Mixed pair of South Polar Skua male (left) and Brown Skua female

Speciation and hybridisation in skuas (*Catharacta* spp.)

Dissertation

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von Diplom-Biologe Markus Ritz
geboren am 17.08.1976 in Dresden

Gutachter:
Prof. Stefan Halle, Jena
Prof. Gerald Heckel, Bern, Schweiz
Prof. Peter de Knijff, Leiden, Niederlande

CONTENT

INTRODUCTION

Speciation and hybridisation

Speciation, the process of species formation, is a central topic in evolutionary biology. Whilst the foundations of evolution, variability and selection, were quickly accepted amongst scientists after the publication of "On the origin of species" (Darwin 1859), it proved much harder to find how species actually diverge and evolve into distinct groups. One reason is that the emergence of a new species can usually not be observed during time scales comparable to a researcher's career. Studies on speciation will thus have to try to reconstruct the past or to confine to a specific stage in speciation. This raises the question at which stage two taxa can be called separate species. So, Darwin went too far in his conclusions in the "Origin" that by studying evolution "*… we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species.*" Whilst it is now widely accepted that taxa are variable and it is worthwhile to study biodiversity irrespective of the level of variation (e.g. genera, species, subspecies, ecotypes,…), there are still reasons to adopt a definition for "species" (Coyne and Orr 2004). Most scientists agree that species are real entities in nature and not human constructs to classify organisms. However, in compliance with the saying that " in a room with ten evolutionary biologists you will hear at least eleven different species concepts" I will not discuss any of the numerous species concepts but only describe the "comprehensive biologic species concept" (CBSC, Johnson et al. 1999) which was introduced with special emphasis on birds. It is a broader version of the biological species concept (Dobzhansky 1937, Mayr 1942) and accounts for the observed stability of species in spite of hybridisation. According to the CBSC an avian species "*…is a system of populations representing an essentially monophyletic, genetically cohesive, and genealogically concordant lineage of individuals that share a common fertilisation system through time and space, represent an independent evolutionary trajectory, and demonstrate essential but not necessarily complete reproductive isolation from other such systems.*"

Three main routes to speciation have been described based on the geographic circumstances during divergence. Sympatric speciation assumes that divergence takes place within a population due to for example disruptive selection. Numerous models have been developed to explore the conditions under which sympatric speciation may occur (e.g. Higashi et al. 1999, Via 2001, Kirkpatrick and Ravigne 2002, Gavrilets 2003). The very restrictive conditions allowing for evolution of reproductive isolation in the presence of gene flow argue against sympatric speciation being a common mode of speciation in animals. Some scientists even deny the possibility of sympatric speciation but a few model groups are discussed as candidates for divergence in the presence of gene flow (Coyne and Orr 2004, Bolnick and Fitzpatrick 2007). Parapatric speciation describes the process, where upon a taxon evolves into two taxa with adjacent ranges. This is a likely scenario if the species has a wide range with ecological breaks. Taxa may then diverge along an ecotone or perhaps a migratory divide. The resulting area of contact would be a primary hybrid zone. However, it is hard, or even impossible, to prove that the two groups were not geographically isolated from each other for at least some time during the past. The probably most common process in birds, allopatric speciation, is based on a geographic separation of groups of organisms. The independent evolution of these allopatric groups will then differ due to founder effects and genetic drift (especially for peripatric speciation) and/or differing selection pressures and result in differing phenotypes. If these groups come into secondary contact, reproductive isolation mechanisms may prevent free interbreeding and two taxonomic units are retained. It has to be noted that the three scenarios are not mutually exclusive. Since speciation is a long-lasting process and taxa ranges vary, combinations of scenarios like allo-sympatric speciation or para-allopatric speciation are possible.

Secondary hybrid zones are formed if two taxa diverged in allopatry, meet in a contact zone and reproductive isolation is not complete. The outcome of secondary contact can be the replacement of one species by the other (Gill 1980), the merging of both taxa into one (new) taxon (Sibley 1957) or the maintenance of two species. The hybrid zone will move in the first case, increase in breadth in the second case, and remain mostly stable in the last case. Hybrid zones can vary in breadth but are often small compared to the species ranges (Barton and Hewitt 1985). Several models have been developed to explain the stability in breadth and position of most hybrid zones. The dynamic equilibrium hypothesis (Mayr 1963, Johnson and Johnson 1985) explains stable hybrid zones by selection against hybrids in combination with gene flow from allopatry into the hybrid zone. In contrast, the bounded hybrid superiority hypothesis (Moore 1977) assumes a higher fitness of hybrids compared to the parental species in the hybrid zone but not outside of it. The increased hybrid fitness is then bounded to a specific area, which is often an ecotone. Barton and Hewitt (1985) broadened the dynamic equilibrium hypothesis and described hybrid zones as tension zones that may move. In the absence of selection against hybrids, the neutral diffusion hypothesis (Endler 1977, Barton and Hewitt 1985) predicts that character clines across the hybrid zone are wide compared to the root of the mean square dispersal distances of the species.

Reproductive isolation barriers evolve as taxa diverge. Such barriers are commonly classified into pre-zygotic barriers (e.g. ecological, phenological, behavioural, morphological isolation) and post-zygotic barriers (e.g. no fertilisation, zygote mortality, F1 inviability, F1 infertility, reduced survival/fitness of F1, F2 breakdown). Depending on the degree of differentiation and the fitness of hybrids several selection factors can be observed. Haldane’s rule describes the observation that in the offspring of mixed pairs the less numerous or sterile sex is with few exceptions the heterogametic one (Haldane 1922). In birds (and butterflies) this sex is the female. The effects of a resulting male-biased gene flow were shown in a hybrid zone between two Chiffchaff taxa (*Phylloscopus collybita*, Helbig et al. 2001, Bensch et al. 2002b). Reproductive character displacement (Brown and Wilson 1956) or reinforcement of reproductive barriers can only occur if hybrids are less fit than the parental taxa. Selection will then favour the expression or recognition of traits that allow safe species identification by mating partners (Saetre et al. 1997, Higgie et al. 2000).

In summary, while in the 1950s most researchers still aimed to belittle hybridisation because it was seen mainly as a treat to the biological species concept, recent decades have witnessed an increase in studies on hybrid zones because they are now regarded as “windows to evolution”. Depending on the degree of reproductive isolation between taxa, hybrid zones are useful in studying pattern and processes during all stages of speciation (Hewitt 2001).

Phylogeography and glaciation

The phylogeography of polar and temperate taxa is closely linked to glaciation. Long-term climatic oscillations (Milankovitsch cycles, Dynesius and Jansson 2000) force species to retreat from glaciers and to eventually survive in small populations until the area is free to re-colonise during an inter-glacial (Hewitt 1999, Hewitt 2000). Due to the resulting repeated bottlenecks, polar taxa can be expected to have a much lower genetic diversity than taxa not affected by ice ages. On the other hand, glaciers force polar taxa to survive glacials in refuges and thus provide the opportunity for allopatric speciation. In consequence, high latitude taxa groups have shallow phylogenies with low genetic diversity within species.

In Europe many species emerged during Quaternary cycles when a huge ice sheet forced taxa to retreat southwards into refuges in the Iberian and Italian Peninsula or in south-eastern Europe (Hewitt 1999, Hewitt 2000). More northerly cryptic refuges have also been proposed (Provan and Bennett 2008). The existence of a large land mass and north-south oriented mountain ranges in the Americas resulted in an east-west separation of taxa during glacials and many present-day sister species. It is widely accepted that glacial cycles played a seminal role for speciation of North American birds although the relative importance of specific periods is still debated (Klicka and Zink 1997, Avise and Walker 1998, Johnson and Cicero 2004, Zink et al. 2004, Lovette 2005, Cicero and Johnson 2006, Zink and Klicka 2006). Our understanding of phylogeographic patterns and processes is much more limited for the southern hemisphere with only 15% of publications between 1997 and 2006 dealing with taxa living south of the equator (Beheregaray 2008). The few studies in Antarctica show a strong influence of glacial cycles although the effects of glaciation differ between taxonomic groups. Whilst the two only antarctic vascular plants (*Deschampsia antarctica*, *Colobanthus quitensis*) did most likely colonise Antarctica after the last glacial maximum (van De Wouw et al. 2008), invertebrates were able to survive glacials in refuges (Cromer et al. 2006, Convey and Stevens 2007). Vertebrates can comparably easy shift ranges and may have survived glaciation of continental Antarctica in refuges and on sub-antarctic islands. The retreat into such refuges with subsequent emergence of distinct lineages and strong population size changes were shown for Adelie penguins (Lambert et al. 2002, Ritchie et al. 2004). Although fragmentation of seabird ranges by ice or land invariable led to phylogeographic structure, other factors may also be effective barriers to gene flow, namely non-breeding distribution, philopatry and behaviour (Friesen et al. 2007).

Skua diversity

Skuas are gull-like, mostly marine birds with a bipolar distribution. They feed opportunistically as predators on birds, mammals and fish, by scavenging or by exploiting carcasses. Skuas can reach an age of up to 30 years (Furness 1987) and delay first breeding for several years. Most species are migratory and several taxa visit the other hemisphere during the non-breeding season.

The phylogenetic position of skuas (family *Stercoraridae*) among shorebirds is still debated. Whilst they were traditionally placed sister to gulls (*Laridae*) which they resemble in morphology, new molecular evidence supported alcids (*Alcinae*) as closest relatives (Ericson et al. 2003, Paton et al. 2003, Thomas et al. 2004a, Thomas et al. 2004b, Fain and Houde 2007). Two different skua morphotypes can be clearly distinguished. Three small, slender, long-tailed species are called jeager (*Stercorarius* spec.) in North America and inhabit only the northern hemisphere. The more bulky and uniformly brownish large skuas (*Catharacta* spec.) inhabit the southern hemisphere (three species) and the northern hemisphere (Great skua, *Catharacta skua*). Common and scientific names of all skua taxa are given in table 1.

Table 1: Common and scientific names of all described skua taxa.

Common name	Scientific name	Hemisphere
Long-tailed Skua	Stercorarius longicaudus	northern
Parasitic Skua	Stercorarius parasiticus	northern
Pomarine Skua	Stercorarius pomarinus	northern
Great Skua	Catharacta skua	northern
Chilean Skua	Catharacta chilensis	southern
Falkland Skua	Catharacta antarctica antarctica	southern
Tristan Skua	Catharacta antarctica hamiltoni	southern
Brown Skua	Catharacta antarctica lonnbergi	southern
South Polar Skua	Catharacta maccormicki	southern

A surprising finding of early work on skua phylogeny was the closer relationship of one small species (Pomarine Skua, *Stercorarius pomarinus*) to the Great Skua than to any of the other two *Stercorarius* species (Fig. 1, Blechschmidt et al. 1993, Cohen et al. 1997). Although the significance of the mitochondrial data set has been debated (Braun and Brumfield 1998) there is compelling evidence that the Pomarine Skua is indeed intermediate also based on morphology, ectoparasites and behaviour (Andersson 1973, Cohen et al. 1997, Andersson 1999a, Andersson 1999b). Extensive hybridisation between a jeager and a skua species could explain the pattern but the factual scenario remains enigmatic. The observed paraphyly of *Stercorarius* and *Catharacta* and subsequent discussions about the most likely skua phylogeny has led to the suggestion to combine all skua taxa into the older genus *Stercorarius* (Andersson 1999b, Sangster et al. 2004). I do not follow this recommendation and argue that monophyly of *Catharacta* and *Stercorarius* cannot be ruled out based on our current knowledge. Therefore, I favour the retention of the traditional taxonomy until the enigma around *pomarinus*/*skua* has been resolved.

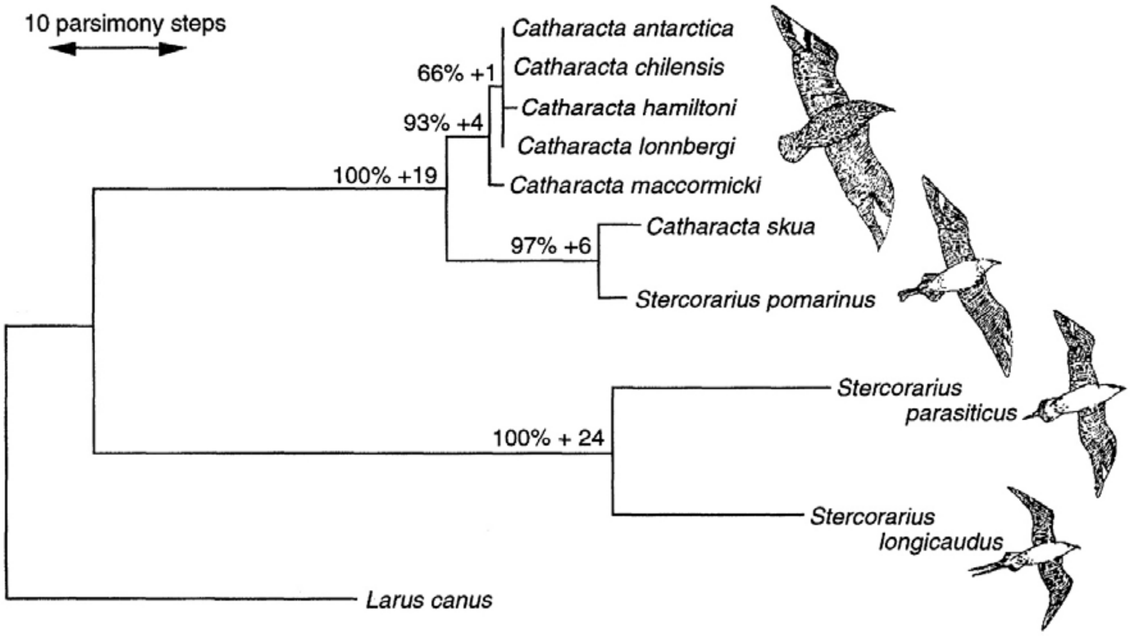


Figure 1: Skua phylogeny based on the mitochondrial genes *cytochrom b* and *12S* (taken from Cohen et al. 1997). Number above branches show bootstrap support and number of additional steps needed to collapse the node.

Southern hemisphere skuas are sometimes treated as a super-species and are currently classified as three species with *Catharacta antarctica* being sub-divided into three sub-species (Furness 1996). All taxa closely resemble large gulls in general appearance but have a hooked bill and sharp claws and a more or less uniformly brownish plumage. The only conspicuous plumage character are white wing patches which are shown during the long call complex – a wing raising posture accompanied by the long-call (Pietz 1985, Furness 1987). The South Polar Skua (*C. maccormicki*) is the smallest and most gracile southern skua and inhabits coastal areas of the Antarctic continent. It is the only taxon known to migrate annually to the northern hemisphere. The Chilean Skua (*C. chilensis*) is the morphologically most distinct southern skua with a black cap, cinnamon under-parts and underwing-coverts and a gull-like behaviour (Moynihan 1962, Devillers 1978). It is only found in coastal areas of Patagonia. The large, bulky Brown Skua (*C. antarctica lonnbergi*) has the largest range spanning the sub-antarctic islands around the world. The Falkland Skua (*C. a. antarctica*) lives on the Falkland Islands and along the Argentine coast. The Tristan Skua (*C. a. hamiltoni*) is restricted to the Tristan Island archipelago. The ranges of the southern taxa are illustrated in manuscript 1, figure 1 of this thesis. A good overview of skua distribution, morphology and biology is given in Furness (1987, 1996).

Mitochondrial phylogeny has revealed a young age of the southern hemisphere skua complex. The South Polar Skua differed in one base pair of the *12S* gene from all other southern taxa which had identical *cytochrome b* and *12S* sequences. This single base pair difference prompted Votier et al. (2004) to conclude that two skuas found at the UK coast were not South Polar Skua, which regularly migrates to the northern hemisphere. Other southern hemisphere taxa could be excluded based on morphometry and the mystic skua individuals were classified as first records of Brown Skua in Europe (Votier et al. 2004).

Hybridisation between southern skua taxa

In line with the assumed recent divergence of southern skua taxa, hybridisation has been reported between all species pairs. Although the Chilean Skua is restricted to South America and the South Polar Skua inhabits Antarctica, Chilean Skuas are occasionally seen in the area of the Antarctic Peninsula and an F1-hybrid between the two species has breed successfully at King George Island since at least 1994 (Reinhardt et al. 1997). The Falkland Skua breeds also outside the Falkland Islands on the Argentine coast and has a partially overlapping range with the Chilean Skua near Puerto Deseado (Devillers 1978, Yorio 2005). A few mixed pairs produce viable offspring, but hybrid fitness has not been investigated. Mixed species pairing involving the Tristan Skua has not been reported. However, it can be doubted that such pairs would be recognised because Tristan Skua are morphologically very similar to Falkland Skua and Brown Skua, which are both closer to potential hybridisation partners. Extensive gene flow occurs between South Polar Skua and Brown Skua. It is known from the western edge of the Ross Sea and in large sympatric populations in the area of the Antarctic Peninsula.

