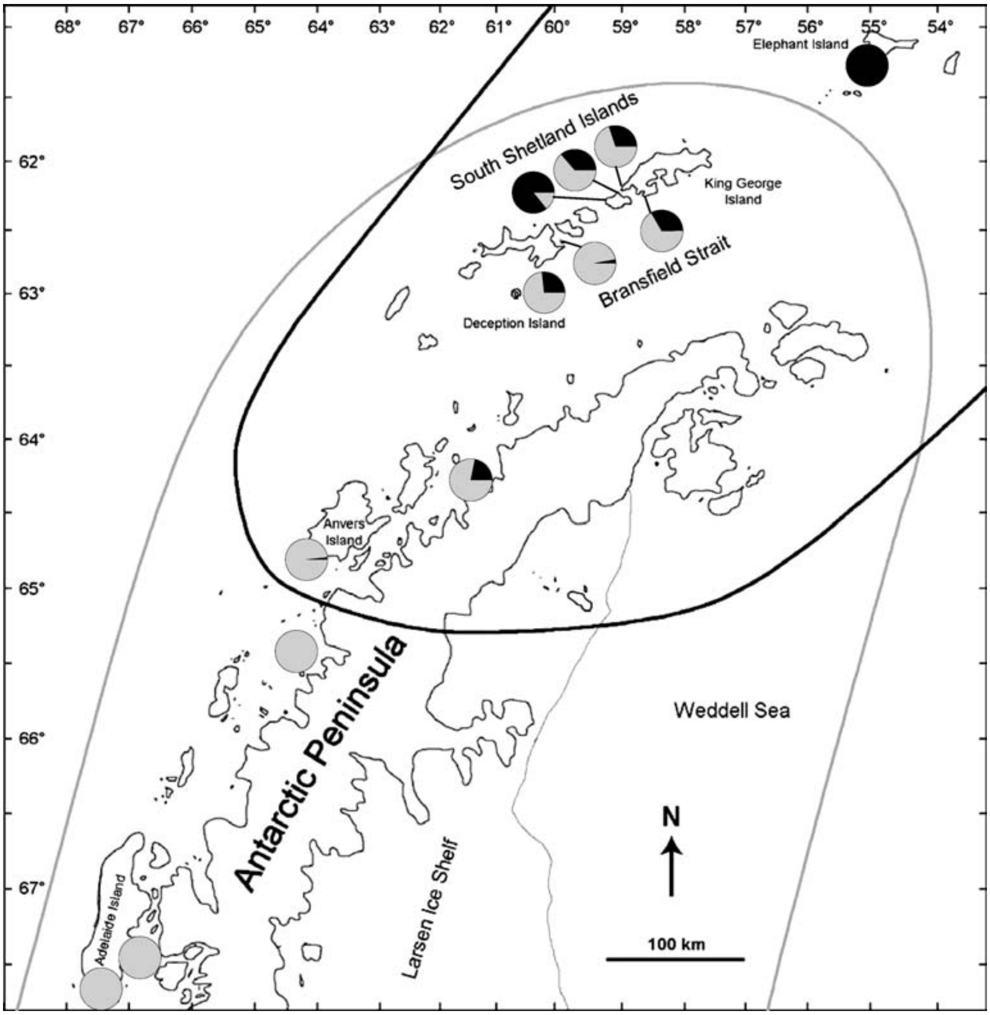

Fig. 1 Species composition of breeding populations of South polar skua (*grey part of pie*) and Brown skua (*black part of pie*) in the area of the Antarctic Peninsula. Number of breeding pairs and source of data are in Table 1. The grey and black solid lines encircle the approximate breeding ranges of South polar skua and Brown skua, respectively

Table 1 Number of South polar skua pairs (SPS), mixed pairs (MP) and Brown skua pairs (BS) in the area of the Antarctic Peninsula. Only colonies known to hold more than ten pairs are included

Location	Coordinates	SPS	MP	BS	Study year	References
Signy Island, South Orkneys	60°43'S 45°36′ W	1–3	Some	> 100	2003–05	British Antarctic Survey (unpublished data)
Elephant Island	61°05′ S 55°10′ W	0	0	190	1983	M. Sanders (pers. com.)
Fildes Peninsula / KGI	62°11′ S 59°00′ W	176	28 (10%)	76	2001	Own data
Potter Peninsula / KGI	62°14′ S 58°40′ W	63	13 (12%)	35	2002	Own data
Northern Nelson Island	62°14′ S 59°00′ W	21	1 (3%)	12	1992	Lumpe and Weidinger (2000)
Harmony Point, Nelson Island	62°18′ S 59°10′ W	10		61	1996	Silva et al. (1998)
Half moon Island	62°36′ S 59°53′ W	103	4 (4%)	3	1996	Garcia Esponda et al. (2000)
Deception Island	62°58′ S 60°39′ W	11		4	2001	Bo and Copello (2000)
Cierva Point	64°09′ S 60°57′ W	93	8 (6%)	26	1996	Quintana et al. (2000)
Anvers Island archipelago	64°46′ S 64°03′ W	app. 650	1 (< 1%)	12	2004	W. Fraser (pers. com.)
Argentine Islands (Vernadsky)	65°14′ S 64°15′ W	50	0	0	2003	V. Bezrukov (pers. com.)
Adelaide Island (Rothera)	67°34′ S 68°08′ W	12	0	0	1998	Milius (2000)
Avian Island, Marguerite Bay	67°46′ S 68°54′ W	880	0	0	2004	W. Fraser (pers. com.)

(Fig. 3, $R^2_9 = 0.20$, $P = 0.18$), Brown skua ($R^2_9 = 0.19$, $P = 0.20$) or mixed pairs ($R^2_9 = 0.02$, $P = 0.67$). The South polar skua was clearly more abundant than the Brown skua over the study period (mean: 43 vs. 29 pairs; paired *t*-test, $t_9 = 2.98$, $P = 0.015$). The number of mixed pairs was not significantly related to the breeding pair number of pure pairs (South polar skua: $r_{10} = 0.59$, $P = 0.067$; Brown skua: $r_{10} = 0.47$, $P = 0.17$). Mixed pairs consisted in all 21 observed pairings of a male South polar skua and a female Brown skua. The annual mean of 10 mixed

Table 2 Measurements of South polar skuas and Brown skuas from two study periods (1984–1985 and 2004) from King George Island/Antarctica. Species assignment was done on the basis of plumage colouration and general appearance

	South polar skua ($n=284$)			Brown skua ($n=280$)		
	Mean	SD	Range	Mean	SD	Range
Culmen (mm)	47.8	1.9	41.5–53.3	53.5	2.0	47.8–58.9
Wing (mm)	398	13	340–436	418	13	373–470
Tarsus (mm)	64.5	2.8	53.7–79.8	74.3	3.1	64.9–83.4
Mass (g)	1177	124	890–1660	1669	182	1050–2150