First records of a sympatric occurrence of South Polar Skua and Brown Skua in the area of the Antarctic Peninsula date back to the beginning of the last century (Bennet 1920, Watson 1975). Former studies concentrated on differences in morphology, behaviour and food between species (Pietz 1984, 1985, 1986, 1987, Peter et al. 1990, Parmelee 1992) and confirmed that mixed species pairs can reproduce successfully. Also, a single ringed F1-hybrid was found to be able to reproduce (Pietz 1987, Parmelee 1988). Interestingly, mixed pairs are nearly invariably formed between a South Polar Skua male and a Brown Skua female (Parmelee 1988). The reasons for this unidirectional hybridisation remain unclear. A comprehensive overview of the hybrid zone has so far been lacking. Furthermore, an objective identification of (unringed) hybrids was not possible due to the close similarity of species. Consequently, any estimates of hybrid fitness, degree of admixture and gene flow across the borders of the hybrid zone are lacking as well.

AIMS OF THE STUDY

This study is centred around questions concerning speciation and hybridisation in skuas. It aims to answer how and when skuas diversified at the southern hemisphere and which factors influenced their divergence. Hybridisation between two of these species, the South Polar Skua and the Brown Skua, was investigated in detail in the hybrid zone in the Antarctic Peninsula region.

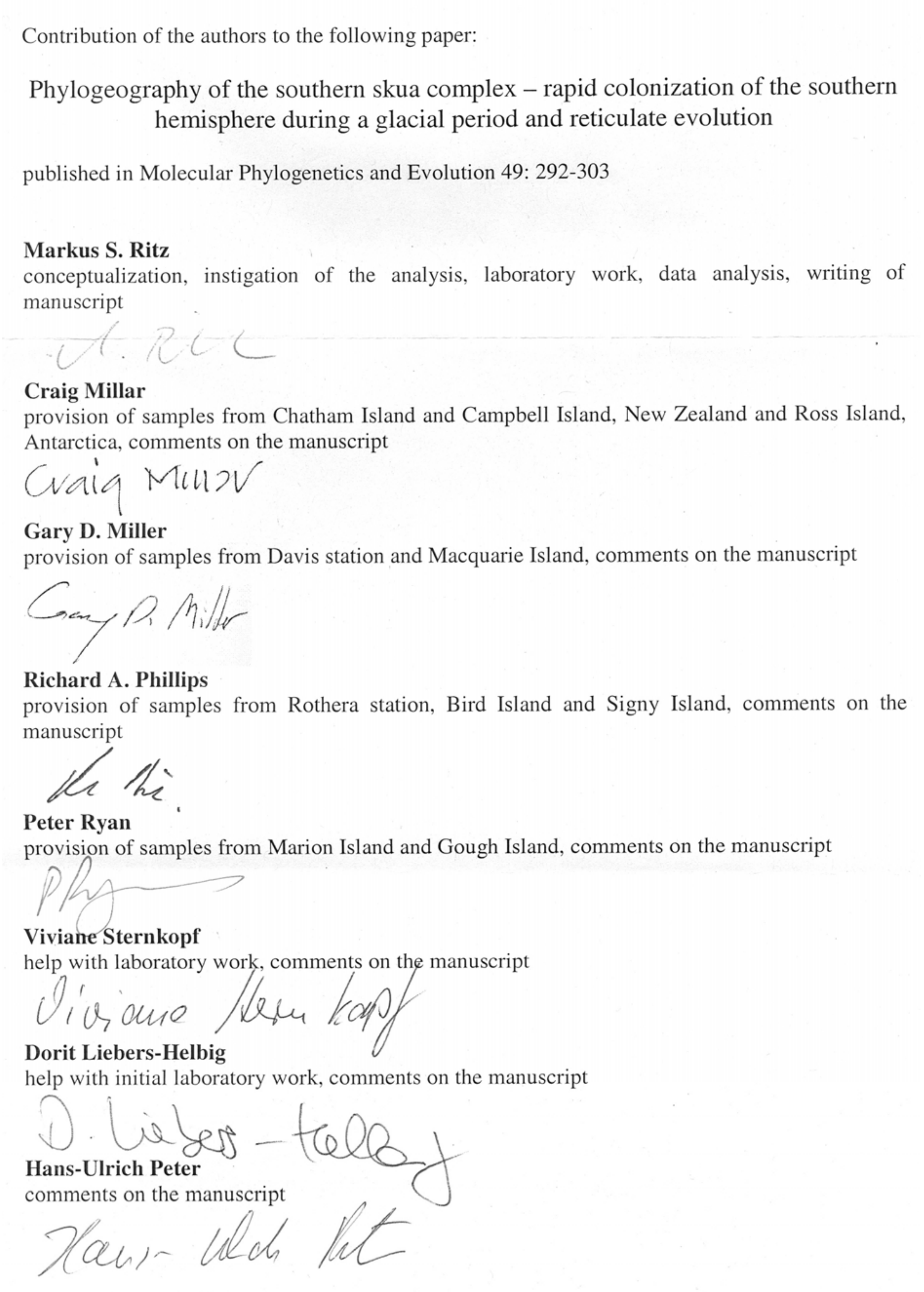
Whilst the initial publications on skua phylogeny revealed that jaegers are the basal group, the relationship among the southern hemisphere taxa remained unresolved (Blechschmidt et al. 1993, Cohen et al. 1997). To get an understanding of how the southern hemisphere was colonised by skuas and which modes and patterns of speciation were important during skua evolution, I performed a phylogeographic study. This involved molecular analysis of 270 skua blood samples from 16 populations covering all described taxa and their ranges. The hypervariable control region I (*HVR I*) of mitochondrial DNA was chosen because it is known to be the fastest evolving gene in birds. **Manuscript 1 (Ritz et al. 2008)**

A single nucleotide polymorphism (SNP) in the *12S* gene of mtDNA between South Polar Skua and Brown Skua was used as the basis to report the first record of Brown Skua in Europe (Votier et al. 2004). Such a SNP would also be a valuable additional marker for hybrid identification. However, amplification of the *12S* gene in morphologically-extreme South Polar Skuas and Brown Skuas from the hybrid zone and subsequent digestion with a specific restriction enzyme (BanI) did not result in the expected band pattern. At the same time, the group working on skuas in Glasgow also wished to verify the SNP between South Polar Skua and Brown Skua. A cooperation was established and samples from eleven morphologically-extreme South Polar Skuas breeding at King George Island were analysed as in Votier et al. (2004) to test for the actual diagnostic value of the potential SNP. **Manuscript 2 (Votier et al. 2007)**

Although several faunistic studies recognized the sympatric occurrence or South Polar Skua and Brown Skua and the existence of mixed species pairs in the area of the Antarctic Peninsula, a comprehensive review of the hybrid zone was lacking. To set a baseline for more detailed studies on hybridisation between both species, I reviewed the available information on the composition of breeding populations and the frequency of mixed pairs in the area. This information was supplemented with data from our long term study populations at King George Island. I included analyses of population size trends, morphometric differences between species and the possible resulting potential to identify hybrids, the frequency of mixed pairs in relation to assumed random mating and comparison of the reproductive output of pair types. **Manuscript 3 (Ritz et al. 2006)**

Identification of hybrids is essential to estimate hybrid fitness which, in turn, is essential to identify the nature of the hybrid zone and to reveal potential isolating mechanisms between species. Since skuas are long-lived and delay first breeding for on average eight years (Ainley et al. 1990), building up a study population with known hybrids based on pedigree would therefore require at least a decade of extensive ringing. Furthermore, since hybridisation between the species can be expected to last already at least one century, considerable introgression seems likely. In conclusion, a molecular based (objective) method to assign pure species individuals and hybrids was required. I chose the whole genome based method amplified fragment length polymorphism (AFLP) to distinguish species and to identify hybrids. **Manuscript 4 (Ritz & Peter, submitted manuscript)**

MANUSCRIPT 1



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Richard A. Phillips
provision of samples from Rothera station, Bird Island and Signy Island, comments on the manuscript

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Viviane Sternkopf
help with laboratory work, comments on the manuscript

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comments on the manuscript

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Phylogeography of the southern skua complex—rapid colonization of the southern hemisphere during a glacial period and reticulate evolution

Markus S. Ritz [a,*], Craig Millar [b], Gary D. Miller [c], Richard A. Phillips [d], Peter Ryan [e], Viviane Sternkopf [f], Dorit Liebers-Helbig [f], Hans-Ulrich Peter [a]

[a] *Institute of Ecology, Friedrich-Schiller University Jena, Dornburger Str. 159, 07743 Jena, Germany*
[b] *Evolutionary Genetics, Department of Zoology, University of Auckland, Private Bag, Auckland, New Zealand*
[c] *Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA*
[d] *British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK*
[e] *DST/NRF Centre of Excellence at the Percy FitzPatrick Institute University of Cape Town, Rondebosch 7701, South Africa*
[f] *Deutsches Meeresmuseum Stralsund, Katharinenberg 14/20, D-18439 Stralsund, Germany*

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ABSTRACT

Whilst we have now a good understanding how past glaciation influenced species at the northern hemisphere, our knowledge of patterns and modes of speciation is far more limited for the southern hemisphere. We provide mtDNA based data on the phylogeography of a circumpolar distributed southern hemisphere seabird group—the southern skua complex (*Catharacta* spp.). Diversification of southern skuas dates between 210,000 yBP and 150,000 yBP and coincides with a glacial spanning 230,000–140,000 yBP. Skuas most likely first inhabited the Antarctic continent, in the course of global cooling and increasing glaciation spread to the sub-antarctic islands and Tristan da Cunha and finally colonized Patagonia and the Falkland Islands at the glacial maximum. Despite significant differences between taxa most populations still exchange genes with neighboring populations of other taxa and speciation is incomplete.

1. Introduction

The rapid improvement of sequencing techniques in the last decade and the availability of suitable markers has provided important insights into the evolution of taxa in space and time and greatly advanced the field of phylogeography. Following the many studies on the northern hemisphere we have now a good understanding of how species separated, expanded and shifted breeding ranges and how these processes were influenced by past glaciation (Avise and Walker, 1998; Hewitt, 2001; Hewitt, 2004a; Hewitt, 2004b). In contrast, our knowledge of such patterns is far more limited for the southern hemisphere. We investigated the phylogeography of a southern hemisphere seabird group—the southern skua complex—inhabiting South America, New Zealand, sub-antarctic islands and Antarctica and show the close connection of its diversification with Antarctic glaciation.

Skuas (Stercoraridae) are gull-like seabirds inhabiting temperate and polar habitats on both hemispheres. Despite considerable research effort, the phylogenetic history of skuas remains enigmatic (Andersson, 1973; Blechschmidt et al., 1993; Cohen et al., 1997; Andersson, 1999a; Andersson, 1999b). Although the three small species of the northern hemisphere (*Stercorarius* spp.) are similar to each other and clearly differentiated from the Great Skua (*Catharacta skua*) of the northern hemisphere and all taxa breeding at the southern hemisphere, a mitochondrial DNA phylogeny revealed a closer relatedness of the Great Skua to one of the small northern skuas, the Pomarine Skua (*S. pomarinus*), than to any of the southern taxa (Blechschmidt et al., 1993; Cohen et al., 1997). The southern taxa formed a monophyletic clade with very short and shallow branches implying a recent and rapid colonization of the southern hemisphere. The aim of our study was to resolve the relationships between the southern skuas and to reconstruct the pattern and modes of colonization.

Although unraveling the enigmatic relationship between Great Skua and Pomarine Skua is beyond the scope of this study, this question has implications for understanding the role of the southern hemisphere during skua evolution. Based on the consensus that the *Stercorarius*-like skua form is the ancestral one, then the Great Skua may have diverged first and later colonized the southern hemisphere. Another possibility is a southern colonization by *Stercorarius*-like founders, a morphological shift towards larger size and dark plumage and a subsequent re-colonization of the northern hemisphere involving extensive hybridisation and backcrossing with *Stercorarius*-like skuas. The second possibility has led to considerable speculation as to the ancestor of the Great Skua

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[*] Corresponding author. Fax: +49 3641949402.
E-mail address: markus.ritz@web.de (M.S. Ritz).

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under this scenario. Various arguments involving geographic proximity, morphology, coloration and migration pattern favor either the Tristan Skua (Fisher and Lockley, 1954), the Chilean Skua (Swales, 1965) or the Falkland Skua (Furness, 1987) as closest relative of the Great Skua.

The southern hemisphere skuas are sometimes treated as a superspecies and the complex currently consists of three described species of which one, *Catharacta antarctica*, is sub-divided into three sub-species (Devillers, 1978; del Hoyo, 1996). The distribution of these five taxa is shown in Fig. 1. The South Polar Skua (*Catharacta maccormicki*) and the three sub-species Falkland Skua (*C. a. antarctica*), Tristan Skua (*C. a. hamiltoni*) and Brown Skua (*C. a. lonnbergi*) are relatively similar to each other with a brown to greyish plumage and varying degrees of white spots at the back and golden hackles at the neck. The most distinct southern skua is the Chilean Skua (*C. chilensis*) with a black cap, cinnamon underparts and underwing-coverts and a gull-like behavior. A detailed morphological description of the taxa is given in Furness (1987). All taxa have relatively small population sizes ranging from 2500 pairs of Tristan Skua to 5000–8000 pairs of South Polar Skua (Furness, 1987; del Hoyo, 1996).

In accordance with the supposed recent origin and an incomplete divergence of the southern taxa, evidence of hybridisation exists for all species pairs. The largest range overlap with extensive hybridisation is found in the area of the Antarctic Peninsula between South Polar Skua and Brown Skua (Ritz et al., 2006). Up to 12% of breeding pairs in populations within a 500 km wide hybrid zone consist of a South Polar Skua male and a Brown Skua female.

Fig. 1. Distribution of the five southern skua taxa and sample locations (red dots) with sample size. Black dots show skua populations not sampled but considered in the automated phylogeographic analysis.

Those pairs produce viable offspring that can reproduce successfully (Pietz, 1987; Parmelee, 1988). Evidence for hybridisation between the two taxa comes also from the opposite side of Antarctica, from Edmonson Point at the western edge of the Ross Sea. A mixed pair bred there among 120 South Polar Skua pairs in several seasons in the late 1990s (Francesco Pezzo pers. comm.). A hybrid zone involving just a few pairs exists between Chilean Skua and Falkland Skua at the Patagonian Atlantic coast. Hybrids are viable but nothing is known about their fitness (Devillers, 1978; Yorio, 2005). Although populations of Chilean Skua and South Polar Skua are separated by the 1000 km wide Drake Passage, hybridisation between these two taxa also occurs. An F1-hybrid has bred successfully since at least 1994 at Potter Peninsula/ King George Island (Reinhardt et al., 1997). Hybridisation involving the Tristan Skua has not been reported but could easily remain undetected due to the very similar morphology of the sub-species.

Although formulating hypotheses about the pattern of diversification of the southern skua taxa is difficult due to the unresolved relationship between the northern and southern hemisphere skuas, some predictions about the phylogeographic structure of the southern taxa can be made. The structuring should be less pronounced in taxa with small population size inhabiting small ranges (Tristan Skua) and strongest in taxa with larger population sizes and a wider distribution (South Polar Skua, Brown Skua). Furthermore, the Brown Skua breeding on remote islands in both the Antarctic and sub-antarctic can be expected to have a more complex phylogeographic structure than the South Polar Skua which primarily inhabits the continental Antarctic coastline. This prediction also arises considering long-term climatic oscillations (Milankovitsch cycles) which repeatedly force species breeding at high latitude to retreat from and re-colonize areas affected by ice ages (Dynesius and Jansson, 2000; Hewitt, 2000; Hewitt, 2004a).