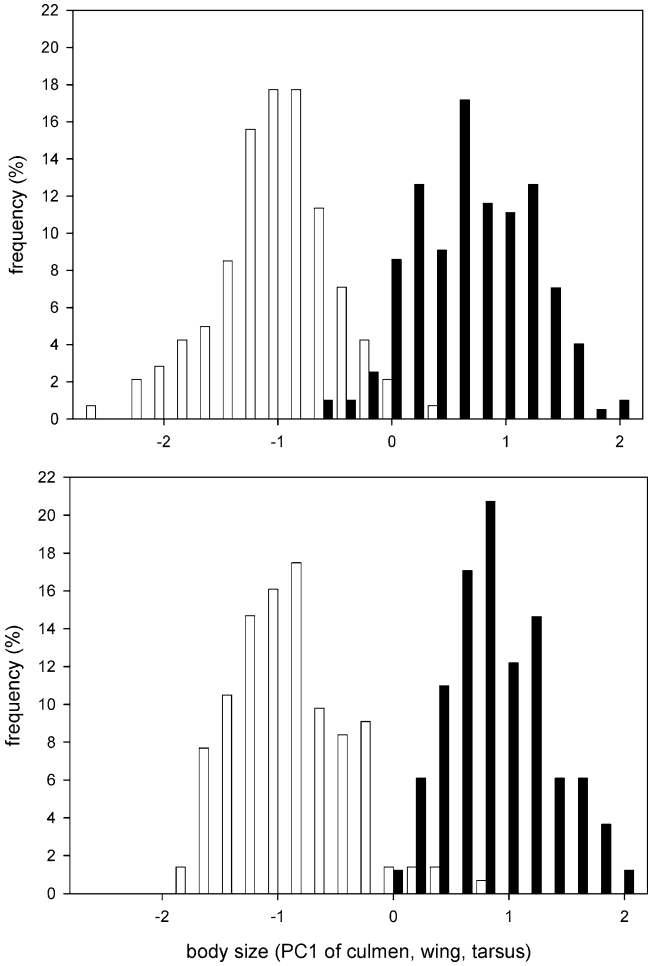

Fig. 2 Frequency distribution of body size for South polar skuas (open bars) and Brown skuas (filled bars) at King George Island, Antarctica. Data shown for the study periods 1984–1985 (upper graph; $n=141$ and 198) and 2004 (lower graph; $n=143$ and 82)

breeding pairs was considerably lower than the 31 expected mixed pairs under the assumption that skuas mate randomly with respect to species (male Brown skua–female South polar skua pairings excluded; $\chi^2_2=25.092$, $P<0.001$).

Mixed pairs showed the strongest annual variation in the number of breeding pairs (coefficient of variation: 49.6%, confidence interval: 48.0–51.1%). Among pure species pairs Brown skuas fluctuated considerably less than South polar skua pairs (Brown skua: 21.0%, 19.4–22.5%; South polar skua: 31.0%, 29.4–32.5%).

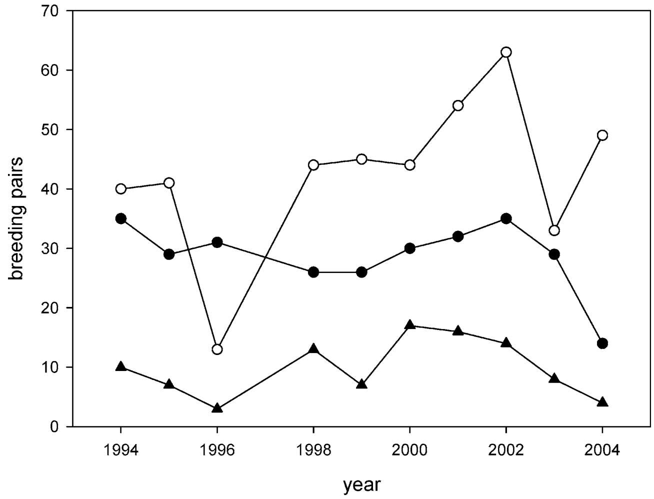

Fig. 3 Numbers of South polar skua (open circles), Brown skua (filled circles) and mixed species breeding pairs (filled triangles) at Potter Peninsula, King George Island, during 1994–2004. No linear trend was detected for any pair type. Years correspond to the second year of the austral season (e.g. 1994 = austral summer 1993/94)

Breeding success of skuas at Potter Peninsula showed no consistent linear trend over time (South polar skua: $R^2_4=0.01$, $P=0.85$, Brown skua: $R^2_6=0.39$, $P=0.14$, mixed pairs: $R^2_6=0.08$, $P=0.54$). The number of fledged chicks per breeding pair did not differ among pair types (Brown skua: 0.60 ± 0.11, South polar skua: 0.57 ± 0.22, mixed pairs: 0.62 ± 0.18; ANOVA, $F_{2,16}=0.02$, $P=0.98$). Brown skua pairs varied less in breeding success than South polar skua and mixed pairs (Fig. 4) but only the difference between Brown skua and mixed pairs was significant (paired *t*-test, Brown skua vs. South polar skua: $t_4=1.99$, $P=0.117$; Brown skua vs. mixed pairs: $t_6=4.99$, $P=0.002$). Fluctuations in breeding success of South polar skua and mixed pairs did not differ (paired *t*-test, $t_4=0.53$, $P=0.62$).

Discussion

Species composition of breeding populations

The species composition of breeding populations inside the hybrid zone showed an increasing frequency of South polar skua breeding pairs to the south.

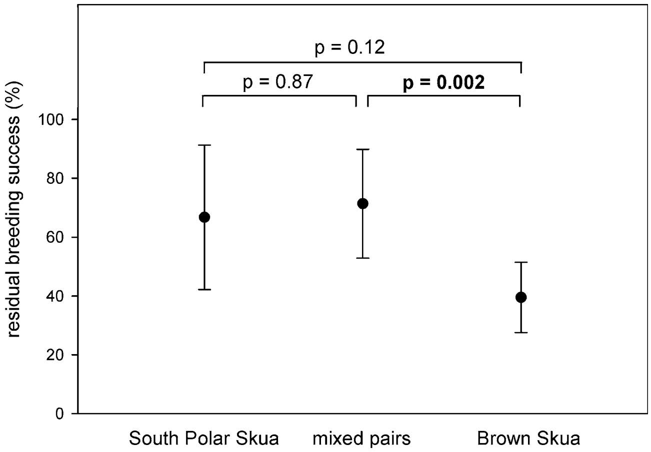

Fig. 4 Mean annual deviation from total breeding success corrected for long-term trends. Residual breeding success ±SE of South polar skua pairs, mixed pairs and Brown skuas pairs at Potter Peninsula. Brown skuas showed lower fluctuations in breeding success than mixed pairs. See text for statistics

Populations from two sites departed markedly from the over all pattern. More than 85% of skua pairs at Harmony Point/Nelson Island were Brown skua pairs (Silva et al. 1998) whereas populations less than 10 km away were made up of one-third Brown skua pairs. Harmony Point is a very small Peninsula and breeding space thus limited. On the other hand, a large penguin rookery of mainly Chinstrap Penguins (*Pygoscelis antarctica*) with more than 90,000 breeding pairs exists and provides a good food supply for Brown skuas, which displace the smaller South polar skua from potential breeding sites. However, the population was estimated in 1991 when South polar skuas were less frequent in the area which may also be the reason for the presence of only one mixed pair. South polar skuas formed the majority of breeding pairs at Half Moon Island (97%, Garcia Esponda et al. 2000). The small Chinstrap rookery (1700 breeding pairs) is probably not able to sustain more Brown skua pairs whereas the island provides good access to marine resources for South polar skuas.

The presented pattern in the skua hybrid zone is typical for hybrid zones in general (Saino and Villa 1992; Rolando 1993; Helbig et al. 2001). The shape of the frequency distribution of hybrids in the hybrid zone usually allows making predictions about the nature of the hybrid zone. If the distribution is in accordance with environmental variables, than a hybrid zone with bounded hybrid superiority seems most likely. A skewed distribution with the highest frequency of hybrids at one end of the hybrid zone was found in this study and indicates a moving hybrid zone. This may be the case since an increase in South polar skua pairs and mixed pairs was observed in the 1980s and 1990s at King George Island (Hahn et al. 2003). This probable result of a South polar skua range expansion is not evident in the population development between 1994 and 2004 at Potter Peninsula and the range expansion has most likely stopped. This assumption is supported by the fact that South polar skua breeding at Signy Island/South Orkneys has declined from nine pairs in 1983 to 1–3 pairs in recent years (Hemmings 1984; BAS unpublished data). However, South polar skua pair numbers can fluctuate greatly even at established colonies (this study) making it difficult to draw definite conclusions. In addition, knowledge about the fitness of hybrids is needed to characterise the hybrid zone and to make predictions about their future.

Morphometrics

A discriminant analyses using tarsus, culmen and mass measurements is able to assign most individuals to the right species. But species assignment in the field was done on the basis of plumage characteristics and overall appearance. It cannot be excluded that doubtful individuals were (later) assigned to a species based on the measurements which would reduce the usefulness of the measurements for species determination. More importantly, the procedure ignores hybrids and is thus unable to identify them. Hybrids are of intermediate size (see Hahn et al. 2003 for fledgling size) which will greatly complicate species assignment based on morphology alone. A newly developed protocol using the molecular method amplified fragment length polymorphism (AFLP) will be able to assign individuals to species or identify them as hybrids on the basis of their genetic background. This will be a reference for determining confidence intervals for species determination with morphological measurements in future studies.