2. Materials and methods

2.1. Samples

Blood, tissue or feathers were taken from 270 breeding adults or chicks from 16 populations of southern hemisphere skuas. Only one chick per clutch was sampled and adults were only sampled if their chicks had not been sampled. Sample locations and sample sizes can be seen in Fig. 1. In addition, DNA was analyzed from all four northern hemisphere skua taxa. This included 12 individuals of *C. skua* from Iceland, NW-Scotland and Foula/Shetland Islands, 6 ind. of *S. pomarinus* from Taimyr Peninsula, 4 ind. of *S. longicaudus* from Taimyr Peninsula and the upper Anadyr river and 2 ind. of *S. parasiticus* from Churchill/Canada and Franz-Josef-Land.

2.2. PCR and sequencing

A 386 bp segment of the hypervariable region 1 in the mitochondrial control region (CR I) was amplified using a similar procedure as in Liebers et al. (2001). In a first step a 2500–3000 bp long fragment which included the entire control region, the *ND6* gene and a part of the 12S rRNA gene was amplified using primers H2 (5′-GCC ATC CTA CGC TCA ATC CCC AAC AA-3′) and DDL-C (5′-CAC CGC CAA GTC CTT AGA GTT T-3′) and the Expand Long template PCR system (Roche) followed by a 15 min digestion with ExoSap (Amersham). PCR conditions were varied slightly with a denaturation temperature of 93 °C and an annealing temperature of 55 °C. After the second PCR with the IRD-labelled primer HLB (5′-GGC CCT GAC ATA GGA ACC AGA GG-3′), the samples were run on a 4% polyacrylamide gel in a Licor 4200 sequencer. All sequences were checked manually for ambiguities and aligned with ClustalW (Thompson et al., 1994).

2.3. Phylogeographic analysis

Five complementary methods were combined to gain insight into historical demographic processes as well as genetic patterns of female-mediated gene flow in the southern skuas.

The model of sequence evolution was chosen using Modeltest 3.7 (Posada and Crandall, 1998) and PAUP* 4.0b10 (Swofford, 2000). The transition/transversion ratio was 3.14, nucleotide base frequencies were A = 0.297, C = 0.307, G = 0.143, T = 0.253 and the model with the highest likelihood was the Hasegawa–Kishino–Yano model (HKY, Hasegawa et al., 1985) with invariable sites ($I = 0.737$) and a gamma distributed substitution rate of variable sites (gamma $\alpha = 0.751$). This translates into a rate heterogeneity among sites of $\rho = 0.887$ (Gu et al., 1995). Because the HKY model is not available in Arlequin 3.11, the genetic distance matrix was computed from the alignment using the similar Tamura & Nei model (Tamura and Nei, 1993) with a gamma distribution.

2.4. Nested clade phylogeographic analysis (NCPA)

The initial haplotype network was constructed with TCS 1.21 (Clement et al., 2000) including gaps as fifths character state. To resolve cladogram ambiguities we applied criteria derived from coalescent theory (Crandall and Templeton, 1993; Pfenninger and Posada, 2002): haplotypes are more likely to be connected to haplotypes (1) of high frequency (frequency criterion) (2) interior of the cladogram (topological criterion) (3) from the same population or geographically close populations (geographical criterion). Nested clade analysis and interpretation of the retrieved deviations from the null hypothesis was done automatically using ANeCA 1.0 (Panchal, 2007) to decrease subjectivity of the procedure. The program uses GeoDis 2.2 (Posada et al., 2000; Posada et al., 2006) and a revised version of the inference key published by Templeton (1998) (available at http://darwin.uvigo.es/software/geodis.html). ANeCA is not able to resolve cladogram ambiguities following the above mentioned rules. Instead, the program deals with ambiguities by including them into clades during the nesting process which has the advantage of paying the tolls for uncertainties in the network but the disadvantage of strongly reducing power for the detection of phylogeographic patterns, especially if loops involve more than a few mutations. ANeCA was therefore run with the original network as well as with the network with manually resolved ambiguities. During the renewed debate about whether NCPA is a valid statistical method (Panchal and Beaumont, 2007; Garrick et al., 2008; Petit, 2008a; Petit, 2008b, Templeton, online first), Templeton supposed that the high rate of false positives detected by Panchal and Beaumont (2007) may be due to their simulations and/or their invalidated implementation of NCPA in ANeCA. All positive inferences in the skua data set were, therefore, rechecked manually and were confirmed.

2.5. AMOVA

Population structure was deduced from analysis of molecular variances (AMOVA) in Arlequin 3.11 (Excoffier et al., 2005). Several groupings of populations were tested in order to maximize the among-group variance component (Φ_{CT}), i.e. to find the grouping that best explains the variance in the sequence data. Not every possible grouping could be tested and instead, groupings resulting from non-genetic knowledge (i.e. taxonomy) were used as well as groupings arisen from the NCA analysis or revealed by a SANOVA (Dupanloup et al., 2002). Differentiation between the groups was tested with conventional F_{ST} statistics and 1000 permutations as well as with an exact test (Raymond and Rousset, 1995) using 100,000 Markov chain steps and a “burn-in” of 10,000 steps.

2.6. Fu's F_S and Tajima's D test for neutral expectations

Fu's F_S (Fu, 1994) and Tajima's D (Tajima, 1989) test statistic check the conformation of the data to neutral evolution. Large significant values indicate a deviation from neutrality. For example, past increases in population size usually lead to an excess of rare alleles and result in negative F_S-values.

2.7. Mismatch distribution

To reveal whether populations underwent a historical population expansion, the observed frequency distribution of pairwise nucleotide differences among individuals (i.e. mismatch distribution, Rogers and Harpending, 1992) was compared with the expected distribution from a population expansion model using Arlequin 3.11 (Excoffier et al., 2005) in populations with at least five sequenced individuals. The parameters for a spatial expansion model were calculated likewise. Harpending's raggedness index (r) was used to test for a deviation from unimodality of the mismatch distribution.

The expansion event was dated using the formula $\tau = 2ut$ where $u = \mu$ (mutation rate per site and year) $\times\, k$ (sequence length). Due to the absence of an μ-estimate for the mitochondrial CR I in skuas, the mutation rate of this gene in the closely related large gulls (*Larus* spec.) was used ($\mu = 4.24 \times 10^{-8}$, Liebers and Helbig, 2002). The 95%-confidence interval around τ was calculated with parametric bootstrapping as implemented in Arlequin 3.11.

2.8. Divergence times and gene flow

The statistical method implemented in the IM software calculates the divergence time of two populations simultaneously with the number of migrants between them (Nielsen and Wakeley, 2001; Hey and Nielsen, 2004). Furthermore, a new version of the program can account for unequal sizes of founder populations and population size changes (Hey, 2005). A disadvantage is the program's inability to deal with indels. The program was run for 30 population pairs for which an "isolation with migration" model seems reasonably assuming a finite sites mutation model (Hasegawa et al., 1985). A pre-run including the splitting parameter was run for each population pair with 100,000 burnin steps, 1,000,000 sampling steps, $t_{\max} = 20$, $M_{\max} = 50$ and $\theta = 50$. Different heating schemes and numbers of Markov chains were tested to explore the parameter space and check for sufficient Markov chain mixing. The final three runs with different random seeds consisted of ten Markov chains, 40 chain sweep attempts per step, a geometric heating scheme ($g_1 = 0.95$, $g_2 = 0.8$), 200,000 burnin steps, three to ten million sampling steps and the prior range adjusted according to the results from the pre-runs. The posterior density curves for parameter t (divergence time) had two clear peaks in a few cases with the estimate from the second peak always being much larger than the estimated TMRCA (time to most recent common ancestor). The parameter space was then restricted to include the first peak only. These settings resulted in effective sample size (ESS) estimates larger than 50 for all parameters and the absence of any trend in the parameter trendlines.

3. Results

3.1. Sequence variation

The analyzed 386 bp sequences contained 48 variable sites (57 including indels) of which 34 were parsimony informative. Of the variable sites 43 had two variants (30 parsimony informative) and 5 three variants (4 parsimony informative). A total of 100 haplotypes (81 excluding indels) were found. The sequence of the most frequent haplotype is deposited in GenBank (Accession No. EU636796). The complete haplotype list with the assignment to the taxa is given in Table S1. There are no fixed differences between the species or the five taxa.

3.2. Nested clade phylogeographic analysis

TCS estimated the 95% connection limit to be eight mutational steps and constructed two separate networks for the outgroup taxa which were 11 (*C. skua* + *S. pomarinus*) and 38 (*S. parasiticus* + *S. longicaudus*) steps away from the southern taxa network, respectively (Fig. 2). No clade in the network of the southern taxa got an outgroup weight higher than 0.1. The network was highly reticulate with 132 ambiguous edges (i.e. involved in loops) out of 194 edges. Although all loops could be resolved following the three rules described above, the differences that led to an assignment of haplotypes to a clade and not to another were often subtle. In some cases adopting a pathway with one more step or a slightly less likely step would have changed the position of major clades in the cladogram. The GeoDis statistics and the inference key cannot account for such uncertainties in the cladogram and the results from the inference key have to be interpreted with some caution in such a case. Two alternative connections are shown in Fig. 2 and the GeoDis analysis was also run for the three alternatively resolved networks to compare the phylogeographic inferences.

The network showed no clear separation of the currently described taxa and especially haplotypes of South Polar Skua and Brown Skua are virtually spread all over it. The Tristan Skua was found in a private haplotype containing 15 individuals (clade 2–16) and in two other places at least 8 steps away from that clade. The Falkland Skua is also relative homogeneous with samples from the Patagonian continent found at the tips but one haplotype placed between Brown Skua haplotypes from Marion Island (clade 3–3). Chilean Skua haplotypes are found in close connection with South Polar Skua and Brown Skua (clade 2–1) but also at the tips of clade 3–7 near Tristan Skua haplotypes. Nested clade phylogeographic analysis revealed several events of contiguous range expansion and restricted gene flow with isolation by distance for the southern skuas (Table 1). Only four inferences could be made for the unresolved network, of which two (for clade 1-7 and 2-8) were identical to the presented network. The other two referred to slightly modified versions of clade 3-5 and 3-7 and identified "allopatric fragmentation" and "restricted gene flow with isolation by distance" as key events. Inferences from the network with two ambiguous connections shown in Fig. 2 were identical for all but four higher order clades. No phylogeographic pattern was found for clade 3-2 and 4-2 and "contiguous range expansion" was found for the two 5-step clades but their nesting design was different. The three alternatively resolved networks gave very similar results. The inferred "long-distance colonization" refers to Tristan Skuas colonizing Patagonia and giving rise to the Chilean Skua. However, a South Polar Skua haplotype with five individuals from Rothera, Davis and Mirny was also found in this clade.

3.3. AMOVA

Nearly two third of the variance in the sequence data is explained by variation within populations irrespective of which grouping is applied (Table 2). Only 9.1% of the variance is explained by the grouping representing the current taxonomic species affiliation. More than one quarter (28.6%) of the variance component is due to variation among populations within groups. Treating all five described taxa (3 species and 2 sub-species) equally increases the variance component of F_{CT} to 11.1%. A further division of the taxon *C. a. lonnbergi* into four groups (Atlantic populations, Indian Ocean

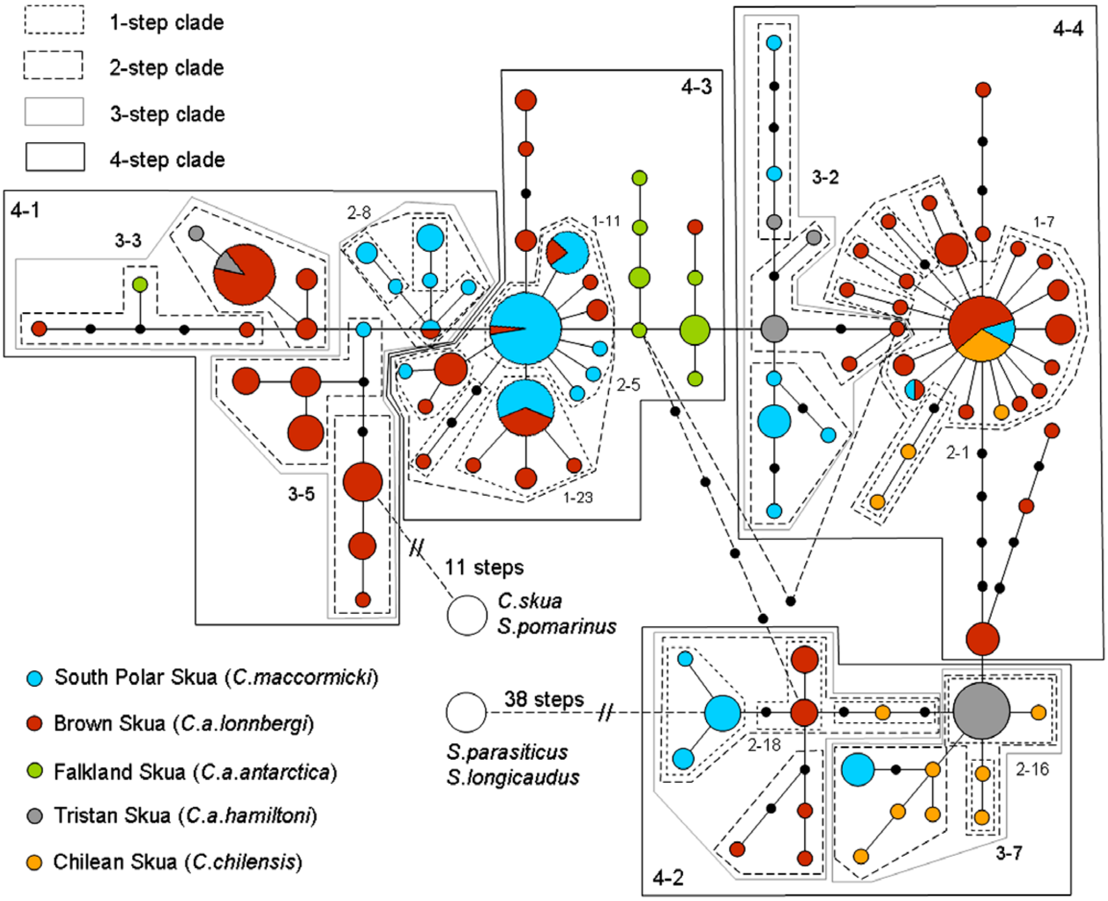

Fig. 2. Haplotype network of mitochondrial control region DNA from 270 southern hemisphere skua individuals. Broken lines connecting haplotypes show alternative resolutions of ambiguities in the initial network. Circles represent haplotypes and circle surface corresponds to haplotype frequency. Black circles show intermediate haplotypes not found in the study. Large white circles belong to the northern hemisphere skua species and their connection to the network, ignoring the 95% connection limit (8 steps), is indicated by broken lines. To increase graph clarity the nesting design is only shown for clades with significant statistical phylogeographic inference and their subclades.

populations, New Zealand populations and the population at Macquarie Island) results in a F_{CT} value more than three times as large as under the species grouping of the current taxonomy. This is achieved at the cost of the proportion of explained variance among populations (within groups). A split of *C. maccormicki*, e.g. into East and West Antarctica populations, always decreases the F_{CT} variance component.

The three species are significantly differentiated from each other (*C. maccormicki* vs. *C. antarctica*: F_{ST} 0.147, $p < 0.001$; *C. maccormicki* vs. *C. chilensis*: F_{ST} 0.420, $p < 0.001$; *C. antarctica*

Table 1
Results of the nested clade phylogeographic analysis using mtDNA data from southern hemisphere skuas

Clade	Chain of inference	Demographic event inferred	Ambiguous network
1–7	1-2-3-4 no	Restricted gene flow with isolation by distance	X
1–11	1-2-11-12 no	Contiguous range expansion	X
1–23	1-2-11-17-4 no	Restricted gene flow with isolation by distance	X
2–1	1-2-3-5-6-7-8 yes	Restricted gene flow/dispersal but with some long-distance dispersal	X
2–5	1-2-11-12 no	Contiguous range expansion	X
2–8	1-2-3-4 no	Restricted gene flow with isolation by distance	X
2–16	1-2-11-12 no	Contiguous range expansion	X
2–18	1-19-20-2-3-4 no	Restricted gene flow with isolation by distance	X
3–2	1-2-3-4 no	Restricted gene flow with isolation by distance	
3–3	1-2-11-12 no	Contiguous range expansion	X
3–5	1-2-3-5-6-7 yes	Restricted gene flow/dispersal but with some long-distance dispersal	X
3–7	1-2-11-12-13 yes	Long-distance colonization	X
4–1	1-19-20-2-3-5-6-7-8 yes	Restricted gene flow/dispersal but with some long-distance dispersal over intermediate areas not occupied by the species; or past gene flow followed by extinction of intermediate populations	X
4–2	1-2-11-12 no	Contiguous range expansion	
5–1	1-19-20-2-11-12 no	Contiguous range expansion	(X)
5–2	1-2-11-12 no	Contiguous range expansion	(X)

Clade numbers correspond to Fig. 2.
An "X" in the last column indicates that the inferred demographic event was also found under the network with the alternative connections shown in Fig. 2.

Table 2
Nested AMOVA with mtDNA data of southern hemisphere skuas

Grouping	Level of variation	df	SS	Explained variance
Three species	Among groups (F_{CT})	2	70.9	$9.1\%^{*}$
	Among populations (F_{SC})	13	179.4	$28.6\%^{***}$
	Within populations (F_{ST})	254	527.6	$62.3\%^{***}$
Five southern taxa	Among groups (F_{CT})	4	110.1	$11.1\%^{*}$
	Among populations (F_{SC})	11	140.1	$26.1\%^{***}$
	Within populations (F_{ST})	254	527.6	$62.8\%^{***}$
Five taxa + division of *C. a. lonnbergi* in Atlantic/Indian Ocean/New Zealand/Macquarie Isl.	Among groups (F_{CT})	7	113.3	$28.9\%^{***}$
	Among populations (F_{SC})	8	36.9	$8.2\%^{***}$
	Within populations (F_{ST})	254	527.6	$62.9\%^{***}$

The Tamura & Nei model of sequence evolution with gamma distributed mutation rates was used.
* $p < 0.05$.
*** $p < 0.001$.

Table 3
Population pairwise genetic distance (Tamura & Nei model with $\alpha = 0.751$)

	C. maccormicki				*C. antarctica lonnbergi*						*C. a. antactica*		*C. a. hamiltoni*	*C. chilensis*
	Rothera	Davis	Mirny	Ross	Bird	Signy	Marion	Campbell	Chatham	Macquarie	Falklands	Viana	Gough	Beagle
Rothera		−0.608	0.07	0.105	0.958	−0.414	1.318	2.238	1.423	−1.172	0.104	0.434	1.185	1.052
Davis	−0.051		−3.793	−0.326	1.537	0.437	0.593	1.815	1.492	0.192	−0.76	−0.056	1.265	1.626
Mirny	0.084	−0.010		−0.012	1.22	0.044	1.13	2.303	1.583	−0.915	−0.084	0.306	1.094	1.189
Ross	0.039	0	**0.041**		1.62	0.327	1.227	2.491	1.633	−0.126	0.113	0.465	1.296	1.557
Bird Island	**0.341**	**0.379**	**0.451**	**0.414**		0.249	2.187	2.175	1.038	0.633	1.353	1.618	0.997	0.194
Signy	**0.069**	**0.099**	**0.194**	**0.173**	**0.132**		1.311	1.636	1.018	0.093	−0.031	0.399	0.865	0.46
Marion	**0.441**	**0.405**	**0.412**	**0.280**	**0.531**	**0.416**		2.164	1.675	1.169	0.502	0.78	1.514	2.319
Campbell	**0.677**	**0.668**	**0.600**	**0.536**	**0.583**	**0.522**	**0.606**		0.549	1.666	2.458	2.776	2.195	2.101
Chatham	**0.418**	**0.428**	**0.452**	**0.401**	**0.335**	**0.317**	**0.475**	**0.431**		1.015	1.129	1.68	1.407	1.206
Macquarie	**0.027**	0.015	**0.091**	**0.091**	**0.242**	**0.042**	**0.398**	**0.533**	**0.316**		−0.258	0.256	0.729	0.66
Falklands	**0.208**	0.195	**0.200**	**0.100**	**0.439**	**0.218**	**0.295**	**0.758**	**0.411**	**0.187**		0.377	1.228	1.543
Viana	0.246	0.218	**0.241**	**0.147**	0.448	**0.242**	**0.335**	**0.778**	**0.451**	**0.218**	−0.03		1.374	1.781
Gough	**0.412**	**0.39**	**0.418**	**0.399**	**0.358**	**0.331**	**0.469**	**0.614**	**0.430**	**0.308**	**0.446**	**0.449**		0.358
Beagle	**0.367**	**0.381**	**0.447**	**0.429**	0.100	**0.200**	**0.552**	**0.602**	**0.371**	**0.255**	**0.477**	0.480	**0.194**	

Estimated divergence time (τ, above diagonal) and pairwise F_{ST} (below diagonal), bold values for genetic distance are significant at $p < 0.05$ with an exact test (Raymond and Rousset, 1995). Only populations with at least five sequenced individuals are shown.

Table 4
Genetic diversity indices for the sampled populations

Taxon	Population	N	$h \pm$ SE	$\pi \pm$ SE	k	Fu's F_S	Tajima's D
South Polar Skua *Catharacta amaccormicki*	Rothera	10	0.867 ± 0.107	0.75 ± 0.5	4.06 ± 2.2	−1.73	−1.28
	Mirny station	10	0.933 ± 0.077	0.86 ± 0.5	5.18 ± 2.7	$-2.21^{(*)}$	−1.16
	Davis station	28	0.896 ± 0.031	1.02 ± 0.6	6.12 ± 3.0	−1.95	−0.65
	Ross Island	36	0.833 ± 0.043	0.84 ± 0.5	4.86 ± 2.4	−2.21	−0.04
	Forster station	2	1.0 ± 0.5	0.53 ± 0.6	2.27 ± 1.9		
	populations pooled	86	0.894 ± 0.023	0.91 ± 0.5	5.38 ± 2.6	-11.86^{**}	−0.82
Brown Skua *C. antarctica lonnbergi*	Bird Island	24	0.913 ± 0.048	0.94 ± 0.6	5.79 ± 2.9	-7.34^{**}	$-1.52^{(*)}$
	Signy Island	25	0.936 ± 0.030	1.07 ± 0.6	6.05 ± 2.9	-5.40^{*}	−0.23
	Macquarie Is.	22	0.935 ± 0.031	1.08 ± 0.6	6.36 ± 3.1	$-2.97^{(*)}$	0.13
	Chatham Island	19	0.795 ± 0.060	0.99 ± 0.6	5.87 ± 2.9	1.41	0.99
	Campbell Island	11	0.618 ± 0.103	0.19 ± 0.1	0.82 ± 0.6	−0.02	0.19
	Crozet Island	2	1.0 ± 0.5	1.94 ± 2.0	13.0 ± 9.5		
	Marion Island	28	0.669 ± 0.096	0.74 ± 0.4	4.67 ± 2.4	−0.41	0.18
	Atlantic populations	49	0.935 ± 0.024	1.08 ± 0.6	6.5 ± 3.1	-15.30^{***}	−1.12
	New Zealand populations	30	0.945 ± 0.012	0.97 ± 0.6	3.7 ± 1.9	0.67	0.92
	Indian Ocean populations	30	0.712 ± 0.088	0.79 ± 0.5	4.9 ± 2.5	−1.35	0.13
	Populations pooled	131	0.964 ± 0.007	1.38 ± 0.7	8.69 ± 4.0	-25.14^{***}	−0.83
Falkland Skua *C. a. antarctica*	Isla Viana	5	0.900 ± 0.161	0.59 ± 0.4	2.74 ± 1.7	−0.56	0.96
	Falkland Islands	7	0.904 ± 0.103	0.46 ± 0.3	2.15 ± 1.4	−1.26	0.24
	Populations pooled	12	0.894 ± 0.077	0.50 ± 0.3	2.32 ± 1.4	-3.41^{**}	−0.21
Tristan Skua *C. a. hamiltoni*	Gough Island	23	0.569 ± 0.114	0.77 ± 0.5	4.86 ± 2.5	2.21	0.47
Chilean Skua *C. chilensis*	Beagle Channel	18	0.862 ± 0.080	0.89 ± 0.5	5.48 ± 2.8	$-3.21^{(*)}$	0.45

For each population the number of sequenced individuals, haplotype diversity (h), nucleotide diversity ($\pi \times 10^{-2}$), the average number of pairwise nucleotide differences (k), and Fu's F_S and Tajima's D test statistic for selective neutrality is given.
$^{(*)}p < 0.1$; $^{*}p < 0.05$; $^{**}p < 0.02$; $^{***}p < 0.001$.

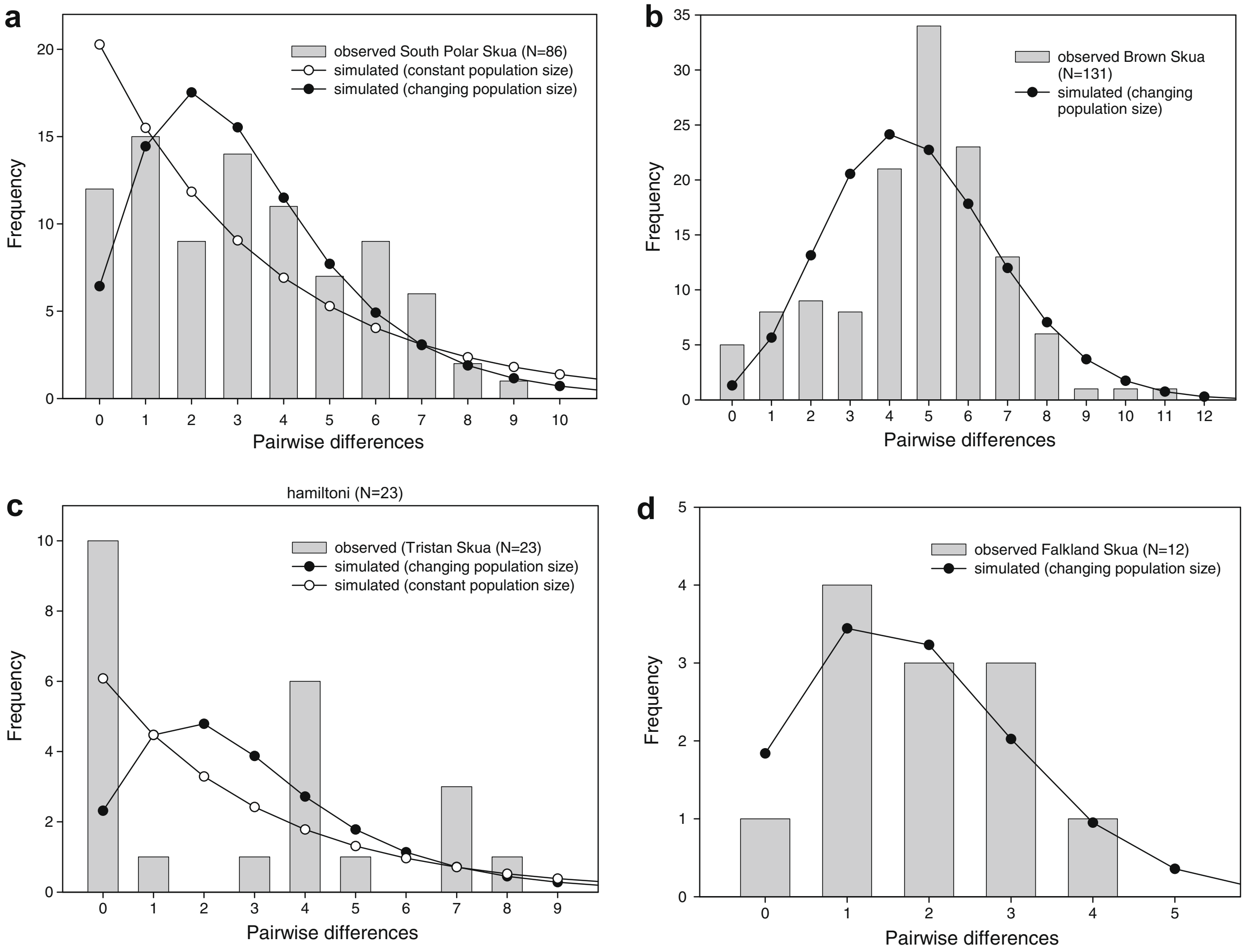

Fig. 3. Mismatch distribution for the five investigated southern hemisphere skua taxa (a–e, populations pooled) and two subsets of the Brown Skua (f and g). The distributions indicate past population size changes and/or geographic fragmentation.

vs. *C. chilensis*: F_{ST} 0.149, $p < 0.001$). This holds true when the five described taxa (species + sub-species) are compared (F_{ST} 0.15-0.51, all p-values < 0.001). Pooling populations in accordance with the grouping with the highest F_{CT}-value from the AMOVA (Table 3) also results in significant differences among all groups (F_{ST} 0.07-0.54, all p-values < 0.01). Table 3 presents F_{ST}-values for all population pairs together with the estimated divergence time (τ).

3.4. Molecular diversity, Fu's F test, Tajima's D

The skua population at Tristan da Cunha had the smallest haplotype diversity among the populations investigated (Table 4). Only one population (Bird Island) had a significantly negative Fu's *F*. Pooling populations resulted in more signs of past population size changes and/or differentiations.

3.5. Mismatch distribution

Mismatch distributions of the five taxa investigated indicate past population size changes and/or fragmentation (Fig. 3). The mismatch distribution statistics revealed incidences of demographic and/or spatial population expansion for nearly every investigated population (Table S2). Note that the statistic assumes a single event and that time estimates have extremely wide confidence intervals. Harpending's raggedness index confirmed a multimodal mismatch distribution for the pooled Brown Skua individuals (Table S2). Inspection of subsets of Brown Skua populations revealed that populations within the subsets had different population size histories (Fig. 3f and g).

3.6. Divergence times and gene flow

Table 5 shows the estimates for divergence time and time to most recent common ancestor (TMRCA) for 30 skua population pairs assuming an isolation with migration model. TMRCA estimates span 219,000–130,000 yBP. Population divergence times are in the range of 80,000–10,000 yBP. In contrast, the Brown Skua population at Chatham Island/New Zealand is remarkably well differentiated from the neighboring populations (1000–3700 km distant) with divergence time estimates of 143,000–115,000 yBP. The South Polar Skua population in East Antarctica (Davis station) is well differentiated from the Brown Skua population at the sub-antarctic Marion Island. These two populations are approximately 4200 km apart. Maternal gene flow is biased for many population pairs and unidirectional for South Polar Skua populations. Typically, introgression is from Brown Skua and Chilean Skua populations into South Polar Skua populations (Fig. 4a and b). Macquarie Island is exceptional with introgression from South Polar Skua alleles into the Brown Skua population (Fig. 4c).

4. Discussion

The different analytical approaches consistently confirm that the southern skua complex consists of young taxa which have rap-

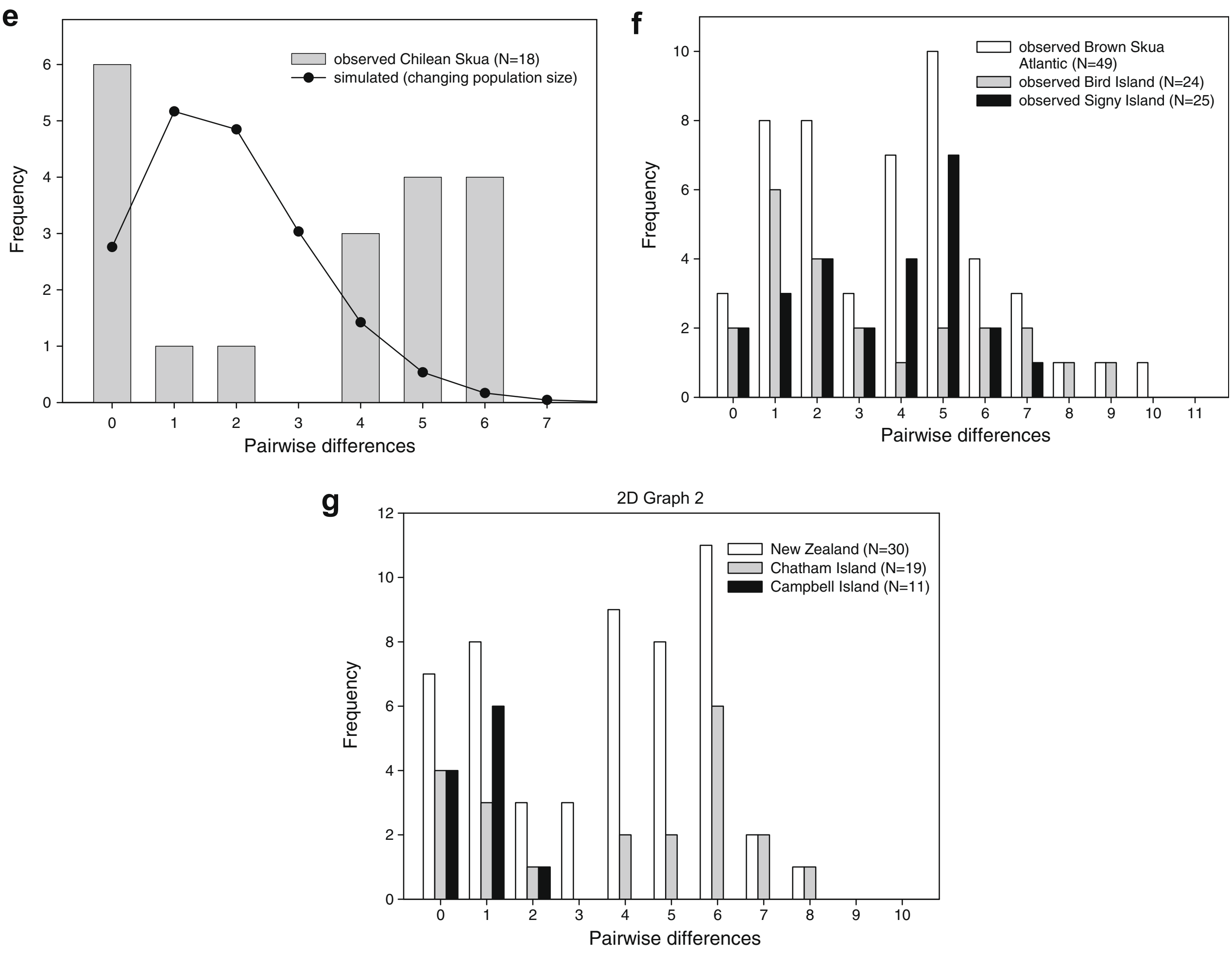

Fig. 3 (*continued*)

idly colonized the southern hemisphere. Beside significant population and taxa differentiation, evolution of the southern skuas is highly reticulate.