Breeding population at Potter Peninsula

No trend since 1994 could be observed in the number of mixed pairs and of breeding pairs of South polar skua and Brown skua at Potter Peninsula. This suggests that the breeding range expansion of the South polar skua associated with increasing numbers of breeding pairs at King George Island (Woehler et al. 2001; Hahn et al. 2003) stopped or breeding pair numbers reached a saturation level. The first option is more likely because the number of breeding pairs does not seem to be limited by the available space for nesting at Potter Peninsula. Furthermore, reproductive seasons with low offspring output or even complete breeding failure suggest that the food supply for pelagic surface feeding birds is no longer as good as it was immediately after the closure of Antarctic waters to fishery. Additionally, breeding success was, at least at Potter Peninsula, not higher in South polar skua pairs as would be expected if the species is still spreading. We propose that the hybrid zone between the two skua species has reached a new steady state and will not change in the near future. However, detailed information on the fitness of hybrids is needed to confirm this idea. It is still possible that gene flow from one species into the other will move the hybrid zone or change its extent. Furthermore, climate change, which is especially strong in the area of the Antarctic Peninsula (Vaughan et al. 2003), is likely to affect the food resources of both skua species and has the potential to cause range changes.

The earlier finding that mixed pairs always consist of a male South polar skua and a female Brown skua (Pietz 1984; Parmelee 1988; Hahn et al. 2003) is supported with our large sample of additional cases. The reason for this unidirectional hybridisation is still unclear. Brown skuas do not mate assortatively with respect to body size (Phillips et al. 2002). The most likely reasons are inaccurate species recognition along with the earlier arrival of Brown skuas at the breeding grounds (Neilson 1983; Parmelee 1992). Unpaired Brown skua females could decide to pair with a South polar skua male before South polar skua females arrive and are likely to win fights with returning South polar skua female. The greater size found in male South polar skuas paired with Brown skuas compared to males paired with conspecifics (Hahn et al. 2003) can then be seen as the tendency of Brown skua females to minimise the risk of false matings by using body size as indicator of species affiliation. But the former result also could have arisen if some males in mixed pairs were actually hybrids, since hybrids cannot be detected objectively to date. Further studies on mate choice criteria in skuas are necessary to fully understand the findings.

The number of mixed breeding pairs was independent from the number of South polar skua and Brown skua pairs but fluctuated more strongly than pure species pairs. Obviously, not one sex alone decides whether to breed or not to breed in a season. Stronger fluctuations in mixed breeding pairs might emerge if the male South polar skua decides to suspend breeding for other reasons than the female Brown skua. Pair mates of pure pairs are more likely to agree in their yearly decision on reproduction. An alternative explanation is lower mate fidelity in mixed pairs. Mixed pair members might perceive their mating error and decide to change mates in the next season. Skuas with new mates delay egg laying or skip breeding in the first season (Catry et al. 1997). However, mate fidelity in pure pairs is high (Wood 1971; Parmelee and Pietz 1987; Pietz and Parmelee 1994) and long-term studies have to reveal whether mixed pairs have a lower mate fidelity than pure pairs.

The finding that breeding success of Brown skuas varied least is not surprising. Both species depend on the overall food supply in the season but the Brown skua has the more predictable resource (Pietz 1987; Young 1994). Availability of penguin eggs and chicks varies less between years than the access to pelagic fish. More astonishing is the finding that the long-term breeding success did not differ among the pair types in our study. Mixed pairs thus had no direct fitness loss in terms of reproductive success. The data could be blurred if Brown skua females of mixed pairs engage in extra-pair copulations more often than Brown skua females of pure species pairs. This pattern was found in hybridising flycatchers (Veen et al. 2001) where nests of mixed pairs had a strongly increased rate of extra-pair young compared to pure species pairs. Rate of extra-pair young in allopatric South polar skuas and Brown skuas was found to be low (Millar et al. 1994, 1997) but no studies on extra-pair young in sympatric skua populations have been published. Furthermore, data on survival and reproductive success of hybrids are needed to fully understand the nature of the skua hybrid zone in the Antarctic Peninsula region.