When reconstructing population histories it should be kept in mind that divergence time estimates are sensitive to the mutation rate used, which is not necessarily constant across related taxa

Table 5

TMRCA estimates (time to most recent common ancestor, above diagonal) and population divergence time (below diagonal) between southern hemisphere skua populations calculated under an isolation with migration model allowing for population size changes (IM, Hey, 2005)

		South Polar Skua *Catharacta maccormicki*			Brown Skua *Catharacta antarctica lonnbergi*						Falkland Skua *C. a. antarctica*	Tristan Skua *C. a. hamiltoni*	Chilean Skua *C. chilensis*
		Rothera	Davis	Ross	Bird	Signy	Macquarie	Chatham	Campbell	Marion	Falklands	Gough	Beagle
South Polar Skua *Catharacta maccormicki*	Rothera	—	189,000	183,000	219,000	174,000					130,000	182,000	162,000
	Davis	9000	—	186,000			213,000			206,000		207,000	
	Ross	14,000	14,000	—			212,000	207,000	178,000				
Brown Skua *Catharacta antarctica lonnbergi*	Bird	43,000			—	188,000				219,000	183,000	202,000	185,000
	Signy	32,000			73,000	—					146,000	174,000	166,000
	Macquarie		21,000	30,000			—	197,000	159,000	210,000			
	Chatham			143,000			130,000	—	133,000				
	Campbell			17,000			6000	115,000	—				
	Marion		181,000		70,000		57,000			—		182,000	
Falkland Skua *C. a. antarctica*	Falklands	84,000			74,000	74,000					—	149,000	151,000
Tristan Skua *C. a. hamiltoni*	Gough	39,000	/		73,000	74,000				20,000	37,000	—	157,000
Chilean Skua *C. chilensis*	Beagle	26,000			52,000	30,000					62,000	20,000	—

All values are years BP. /—no result (flat posterior probability distribution).

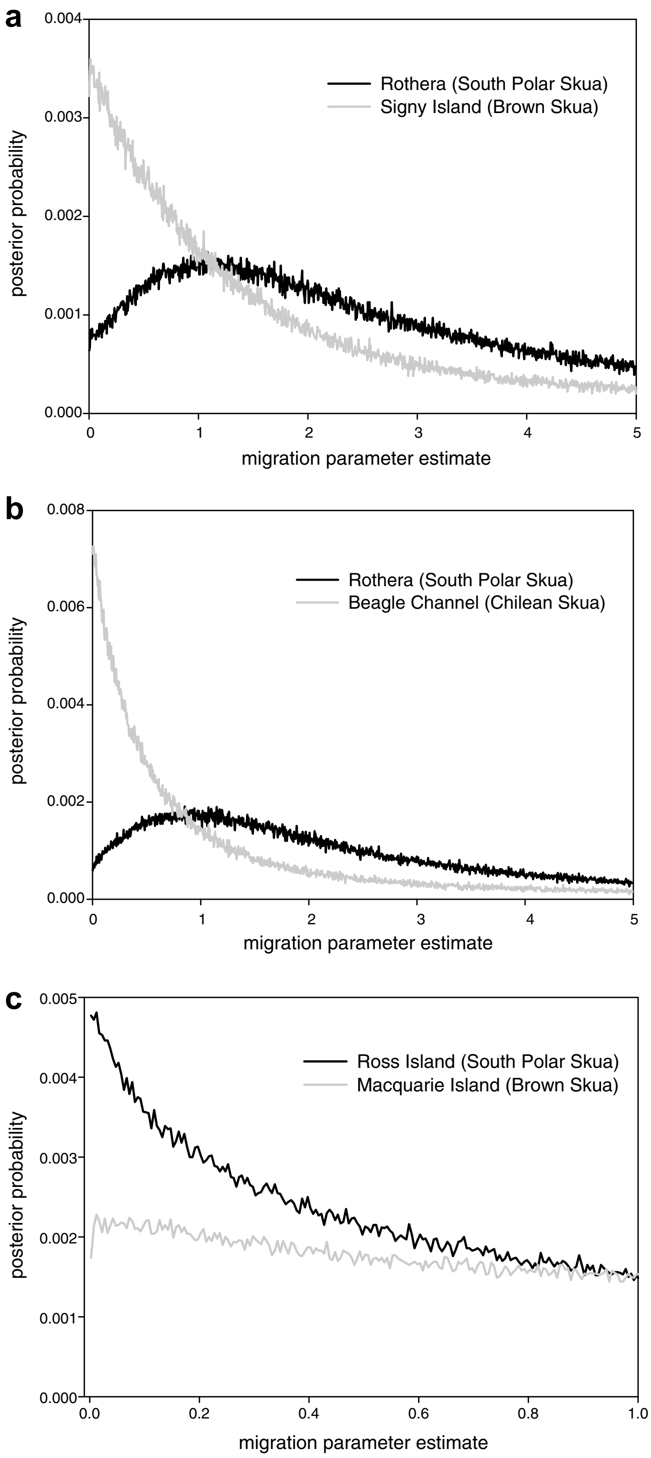

Fig. 4. Examples for unidirectional gene flow between skua population pairs under an isolation with migration model. Peaks in the posterior probability distribution indicate the most likely estimate for the migration parameter *m* (a) migration from Signy into Rothera (b) migration from Beagle into Rothera (c) limited migration from Ross into Macquarie.

(Ritchie et al., 2004). Mutation rate in skuas could not be calibrated using sub-fossil material or fossil records but was taken from gulls (*Larini*). Skuas and gulls are close relatives although their detailed phylogenetic relationship remains controversial (Ericson et al., 2003; Paton et al., 2003; Thomas et al., 2004a; Thomas et al., 2004b). Confidence-intervals of TMRCA estimates are usually large (Basu and Majumder, 2003, Fig. 5) and single estimates are therefore difficult to assign to practicably narrow time windows. However, the combination of estimates from 30 population pairs consistently predicted the diversification of southern skuas to have taken place during about 210,000 to 150,000 yBP (Fig. 5). This time period coincides well with a glacial period in Antarctica between 230,000 and 140,000 yBP. Due to the time lag between temperature and a response of the Antarctic ice body, the Antarctic ice shield was estimated to be smallest at around 210,000 yBP and built up continuously until 140,000 yBP (Oerlemans, 2005). The increasing ice load of Antarctica pushed the continent down and the ice-bonded water resulted in a sea level drop of 80–120 m between interglacials (Jouzel et al., 2007). Furthermore, isostatic glaciation models predict that the sinking Antarctic continent induced northbound flows of magma causing a small forebulge within a 200–1000 km wide zone around the ice grounding line (Lambeck, 1993; Parizek and Alley, 2004). In summary, availability of nesting habitats at the Antarctic continent was comparable to the recent situation at around 210,000 yBP but decreased continuously afterwards. Many of the remaining ice-free parts of Antarctica were probably not usable by skuas because the sea ice zone extended far north and inhibited foraging. At the same time, more (and larger) sub-antarctic areas became available. This pattern fits well with the pattern of diversification of southern skuas. South Polar Skuas spread all around Antarctica when the continent provided habitable conditions. With decreasing temperatures and increasing glaciation skuas were forced to colonize sub-antarctic islands and reached the current distribution at the glacial maximum. South Polar Skuas most likely survived this period in Antarctic refuges. The allopatric fragmentation combined with different ecological conditions then resulted in population divergence and subsequent speciation.

Although rooting of the haplotype network is unreliable if the outgroup is far away from the ingroup (Castelloe and Templeton, 1994; Tarrio et al., 2000; Cassens et al., 2003) it is notable that the northern hemisphere skuas form two outgroups rather than one. Furthermore, these two groups are connected to the network on opposite sides. This is in agreement with an assumed colonization of the southern hemisphere by a small northern species and a subsequent re-colonization of the northern hemisphere by a southern-like skua leading to *C. skua*.

Identification of the most ancestral southern skua taxa involves a degree of speculation. The *S. parasiticus*/*S. longicaudus* group connects to the southern network via South Polar Skua haplotypes from East Antarctica (clade 2–18) but is 38 mutational steps away and therefore cannot be relied upon. Support for the South Polar Skua as the ancestor of the southern skuas comes from ecological and morphological consideration. The South Polar Skua is the only southern taxon known to regularly migrate to the northern hemisphere (Furness, 1987, own unpublished data). It is also the lightest and most long-winged southern taxon and is generally described as slender and gracile in comparison to the more bulky appearance of, for example the Brown Skua (Furness, 1987). In addition, estimates of TMRCA for population pairs also point to the South Polar Skua as oldest taxon. The separation start of South Polar Skua populations is estimated to be before 185,000 yBP. The time estimates for the three South Polar Skua population pairs are nearly identical, corresponding to a rapid spread of the species around the Antarctic continent. However, the start of the genetic divergence between South Polar Skua and Brown Skua populations seems to have been at approximately the same time as that between the South Polar Skua populations. In conclusion, although other possibilities cannot be excluded with complete confidence, the most likely scenario includes the South Polar Skua as oldest southern skua taxon.

Our findings support a colonization scenario for Tristan da Cunha from Brown Skua populations. This agrees with the conclu-

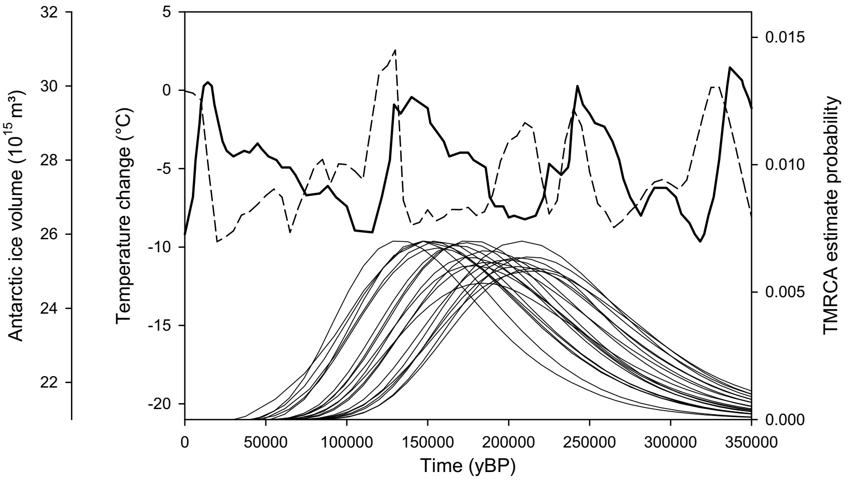

Fig. 5. Antarctic temperature change (compared to 1950, dashed line) reconstructed from the EPICA (European Project for Ice Coring in Antarctica) Dome C Ice core (Jouzel et al., 2007), reconstructed ice shield volume (solid line, after Oerlemans, 2005) and posterior probability distributions of TMRCA (time to most recent common ancestor, distribution curves at the bottom) estimates between 21 southern skua populations (only population pairs belonging to different taxa). Most of the divergence events fall in the cooling period with increasing glaciation 210,000–150,000 yBP.

sion of Swales (1965) based on morphology and distinctive moult patterns.

The most likely candidate for the youngest southern taxon is the Falkland Skua. TMRCA estimates date around 150,000 yBP but a larger sample size is needed to confirm this. Furthermore, the geographic position of the Falklands, and the overlap in non-breeding distribution of Falkland Skua with Brown Skua (Phillips et al., 2007) suggests a higher likelihood of genetic exchange with other taxa, potentially hampering the exact disclosure of historic processes. However, glaciation of Antarctica was near its maximum at 150,000 yBP whilst the Falklands were probably never heavily glaciated (McDowall, 2005). This may have facilitated colonization of the Falklands from skua populations at the Antarctic Peninsula, South Georgia and the Patagonian fjords. The Chilean Skua also seems to be of comparably recent origin and haplotypes are found at the tips of the haplotype network implying a colonization of South America from Tristan da Cunha and Brown Skua populations.

In conclusion, the most parsimonious colonization scenario of the southern hemisphere is the following: a *Stercorarius*-like ancestor founded a southern population, subsequently spread around Antarctica and split into *C. maccormicki* and *C. a. lonnbergi* approximately 200,000 years ago. The Tristan da Cunha archipelago was probably colonized from sub-antarctic island populations. Another long distance colonization event led to the Chilean Skua at the South American continent. The Falkland Skua is most likely a product of immigration from multiple populations at around 150,000 yBP.

The outgroup comprising *C. skua* and *S. pomarinus* is only 11 steps from the network, which corresponds to a 91.7% parsimony probability. Interestingly, the connection is to New Zealand Brown Skuas (clade 3–5) implying again a re-colonization of the northern hemisphere via the Pacific. But this seems unlikely considering the absence of Great Skuas from eastern Siberia and the (current) non-migratory behavior of New Zealand skuas. However, migratory tendencies, or lack of them, can evolve amazingly rapidly and have been proposed as a special route to speciation (Berthold et al., 1992; West-Eberhard, 2003; Bearhop et al., 2005; Kondo et al., 2008). Additional (nuclear) markers may help to solve this mystery in the future.

Conclusions about demographic processes and phylogeographic structure of taxa have to be interpreted with caution if the population history of these taxa is (potentially) complex (Wakeley and Hey, 1998; Knowles, 2004). Population sub-division can result in ragged mismatch distributions (Marjoram and Donnelly, 1994) and impede the uncovering of historical demographic processes. In Adelie penguins *Pygoscelis adeliae*, for example, range expansion erased phylogeographic structure (Ritchie et al., 2004). Our data show that the history of southern skua populations has indeed been eventful. Nearly all populations have undergone demographic and/or spatial expansions. Mismatch distributions show that the demographic histories of skua populations have been different even if the populations are in proximity and exchange genes. For example, the timing of a population size change was different for Brown Skua populations from Bird Island and Signy Island, respectively. Whilst a substantial population size change occurred at Chatham Islands, such an event was absent or at least much more recent in the skua population at the other New Zealand island—Campbell Island (Fig. 3). Nevertheless, nested clade phylogeographic analysis provides evidence that contiguous range expansion and restricted gene flow with isolation by distance have been important processes during the evolution of southern skuas. The inferred events were largely insensitive to alternative connections in the haplotype network. Given the circumpolar distribution of skuas and the occupancy of remote islands, these results are not unexpected.

In agreement with predictions from long-term climatic oscillations (Milankovitsch cycles) and geographic considerations, the South Polar Skua is considerably less phylogeographically structured than the Brown Skua. Whether this difference is due to the two glacials having greater effects on the South Polar Skua or the disjunctive distribution of the Brown Skua at sub-antarctic islands promoting differentiation cannot be answered easily.

The very recent estimates for population divergence times and the ongoing gene flow highlights the need to distinguish between the timing of allelic divergence (gene coalescence, TMRCA) and the timing of population divergence (τ). TMRCA always predates the cessation of gene flow and the time lag between these two events can vary considerably between population pairs (Edwards and Beerli, 2000). Although the South Polar Skua and the Brown Skua were most likely the first taxa which separated, the two taxa still exchange genes in an extensive hybrid zone (Ritz et al., 2006, Fig. 4) and population differentiation is still incomplete after 200,000 years. On the other hand, Brown Skuas from Chatham Island/New Zealand are remarkably well differentiated even from the neighboring population at Campbell Island (Table 5). New

Zealand skuas are unusual in that many, particularly those from the Chatham Islands, are year-round residents at the colony (Furness, 1987; Hemmings, 1990). The absence of substantial migration may have led to an especially low dispersal frequency of skuas from the Chatham Islands (Young, 1998) and a resulting low gene exchange with other populations (Friesen et al., 2007). In contrast, both tracking data and band recoveries indicate overlap in wintering ranges of Falklands Skuas and Brown Skuas from several South Atlantic colonies (Phillips et al., 2007, authors unpublished data). Furthermore, the small population size of c. 130 breeding pairs (del Hoyo, 1996; Young, 1998) at the Chatham Islands favors inbreeding and bottleneck effects. A further reduction of gene flow may be caused by the extraordinary high frequency of cooperative breeding in this population (Hemmings, 1994).

The status of the Brown Skua population at Macquarie Island deserves special attention. Brown Skuas from this island are well differentiated from Brown Skuas of the two New Zealand populations and experienced immigration from South Polar Skuas. This is remarkable because current and historical gene flow between Brown Skua and South Polar Skua is mostly the other way around (Parmelee, 1988; Ritz et al., 2006, Fig. 4). This pattern probably arose from the recent dramatic population history. Animal based oil production at Macquarie Island until 1920 resulted almost in the extinction of seals and penguins as an important food source for Skuas (Cumpston, 1968). Therefore, the Brown Skua population size at Macquarie Island was most likely much reduced until c. 1940 when seal and bird population recovered. In the case of Brown Skuas, the recovery by intrinsic population growth was probably supported by immigration from more southerly population and not from New Zealand populations which were then in decline, too.

4.1. Taxonomy

Our data confirm significant differences between the currently described taxa. But many populations still exchange genes with populations from other taxa although at a lower rate than with populations from the same taxon. Depending on which species concept is applied, the southern skuas could be lumped into one species, *C. antarctica*, or the three current sub-species could be given species status. However, the current taxonomy does not reflect diversity at the molecular (maternal) level within the Brown Skua *C. a. lonnbergi*. Some sets of populations of *C. a. lonnbergi* are well differentiated from each other. This can be seen as evidence that this taxon should be further sub-divided to give e.g. New Zealand Skuas the same status as Tristan Skuas. However, further sampling from e.g. South Sandwich Islands, Bouvet Island and Kerguelen Island would be needed to judge whether Atlantic and Indian Ocean Brown Skua populations are indeed different. The more likely scenario is a cline over the taxon's vast range.

Our results give more evidence for a "once around the world" speciation scenario within the skuas *Stercoraridae*, than for the acquisition of the Great Skua-like morphology twice (in the Great Skua and the southern taxa). This argues for the retention of the genus name *Catharacta*. However, these side results of our study have no statistically strong support and more research effort is needed to resolve the exciting enigma surrounding the phylogenetic positions of *S. pomarinus* and *C. skua*.

5. Conclusions

Of course, our data only reveal the matrilineal aspect of population histories (Ballard and Whitlock, 2004) and could be supplemented by multi-locus nuclear marker data that would better account for gene flow effected by male emigration and immigration (Edwards and Beerli, 2000).

We could show that diversification of the southern skuas dates between 210,000 yBP and 150,000 yBP and coincides with a glacial spanning 230,000–140,000 yBP. Skuas probably first inhabited the Antarctic continent, spread to the sub-antarctic islands and Tristan da Cunha and finally colonized the Patagonian coast and the Falkland Islands at the glacial maximum. Most populations show signs of strong population size changes and still exchange genes with neighboring populations of other taxa. After a rapid colonization of the southern hemisphere, evolution of southern skua taxa is (still) reticulate and speciation incomplete. Indeed, the southern skua complex may serve as model system for recently evolved taxa to get deeper insights into processes and patterns in the early phase of speciation.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2008.07.014.

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MANUSCRIPT 2

Supplementary DNA evidence fails to confirm presence of Brown Skuas *Stercorarius antarctica* in Europe : a retraction of Votier *et al.* (2004)

STEPHEN C. VOTIER, MARTYN KENNEDY, STUART BEARHOP, RICHARD G. NEWELL, KATE GRIFFITHS, HELEN WHITAKER, MARKUS S. RITZ & ROBERT W. FURNESS

The role of the authors was as follows, SCV, SB, RGN, RWF: instigated the study and wrote the ms, MK: conducted the analysis and commented on the ms, KG, HW: extracted DNA and commented on the ms, MSR: collected tissue samples from Antarctic Peninsula skuas and commented on the analysis and the ms.

I confirm the above is correct:

Stephen Votier

17/09/2008

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Short communication

Supplementary DNA evidence fails to confirm presence of Brown Skuas *Stercorarius antarctica* in Europe: a retraction of Votier *et al.* (2004)

STEPHEN C. VOTIER,[1*] MARTYN KENNEDY,[2]
STUART BEARHOP,[3] RICHARD G. NEWELL,[4]
KATE GRIFFITHS,[5] HELEN WHITAKER,[6]
MARKUS S. RITZ[7] & ROBERT W. FURNESS[5]

[1] *Marine Biology and Ecology Research Centre, School of Biological Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK*
[2] *Allan Wilson Centre for Molecular Ecology and Evolution, Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand*
[3] *Centre for Ecology & Conservation, University of Exeter in Cornwall, Tremough Campus, Penryn TR10 9EZ, UK*
[4] *Old Beach Farm, Green End, Landbeach, Cambridge CB4 8ED, UK*
[5] *Institute of Biomedical and Life Sciences, Graham Kerr Building, University of Glasgow G12 8QQ, UK*
[6] *Department of Genetics, JC Smuts Building, University of Stellenbosch, Stellenbosch 7602, South Africa*
[7] *Institute of Ecology, Friedrich-Schiller-University, Dornburger Str. 159, D-07743 Jena, Germany*

Recently we inferred from molecular evidence that two skuas (*Stercorarius*: changed from *Catharacta*, Sangster *et al.* 2004) discovered in the UK were sister taxa of a group comprising the Brown Skua *Stercorarius antarctica* and Chilean Skua *S. chilensis* group (Votier *et al.* 2004). Plumage characteristics excluded Chilean Skua, thereby suggesting that they were Brown Skuas. This finding was significant because these would have been the first North Atlantic records of this species. These immature birds were not identifiable by conventional methods; we know very little about the morphology of immature skuas, because they do not return to the breeding grounds during their first 2–3 years of life (Ainley *et al.* 1990, Marchant & Higgins 1996, Hamer 2001). Also, although breeding skuas in both hemispheres have been tracked electronically (Furness *et al.* 2007, P. Catry *et al.* pers. comm.), their distribution at sea remains something of a mystery.

Following the acquisition of further sequence data, phylogenetic analysis reveals that although the two UK birds have quite different mitochondrial DNA (mtDNA) from the northern hemisphere Great Skua *S. skua*, we cannot determine the southern taxon of origin. Therefore, on the basis of the available molecular evidence we cannot be certain that these birds belonged to the Brown Skua group, and we retract this earlier conclusion.

MATERIALS AND METHODS

DNA was extracted from the blood of 11 South Polar Skuas *S. maccormicki* breeding at King George Island (62°14′S, 58°40′W), Antarctic Peninsula – an area where South Polar and Brown Skuas exhibit high levels of introgression (Ritz *et al.* 2006a). To reduce the risk of sampling a hybrid we selected the smallest out of 240 individuals sampled; F1 generation hybrids tend to be intermediate in size between the two species and therefore larger than pure South Polar Skuas (Hemmings 1984, Parmelee 1988, Jiguet *et al.* 1999). Two mitochondrial gene regions were PCR amplified, the *cytb* short fragment (*c.* 308 bp) and a *12S* ribosomal RNA fragment (*c.* 390 bp). These were then purified (Qiaquick® PCR purification kit, Qiagen), and sequenced from each skua using an internal reverse primer for *12S* (Kennedy *et al.* 2000) and the reverse PCR primer for *cytb*.

These sequences were incorporated into our previous dataset (Votier *et al.* 2004), which was based on the pre-existing dataset of Cohen *et al.* (1997). Following Cohen *et al.* (1997), we made a consensus of the sequences from the 11 Antarctic Peninsula South Polar Skuas (i.e. we present these as a single taxon). The *12S* and *cytb* short sequences have been submitted to GenBank (Accession numbers DQ812941 and DQ812954, respectively). Phylogenetic analyses were conducted using PAUP* version 4.0b10 (Swofford 2002). The near-identity of the sequences meant that maximum parsimony (MP) was inappropriate, and we present the neighbour-joining (NJ) tree, constructed using GTR-corrected distances with 1000 bootstrap replicates (using a heuristic search with ten random addition sequence replicates and TBR branch swapping).

RESULTS

Our alignment contained 696 columns/sites of sequence data, of which 99 were variable and 33 were parsimony informative. The *S. maccormicki* Antarctic Peninsula sequences were almost identical, and differed from *S. a. hamiltoni* and the Scilly specimen by single substitutions in the *cytb* gene. The NJ analyses grouped the Antarctic Peninsula South Polar Skua within the Brown and Chilean Skua group (Fig. 1), rather than with the South Polar Skua sequence of Cohen *et al.* (1997). Apart from the addition

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*Corresponding author.
Email: stephen.votier@plymouth.ac.uk

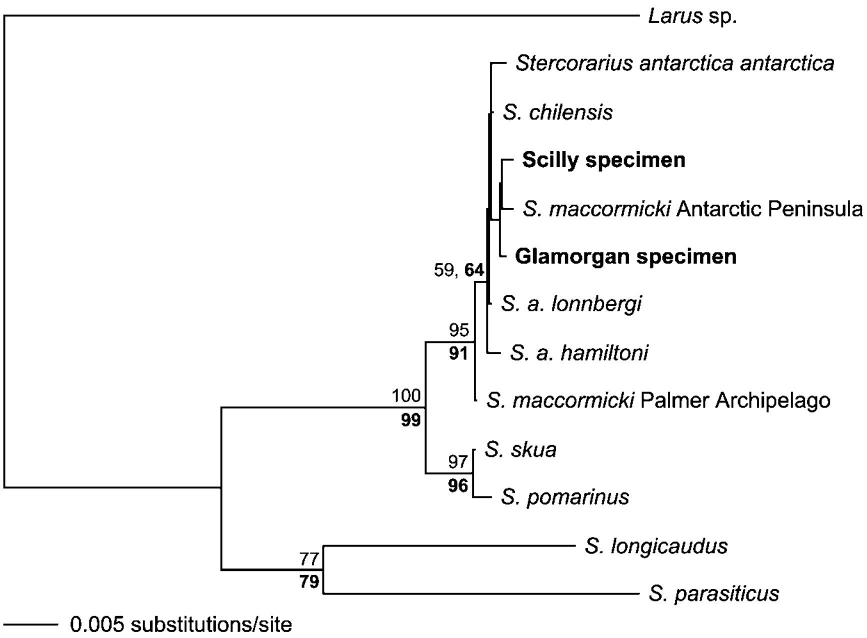

Figure 1. Neighbour-joining (NJ) phylogenetic tree based on mtDNA for 13 samples (two unknown UK specimens and 11 South Polar Skuas of known provenance) added to the dataset of Cohen *et al.* (1997). Branch lengths are proportional to the inferred number of substitutions per site. Numbers represent support values (≥ 50%) from 1000 NJ bootstraps (standard type) and from 1000 maximum-parsimony bootstraps (bold type).

of the UK birds (labelled as Scilly specimen and Glamorgan specimen in the phylogenetic tree) and Antarctic Peninsula South Polar Skuas, the topology and bootstrap values found are concordant with those presented by Cohen *et al.* (1997). The Brown, Chilean and Antarctic Peninsula South Polar Skuas all share a 'T' at base 92 of the *12S* sequences, while the South Polar sequence of Cohen *et al.* (1997) and Great Skua, Pomarine Skua *S. pomarinus*, Long-tailed Skua *S. longicaudus*, Arctic Skua *S. parasiticus* and the outgroup *Larus* sp. all share a 'C' in that position. Whereas the consensus sequence for our Antarctic Peninsula South Polar Skua is the product of 11 individuals' sequences (all of which had a 'T' in that position), the separation of South Polar Skua from the Brown and Chilean Skuas in the Cohen *et al.* (1997) dataset is based on a single *12S* sequence.

DISCUSSION

With the addition of new mtDNA sequence data from South Polar Skuas breeding on the Antarctic Peninsula, we can no longer discriminate between Brown, Chilean and South Polar Skua. Therefore, although the two UK skuas are not Great Skuas, we cannot say with certainty that they have maternal Brown Skua (rather the South Polar) lineages. Although a number of trees grouped the two UK skuas with the South Polar Skuas from the Antarctic Peninsula (Fig. 1, and phylogenetic trees not shown), these generally resulted in an unresolved polytomy, so we can only assign the UK birds to the southern hemisphere group of skuas. Therefore, what appeared to be an important piece in the jigsaw that represents our understanding of the movements and identification of large skuas has proved to be unreliable.

Single base differences are an inappropriate method for separating South Polar and Brown Skuas because of the likelihood of nucleotide polymorphisms, and additional material from more variable sequences is essential.

The small level of divergence among all the southern hemisphere *Stercorarius* taxa reveals that speciation has been rapid and recent; for this reason the systematics of skuas have provoked much debate. Recent work comparing sequences of a hypervariable region of mtDNA (HVR I) showed strong gene flow and little genetic differentiation among southern hemisphere taxa (Ritz *et al.* 2006b), further highlighting their recent separation. The findings of our study highlight how the application of molecular techniques to identify extralimital taxa can produce equivocal results when not interpreted alongside sufficiently representative datasets.

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Markus S. Ritz
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Steffen Hahn
data sampling during the seasons 1999, 2000 and 2001, comments on the manuscript

Tim Janicke
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Hans-Ulrich Peter
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ORIGINAL PAPER

**Markus S. Ritz · Steffen Hahn · Tim Janicke
Hans-Ulrich Peter**

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.