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References

Baker SC, Barbraud C (2001) Foods of the South Polar skua *Catharacta maccormicki* at Ardery Island, Windmill Islands, Antarctica. Polar Biol 24:59–61

Bennet AG (1920) Breves notas sobre las aves antarticas. Hornero 2:25–34

Blechschmidt K, Peter H-U, de Korte J, Wink M, Seibold I, Helbig AJ (1993) Untersuchungen zur molekularen Systematik der Raubmöwen (Stercorariidae). Zool Jb Syst Jena 120:379–387

Bo MS, Copello S (2000) Distribution and abundance of breeding birds at Deception Island, South Shetland Islands, Antarctica, February to April 2000. Mar Orn 29:39–42

Catry P, Ratcliffe N, Furness RW (1997) Partnerships and mechanisms of divorce in the great skua. Anim Behav 54:1475–1482

Cohen BL, Baker AJ, Blechschmidt K, Dittmann DL, Furness RW, Gerwin JA, Helbig AJ, de Korte J, Marshall HD, Palma RL, Peter H-U, Ramli R, Seibold I, Willcox MS, Wilson RH, Zink RM (1997) Enigmatic phylogeny of skuas (Aves: Stercorariidae). Proc R Soc Lond B 264:181–190

Croxall JP, Prince PA, Hunter I, McInnes SJ, Copestake PG (1984) The seabirds of the Antarctic Peninsula, Islands of the Scotia Sea, and Antarctic Continent between 80°W and 20°W: their status and conservation. In: Croxall JP, Evans PGH, Schreiber RW (eds) Status and conservation of the world's seabirds. International Council for Bird Preservation, Cambridge, pp 635–664

Fridolfsson A-K, Ellegren H (1999) A simple and universal method for molecular sexing of non-ratite birds. J Avian Biol 30:116–121

Garcia Esponda CM, Coria NR, Montalti D (2000) Breeding birds at Halfmoon Island, South Shetland Islands, Antarctica, 1995/96. Mar Orn 28:59–62

Griffiths R, Daan S, Dijkstra C (1996) Sex identification in birds using two CHD genes. Proc R Soc Lond B 263:1251–1256

Hahn S, Ritz MS, Peter H-U (2003) Living in mixed pairs - Better for fitness? A study in Skuas. In: Huiskes AHL, Gieskes WWC, Rozema J, Schorno RML, van der Vies SM, Wolff WJ (eds) Antarctic Biology in a Global Context. Backhuys, Leiden, pp 229–233

Helbig AJ, Salomon M, Bensch S, Seibold I (2001) Male-biased gene flow across an avian hybrid zone: evidence from mitochondrial and microsatellite DNA. J Evol Biol 14:277–287

Hemmings AD (1984) Aspects of the breeding biology of McCormicks skua *Catharacta maccormicki* at Signy Island, South Orkney Islands. Br Antarct Surv Bull 65:65–79

Lumpe P, Weidinger K (2000) Distribution, numbers and breeding of birds at the northern ice-free areas of Nelson Island, South Shetland Islands, Antarctica, 1990–1992. Mar Orn 28:41–46

Milius N (2000) The birds of Rothera, Adelaide Island, Antarctic Peninsula. Mar Orn 28:63–67

Millar CD, Anthony I, Lambert DM, Stapleton PM, Bergmann CC, Bellamy AR, Young EC (1994) Patterns of reproductive success determined by DNA fingerprinting in a communally breeding oceanic bird. Biol J Linnean Soc 52:31–48

Millar CD, Lambert DM, Young EC (1997) Minisatellite DNA detects sex, parentage, and adoption in the south polar skua. J Hered 88:235–238

Mund MJ, Miller GD (1995) Diet of the south polar skua *Catharacta maccormicki* at Cape Bird, Ross Island, Antarctica. Polar Biol 15:453–455