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

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M. S. Ritz (✉) · S. Hahn · T. Janicke · H.-U. Peter
Institute of Ecology, Friedrich-Schiller University Jena,
Dornburger Str. 159, 07743 Jena, Germany
E-mail: markus.ritz@uni-jena.de
Tel.: +49-3641-949427
Fax: +49-3641-949402

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

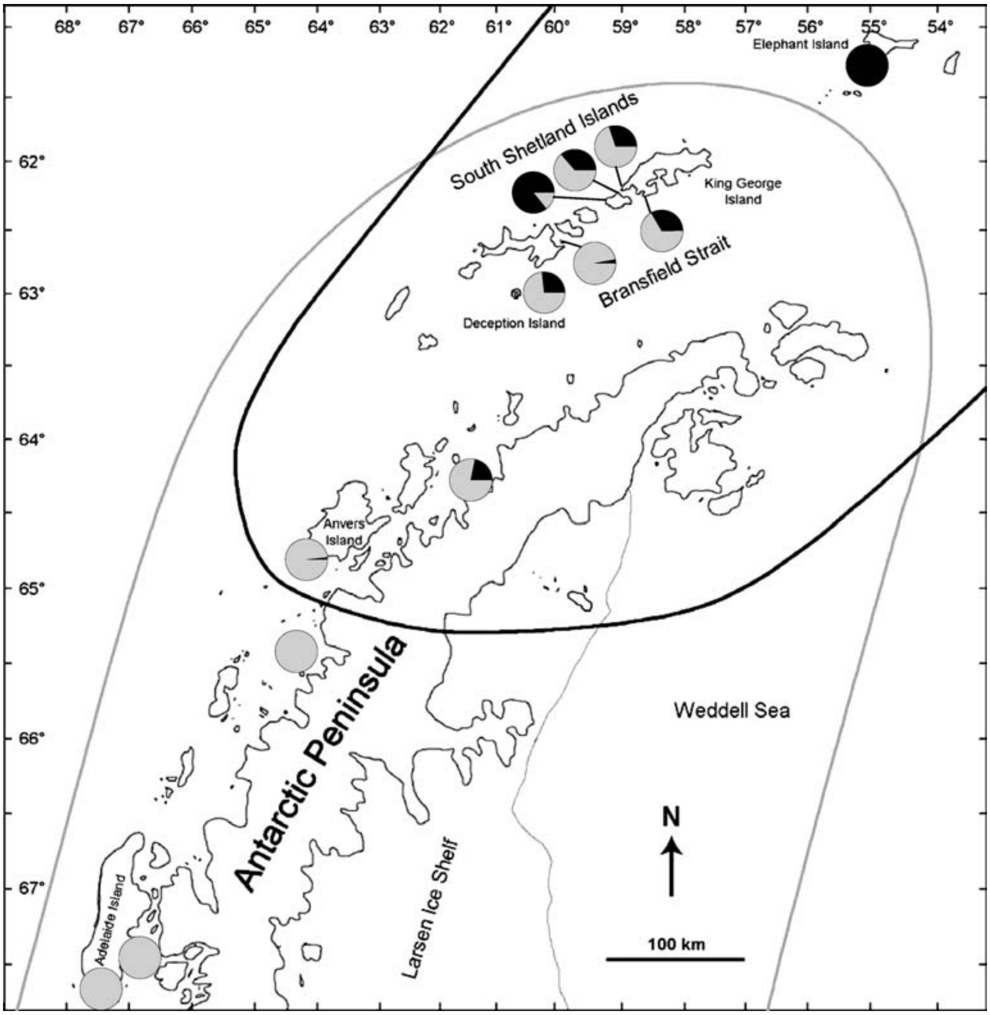

Fig. 1 Species composition of breeding populations of South polar skua (*grey part of pie*) and Brown skua (*black part of pie*) in the area of the Antarctic Peninsula. Number of breeding pairs and source of data are in Table 1. The grey and black solid lines encircle the approximate breeding ranges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

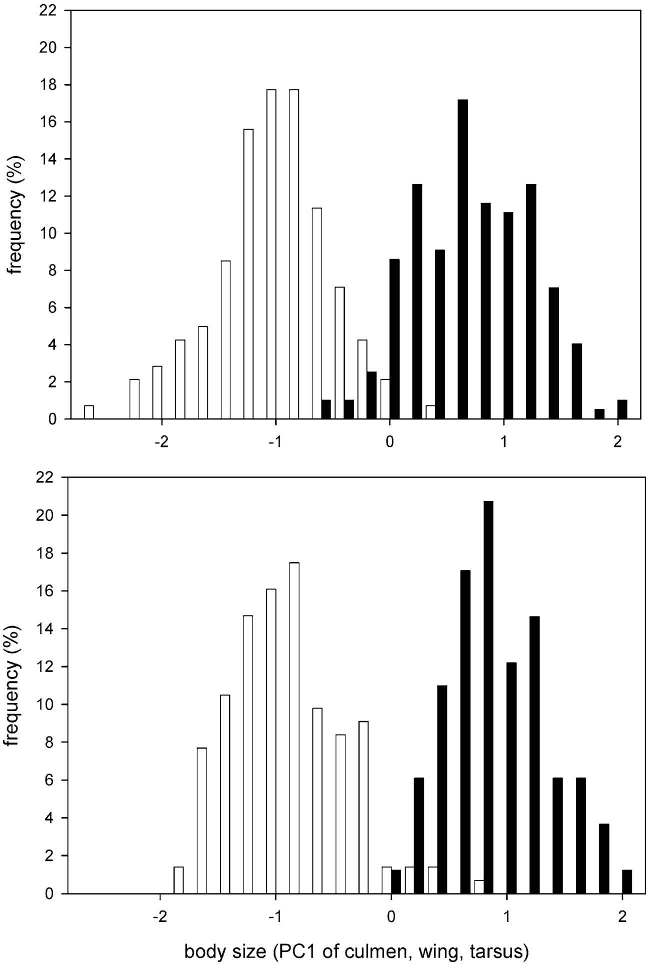

Fig. 2 Frequency distribution of body size for South polar skuas (open bars) and Brown skuas (filled bars) at King George Island, Antarctica. Data shown for the study periods 1984–1985 (upper graph; $n=141$ and 198) and 2004 (lower graph; $n=143$ and 82)

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%).

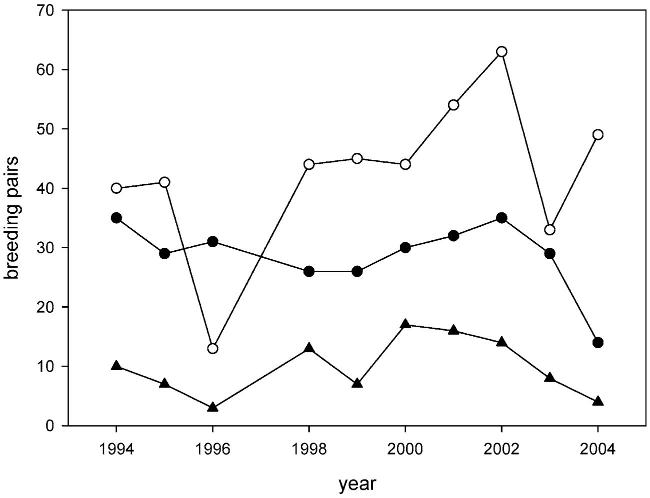

Fig. 3 Numbers of South polar skua (open circles), Brown skua (filled circles) and mixed species breeding pairs (filled triangles) at Potter Peninsula, King George Island, during 1994–2004. No linear trend was detected for any pair type. Years correspond to the second year of the austral season (e.g.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

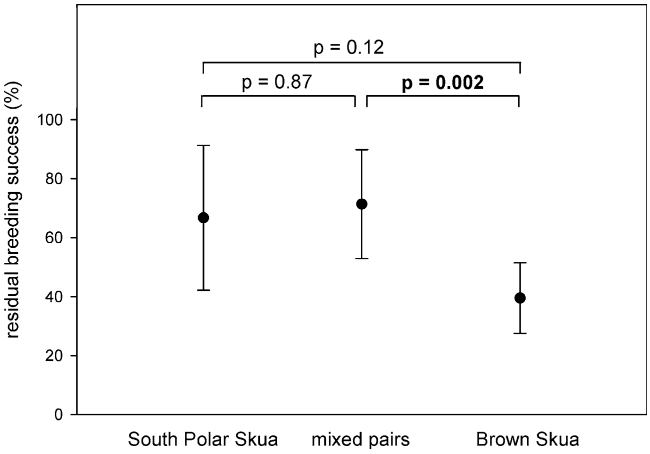

Fig. 4 Mean annual deviation from total breeding success corrected for long-term trends. Residual breeding success ±SE of South polar skua pairs, mixed pairs and Brown skuas pairs at Potter Peninsula. Brown skuas showed lower fluctuations in breeding success than mixed pairs. See text for statistics

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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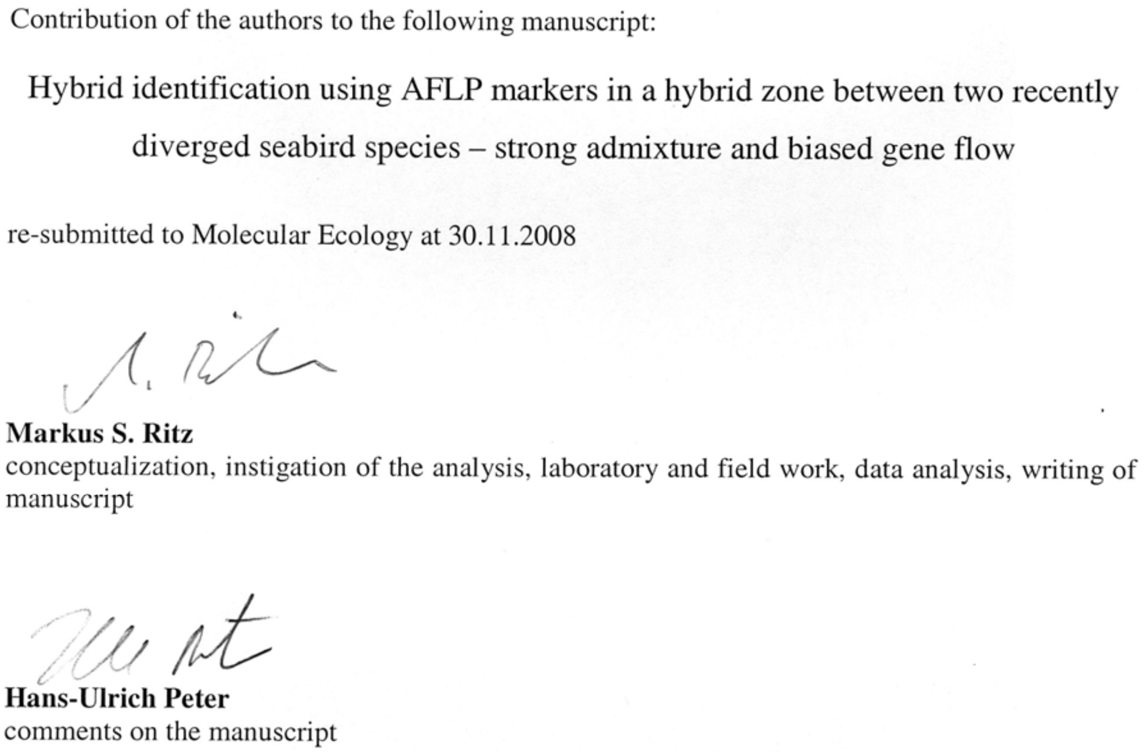

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Hybrid identification using AFLP markers in a hybrid zone between two recently diverged seabird species – strong admixture and biased gene flow

Markus S. Ritz
Hans-Ulrich Peter

Polar & Bird Ecology group, Institute of Ecology, Friedrich-Schiller University Jena, Dornburger Str. 159, 07743 Jena, Germany, email: markus.ritz@web.de, Fon: 0049 3641 949427 Fax: 0049 3641 949402, author of correspondence

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Abstract

Species discrimination and hybrid identification are prerequisites for studies on hybrid zones. We established an AFLP based genetic reference to discriminate South Polar Skuas (*Catharacta maccormicki*), Brown Skuas (*C. antarctica lonnbergi*) and their hybrids in a hybrid zone at the Antarctic Peninsula. Morphometric measurements of blood sampled individuals were tested for their discriminatory power to assign individuals. The 25 informative AFLP markers used can unambiguously assign individuals to one of the species and identify hybrids but can not distinguish between different hybrid categories. (Heterogametic) female hybrids were not significantly less frequent. The degree of admixture was found to be very high in the investigated sympatric population and introgression was biased with higher gene flow from Brown Skua into South Polar Skua than vice versa. Parental species can be distinguished unambiguously based on mass and five morphometric measurements but hybrids show a very broad range of measurements and can closely resemble one of the parental species.

Introduction

Hybrid zones are increasingly recognised as ideal arenas to study various aspects of speciation (Hewitt 1988, Harrison 1993). Studies on hybrid zones have greatly improved our knowledge on the strength and relative importance of various pre- and post-zygotic isolation mechanisms. For example, the development of intrinsic post-zygotic barriers causing sterility and inviability is correlated with divergence time and evolves at a late stage during speciation in birds (Price and Bouvier 2002, Lijtmaer et al. 2003). In contrast, which barrier is the first one to arise when two bird taxa start to diverge is rarely known (Coyne and Orr 2004). The under-representation of studies on hybrid zones involving taxa in an early stage of speciation is explainable by the difficulties to distinguish between them and to identify their hybrids. But an important prerequisite to study e.g. mate choice and reproductive isolation, reproductive character displacement and introgression in hybrid zones is the correct assignment of individuals to parental species or different hybrid categories. We show that AFLP can be used to discriminate between two very recently diverged and morphologically similar Antarctic seabird species and their hybrids. Based on the assignment we report the degree of admixture and direction of introgression in a sympatric population.

Skuas (Stercoraridae) are long-lived, gull-like predatory seabirds and have a bipolar distribution with three small species (*Stercorarius* spp.) and one large species (Great Skua, *Catharacta skua*) at the northern hemisphere. The southern hemisphere is inhabited by five taxa which all belong to the genus *Catharacta* and are currently classified as three species of which one is subdivided into three sub-species (Blechschmidt et al. 1993, del Hoyo 1996, Cohen et al. 1997). The southern taxa have diverged during the Antarctic glacial period 210,000 – 140,000 yBP and gene flow has not ceased between most of the taxa (Ritz et al. 2008). The two species investigated in this study inhabit Antarctica (South Polar Skua, *Catharacta maccormicki*) and the sub-antarctic islands (Brown Skua, *C. antarctica lonnbergi*) and interbreed successfully in an approximately 500 km wide hybrid zone in the area of the Antarctic Peninsula (Ritz et al. 2006a). The species were reported to vary in a single position among 1405 bp of *cytochrom b* and *12S* (Cohen et al. 1997) but this difference was later found to be not diagnostic for species (Votier et al. 2007). Both skua species have an inconspicuous brownish plumage which varies slightly between taxa. The smaller, more gracile South Polar Skua (*Catharacta maccormicki*) is lighter and has golden hackles at the neck whilst the large and more bulky Brown Skua (*C. antarctica lonnbergi*) shows white spots at the back. All plumage characteristics and morphometric measurements vary greatly within species and overlap between species (Peter et al. 1990, Ritz et al. 2006a) and assignment of individuals to species involves always the combination of several measurements. However, hybrids can not be identified with high confidence based on morphology. In this work we aim to set a genetic reference for species determination and hybrid identification. On the basis of the molecular assignment we compare morphometric measurements between the two species and hybrids.

Mixed pairs consist nearly always of a South Polar Skua male and a Brown Skua female (Ritz et al. 2006a). The resulting unidirectional gene flow was confirmed by a population genetic analysis based on maternally inherited mitochondrial control region DNA (Ritz et al. 2008). Because mixed pair members have no obvious fitness disadvantage concerning mean reproductive success (Ritz et al. 2006a, Hahn et al. 2007) and hybrids are fertile (Pietz 1987, Parmelee 1988, MS Ritz own data) the introgression of Brown Skua genes into the South Polar Skua gene pool can be expected to extend beyond the F1-generation. No evidence exists so far that South Polar Skuas and Brown Skuas mate assortatively with respect to body size (Phillips et al. 2002, MS Ritz own data). However, body size is positively correlated with fighting success in skuas (Hahn and Bauer 2008) and the larger Brown Skuas and hybrids can be expected to be superior in intra-sexual competition for mating partners. Therefore, we predict a higher back-cross rate with South Polar Skua and hybrids should consequently be genetically more similar to South Polar Skua than to Brown Skua also at the nuclear level.

Materials and methods

Samples

DNA samples used to verify informative markers stem from three allopatric populations. The South Polar Skua population at Rothera station (Adelaide Island, n = 9) is located 350 km south of the southern edge of the hybrid zone and the second population (Vernadsky station, n = 14) is just a few kilometres south of the site with the most southerly record of mixed pairing (Anvers Island). The allopatric population of Brown Skua (Bird Island / South Georgia, n = 20) is 1.400 km north of the hybrid zone. Within the hybrid zone, 263 samples from two close-by populations at King George Island (Fildes Peninsula, Potter Peninsula) were genotyped. Of the 233 adults sampled 140 individuals were initially classified as South Polar Skua, 85 as Brown Skua and eight as hybrids based on plumage and habitus. In addition, 30 chicks from eleven mixed pairs (sampled during up to three seasons) were analysed to provide a hybrid reference.