Neilson DR (1983) Ecological and behavioral aspects of the sympatric breeding of the South Polar Skua (*Catharacta maccormicki*) and the Brown Skua (*Catharacta lonnbergi*) near the Antarctic Peninsula. MSC thesis, University of Minnesota, 79 pp

Parmelee DF (1988) The hybrid skua: a southern ocean enigma. Wilson Bull 100:345–356

Parmelee DF (1992) Stercorariinae. In: Parmelee DF (ed) Antarctic birds: ecological and behavioral approaches. University of Minnesota Press, Minneapolis, pp 135–157

Parmelee DF, Pietz PJ (1987) Philopatry, mate and nest-site fidelity in the Brown Skuas of Anvers Island, Antarctica. Condor 89:916–919

Peter H-U, Kaiser M, Gebauer A (1990) Ecological and morphological investigations on South Polar Skuas (*Catharacta maccormicki*) and Brown Skuas (*Catharacta skua lonnbergi*) on Fildes Peninsula, King George Island, South Shetland Islands. Zool Jb Syst Jena 117:201–218

Phillips RA, Dawson DA, Ross DJ (2002) Mating patterns and reversed size dimorphism in Southern Skuas (*Stercorarius skua lonnbergi*). Auk 119:858–863

Phillips RA, Phalan B, Forster IP (2004) Diet and long-term changes in population size and productivity of brown skuas *Catharacta antarctica lonnbergi* at Bird Island, South Georgia. Polar Biol 27:555–561

Pietz PJ (1984) Aspects of the behavioral ecology of sympatric South Polar Skua and Brown Skua near Palmer Station, Antarctica. PhD thesis, University of Minnesota, 176 pp

Pietz PJ (1987) Feeding and nesting ecology of sympatric South Polar and Brown skuas. Auk 104:617–627

Pietz PJ, Parmelee DF (1994) Survival, site and mate fidelity in South Polar Skuas *Catharacta maccormicki* at Anvers Island, Antarctica. Ibis 136:32–38

Quintana RD, Cirelli V, Orgeira JL (2000) Abundance and spatial distribution of bird populations at Cierva Point, Antarctic Peninsula. Mar Orn 28:21–27

Reinhardt K (1997) Food and feeding of Antarctic skua chicks *Catharacta antarctica lonnbergi* and *C. maccormicki*. J Ornithol 138:199–213

Rising JD, Somers KM (1989) The measurement of overall body size in birds. Auk 106:666–674

Rolando A (1993) A study on the hybridization between carrion and hooded crow in northwestern Italy. Ornis Scan 24:80–83

Saino N, Villa S (1992) Pair composition and reproductive success across a hybrid zone of Carion Crows and Hooded Crows. Auk 109:543–555

Silva MP, Favero M, Casaux R, Baroni A (1998) The status of breeding birds at Harmony Point, Nelson Island, Antarctica in summer 1995/96. Mar Orn 26:75–78

Vaughan DG, Marshall GJ, Connolley WM, Parkinson C, Mulvaney R, Hodgson DA, King JC, Pudsey CJ, Turner J (2003) Recent rapid regional climate warming on the Antarctic Peninsula. Clim Change 60:243–274

Veen T, Borge T, Griffith SC, Saetre G-P, Bures S, Gustafsson L, Sheldon BC (2001) Hybridization and adaptive mate choice in flycatchers. Nature 411:45–50

Watson GE (1975) Birds of the Antarctic and Sub-Antarctic. American Geophysical Union, Washington

Woehler EJ, Cooper J, Croxall JP, Fraser WR, Kooyman GL, Miller GD, Nel DC, Patterson DL, Peter H-U, Ribic CA, Salwicka K, Trivelpiece WZ, Weimerskirch H (2001) A statistical assessment of the status and trends of Antarctic and subantarctic seabirds. Report on SCAR BBS Workshop on Southern Ocean seabird populations. May 1999, Bozeman, Montana

Wood RC (1971) Population dynamics of breeding South Polar Skuas of unknown age. Auk 88:805–814

Young EC (1963) Feeding habits of the South Polar Skua *Catharacta maccormicki*. Ibis 105:301–318

Young EC (1994) Skua and penguin, predator and prey. Oxford University Press, Oxford