AFLP

The PCR protocol followed closely the protocol given in the original description of the amplified fragment length polymorphism (Vos et al. 1995). *Eco*RI primers were fluorescent labelled with IRD700 and IRD800 and the PCR products were run on a 6% polyacrylamid gel in a Licor 4200 sequencer. Band patterns were inspected visually. To pre-screen for primer combinations yielding informative loci, six individuals per species from allopatric populations were run simultaneously. Primer combinations with at least four polymorphic loci (band presence or absence in at least three individuals) were tested in more detail for informative loci. Sex-specific bands could be excluded because all tested individuals were sexed genetically (Fridolfsson and Ellegren 1999). Promising primer combinations from pre-screening were repeated with twelve individuals per species from allopatric populations and 15 individuals per species from the sympatric population at King George Island. To minimise the risk of including hybrids in the sympatric sample, the 15 smallest individuals (South Polar Skua) and 15 largest individuals (Brown Skua) were chosen based on the first axis score of a principal component analysis including mass, head length, culmen length, gonys height, tarsus length and wing length. Loci were scored as being informative with respect to species if they were present in at least one eights and less than seven eights of the individuals and the frequency difference between species was at least 25%. These thresholds ensured that very low frequency alleles are not included as they may disturb the assignment analysis (Anderson and Thompson 2002) and the minimum frequency difference between species of 25% assures against the inclusion of polymorphic markers not informative with respect to species discrimination. Finally, the selected primer combinations were run for 340 sampled individuals. However, samples with ambiguous (faint) bands or unusual band patterns in at least one primer combination were excluded from the analysis (N=34) resulting in an overall sample size of 306 individuals (263 individuals from sympatry + 43 ind. from allopatry). The AFLP procedure was repeated for 62 individuals starting from sample digestion to ensure repeatability. A principle coordinate analysis on all informative loci was performed with SPSS 16 to visualise the clustering of individuals by species and the scattering of hybrids.

assignment statistics using NewHybrids

Assignment of skua individuals was done with the Bayesian assignment algorithm implemented in NewHybrids 1.1 (Anderson and Thompson 2002, Anderson 2008). The program uses a Markov chain Monte Carlo sampler to estimate posterior probabilities for each individual to belong to a certain category. It allows the inclusion of learning samples, data from individuals with known category membership, via the z- and s-option. All NewHybrids runs were repeated at least five times with different random seeds, a burn-in of at least 1,000 sweeps and 30,000 sampling sweeps. The graphical surface of the program allowed real-time inspection of the likelihood trace, Pi distribution and the average category probability of each individual to quickly assess whether the likelihood trace has reached stationarity and different runs yield similar results.

A step-wise approach with an increasing number of learning samples was chosen. The first data set contained no prior information on species identity and was run to assess whether the markers are sufficient to separate all individuals from allopatric populations into distinct categories. The second set included all individuals and contained prior information (z-option) on the samples from allopatry (s-option) and were used to check the identity of likely pure individuals from sympatry. The third set additionally included learning samples of mixed pair offspring with confirmed parental species identity. Between each step, individuals with a posterior probability of belonging to the assigned category of less than 0.8 were removed from the learning sample set. The step-wise procedures accounts for the fact that informative loci should be verified with allopatric samples but that allele frequencies can vary over a species range. An assignment based on training with allopatric samples only may then assign more individuals from sympatry to the wrong species or to hybrids. Furthermore, the historic ranges of the species are not known. While it seems unlikely that the South Polar Skua ever inhabited the sub-antarctic island South Georgia, the range of the Brown Skua may have extended further south during the last inter-glacial and led to introgression into the South Polar Skua. Identification of such individuals among samples from currently allopatric populations will increase assignment success of individuals from sympatry.

Morphometry

Adult skuas with an active nest were caught with a baited snare, blood sampled (50µl) by puncture of the wing vein and measured. Measures taken were mass (to nearest 10 g), head length, culmen length (tip of bill until beginning of feathering at the upper bill’s ridge), gonys height, tarsus length (all to nearest 0.1 mm) and wing length (flatted chord alongside the bird's body to nearest 1 mm). The handling procedure lasted less than 15 min in all cases. Birds were sexed by amplifying sex chromosome linked CHD gene (Griffiths et al. 1996, Fridolfsson and Ellegren 1999) using primer F (5'-GTT ACT GAT TCG TCT ACG AGA-3') and primer R (5'-ATT GAA ATG ATC CAG TGC TTG-3') or if they bred together with an adult with known sex.

To evaluate the power of morphometric measurements to discriminate species and to identify hybrids, discriminant function analyses were run in SPSS 16 with the AFLP based NewHybrids assignment as grouping variable. For a higher stringency the analysis was repeated with individuals only that had a higher than 0.8 posterior assignment probability. Skuas are (reversed) sexual size dimorphic (Furness 1987) and the analysis can be expected to have a higher power if run for sexes separately. However, to potentially allow field researchers to also identify unsexed individuals the analyses were also run with individuals pooled. Mass and the five morphometric measures were entered into the analysis and the prior probability was assumed to be equal for groups.

Results

AFLP loci

In total, 98 primer combinations were pre-screened. 30 of these combinations contained 36 sex specific bands. 47 primer combinations contained potentially informative loci of which 6 primer combinations with 25 informative loci were finally selected (table S1). No locus was diagnostic for species identity. The estimated mean allele frequency difference between species was 28% and was highest for locus 1 of primer combination Eco-C4 and Mse-C4 at 56%.The plot of first two axis of a principle coordinate analysis on the AFLP markers shows a clear separation by species but hybrids overlap with the parental species (figure 1). Note, however, that the first two axes explain only 22.7% of the genetic variance and the Bayesian procedure in NewHybrids uses a different algorithm to assign individuals.

Sampled skua families with known pedigree could be used to verify the identification of hybrids and to explore the assignment potential of hybrid chicks beyond the F1 generation. Of 19 F1-hybrids 16 were identified by the assignment procedure. The three remaining individuals stem from two mixed pair families in which one partner has a higher than 0.2 probability to actually be a hybrid. The chance of identifying a backcross as hybrid is still good (figure 2) but four out of nine backcross chicks were assigned to one of the parental species.

Assignment

The final data set contained prior information for 11 South Polar Skuas and 17 Brown Skuas from allopatry, for 11 South Polar Skuas and 12 Brown Skuas from sympatry, 8 South Polar Skuas and 8 Brown Skuas from mixed pairs and 18 (F1)-hybrid offspring. Only three of 20 Brown Skua samples from allopatry had to be excluded as learning samples because the analysis indicated a higher than 0.2 probability of having mixed ancestry. In comparison, half of the South Polar Skua samples from outside the hybrid zone, but close to the border in case of the samples from Vernadsky station, could not be used as learning samples. Most individuals from the sympatric population show a non-zero probability of admixed origin. If a threshold of 0.8 posterior assignment probability is applied, only half of the individuals (117 out of 232) can be assigned. But all individuals were assigned to one of the two parental species or as hybrid if a threshold of 0.5 posterior assignment probability was applied. The AFLP based assignment revealed a much higher proportion of hybrids in the sympatric population than previously assumed (table 1). While our morphology based assignment during field work does rarely assign individuals to the wrong species (4 out of 232 individuals, 1.7%), it fails to identify hybrids. Of the tentatively as South Polar Skuas and Brown Skuas classified 140 and 84 individuals from sympatry at King George Island, 60 and 25 individuals, respectively, were found to have a higher than 0.5 probability of having a mixed ancestry. Six of the eight as hybrids classified individuals were confirmed by the AFLP analysis, two were assigned to South Polar Skua. The individual plot shows a non-zero probability to be of mixed ancestry for most individuals (figure 3).

Female hybrids (with >0.8 assignment probability) were less frequent than male hybrids but the sex ratio did not differ significantly from parity (table 4, binomial test, $p = 0.072$). The sex ratio was closer to parity if all sexed hybrids (with >0.5 assignment probability) were analysed (48 males vs. 43 females, $p = 0.348$).

Morphometry

A first step concentrated on the discrimination of species based on morphometry in comparison to the genetic reference. Discriminant function analysis based on mass and five morphometric measurements of breeding adults could assign nearly all individuals to species.

One individual among 57 males and 73 females, respectively was assigned to the wrong species when the assignment from NewHybrids was used as reference. Using only 36 males and 52 female for which the posterior assignment probability was higher than 0.8 resulted in no misidentifications (table 2). Without knowledge of the birds sex species discrimination was still perfect (figure 4). The standardized and unstandardized canonical discriminant function coefficients for this analysis are given in table 3.

The second step included pure species and hybrid individuals with a higher than 0.8 assignment probability. Classification success of these discriminant function analyses was lower compared to the analyses discriminating between species only, and was 67% and 81% for males and females, respectively (table 4). The unstandardized canonical discriminant function coefficients are given in table S2 and the resulting scatter plots with demarcation lines separating pure species individuals and hybrids are shown in figure 5. Although more than 90% of pure species adults can be identified based on morphometrics, the method can correctly assign only one third of hybrids. In summary, a field researchers relying on morphometrics alone will miss more than 60% of hybrids and every fourth identified hybrid will be misclassified and actually belong to one of the parental species. Repeating the analysis with all 104 males and 114 females reduces classification success slightly (66% in males, 69% in females) but gives qualitatively similar results (not shown).

Discussion

AFLP loci

The need to screen 98 primer combinations to extract 25 informative loci, of which none is diagnostic, is in agreement with the close relatedness of South Polar Skua and Brown Skua. The two species were found to have their most recent common ancestor 200,000 yBP but the divergence of allopatric populations in the area of the Antarctic Peninsula was estimated at 40,000-30,000 yBP (Ritz et al. 2008). Considering an average age of reproduction of 10 years in skuas (Pietz and Parmelee 1994, own unpublished data) results in a separation of the species just 3000-4000 generations ago. Although AFLP can even be used to distinguish subpopulations (Bensch and Akesson 2005, Bonin et al. 2007) all AFLP studies aiming to identify bird hybrids have been done on more distantly related taxa so far (Bensch et al. 2002b, Haig et al. 2004, Helbig et al. 2005, Vallender et al. 2007, Ruegg 2008). Any attempt to identify hybrids between taxa that diverged less than 3000 generations ago may require a strongly increased AFLP screening effort. Other techniques, like microsatellites and SNPs, although initially labour intensive, may be (additionally) required in such a case.

Assignment

Assignment analysis with samples from allopatric populations without prior information on taxa affiliation confirmed that the selected AFLP loci can unambiguously discriminate between South Polar Skua and Brown Skua. Pedigree analysis confirmed that F1 individuals can be assigned with high confidence and F2 and backcrosses can often still be identified as hybrids. Discrimination between various backcross categories and between backcrosses and parental taxa requires large amount of (diagnostic) markers (Boecklen and Howard 1997, Anderson 2008). No marker was found to be diagnostic for taxon, and hybrid categories had therefore to be combined. In conclusion, although more loci and/or markers can certainly improve the discrimination power, the overall picture will most likely remain unchanged.

Admixture

An important result of this study is the admixed origin of many (or most) of the individuals in the hybrid zone at King George Island. Especially in the South Polar Skua, the assignment probability plot for all individuals (figure 3) shows a continuous slope rather than a steep slope followed by a plateau of individuals with a high probability to belong to the species. This finding argues for strong introgression into South Polar Skua and the individuals at King George Island could, in fact, be seen as hybrid swarm. Brown Skuas are on average less introgressed with 86% of identified Brown Skuas having a higher than 0.8 assignment probability. Unfortunately, our data do not allow to follow the introgression beyond the F1 generation by breaking down hybrids into different hybrid categories. In conclusion, introgression is stronger from Brown Skua into South Polar Skua also at the nuclear level than vice versa but we can not directly reveal a higher frequency of backcrossed individuals in the South Polar Skua group than in the Brown Skua group. This finding is in contrast to expectations considering the relative frequency of species in sympatric populations. The South Polar Skua is around thrice as abundant than the Brown Skua also at the northern edge of the hybrid zone (Ritz et al. 2006a). The rarer species, the Brown Skua, can be expected to become less choosy (Nuechterlein and Buitron 1998, Wirtz 1999) and to engage in pairings with hybrids more readily than the South Polar Skua creating a pattern contrary to the one observed. Obviously, simple frequency dependent mate choice can not explain the biased introgression in this hybrid zone. A superior performance of large hybrids in intra-sexual competition for a mating partner of the smaller species, the South Polar Skua, is a more likely explanation. Another, potentially additive, factor is the offset in arrival at the breeding grounds between the two species (Neilson 1983, Parmelee 1992). Brown Skua females which remained unpaired in the early season encounter many allospecific mates when South Polar Skua males arrive one week later and may decide to form a mixed pair as the probability of not breeding at all increases (and the fitness loss of mixed pairs is most likely minimal). This difference in phenology may turn out to be a pre-zygotic isolation barrier preventing random mating between the two species.

The observed high degree of admixture within the hybrid zone offers an explanation for the formerly found mitochondrial gene flow from Brown Skua into the allopatric South Polar Skua population near Rothera station (Ritz et al. 2008). Although a former extension of the hybrid zone 350 km further south is a possible scenario, gene flow across the border of the hybrid zone via (backcrossed) hybrids seems more likely. Brown Skuas inhabit mainly sub-antarctic islands and are unlikely to have extended their range further south within the cooler past millennia. More importantly, due to reversed sexual size dimorphism F1 females (with Brown Skua mitochondrial DNA) have a higher chance of mating with a high quality South Polar Skua male in comparison to F1 males trying to mate with a Brown Skua female. This will result in a farther spread of Brown Skua mitochondrial DNA into South Polar Skua populations outside the hybrid zone than vice versa. Further studies may test whether the clines of mitochondrial and nuclear DNA are indeed different in breadth and position across the hybrid zone at the Antarctic Peninsula. Examples of disconcordant genetic and morphology clines have been described for e.g. Manakins (Brumfield et al. 2001), Swainson’s thrush (Ruegg 2008) and the Willow warbler (Helbig et al. 2001, Bensch et al. 2006). In the skua hybrid zone, it can be hypothesised that the mitochondrial cline is broadest and has its centre farthest south, followed by the nuclear and the morphological cline.

Haldane’s rule describes the phenomenon that if hybrids have reduced fertility and/or viability, these individuals belong to the heterogametic sex (Haldane 1922). It has been shown that the formation of these intrinsic post-zygotic isolation barrier evolve gradually as species diverge (Coyne and Orr 1997, Sasa et al. 1998, Presgraves 2002, Price and Bouvier 2002, Lijtmaer et al. 2003, Russell 2003). In birds, the time to achieve total female hybrid inviability is long compared to other taxonomic groups and was estimated at 6 million years or 11.9% *cytochrom b* sequence divergence (Price and Bouvier 2002, Lijtmaer et al. 2003). Although female hybrids tended to be underrepresented in this study the sex ratio of hybrids did not differ significantly from parity. In fact, a reduced viability of female hybrids would be surprising in the light of the recent divergence of the two skua species. Most hybridising bird taxa pairs with a *cytochrom b* sequence divergence of 5% are still fully fertile (Price and Bouvier 2002) and South Polar Skua and Brown Skua do not differ in *cytochrom b* (Cohen et al. 1997, Votier et al. 2007). Similarly, no deficiency of females was detected in hybrids between two warbler species that diverged during the middle Pliocene (Bermingham et al. 1992, Smith and Rohwer 2000). Biased gene flow across hybrid zones has been reported to be in agreement with Haldane's rule (Helbig et al. 2001, Bensch et al. 2002b, Helbig et al. 2005). But the conclusions in these studies were drawn from the comparison of mitochondrial versus nuclear gene flow and did not directly test the sex ratio in hybrids. Although Haldane's rule holds certainly true in most taxa, we argue for a stringent test of the sex ratio of hybrids before the application of Haldane's rule in a hybrid zone is hypothesised. Intrinsic and extrinsic pre-zygotic isolation mechanisms usually emerge first (Coyne and Orr 2004) and may produce identical genetic patterns as reduced fertility and/or viability of the heterogametic sex.

Morphometry

Morphometric measurements may be used to distinguish taxa and to identify hybrids. However, the genetic background of individuals is not necessarily highly correlated with their morphology. Cryptic hybridisation may lead to misassignment of hybrids because they closely resemble parental species in phenotype (Chan et al. 2006, Vallender et al. 2007). The establishment of a genetic reference for species identity offers the possibility to check morphometric measurements for their discriminatory power between taxa in sympatry. Discriminant function analysis showed that pure South Polar Skuas and Brown Skuas can be distinguished unambiguously based on mass and five morphometric measurements. However, hybrids can not be identified based on these measurements with high confidence. Instead, genetically identified hybrids can be found to be morphologically very similar to one of the parental species. This is in agreement with a long lasting, extensive hybridisation (Ritz et al. 2006a) with no obvious fitness disadvantage of mixed pairs and hybrids (Pietz 1987, Parmelee 1988, Ritz et al. 2006a, Hahn et al. 2007).

Conclusions

We have shown that AFLP can be used to discriminate between hybrids and pure individuals of two morphologically similar species which have diverged only a few thousand generations ago. In fact, the South Polar Skua and the Brown Skua are, to our knowledge, the closest related bird species ever investigated in a hybrid zone. Accordingly, the degree of admixture was found to be high and hybrids were phenotypically diverse. Application of the AFLP assignment method will allow detailed insight into this early stage of speciation and help to identify the foremost emerging barriers to reproduction.

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Figure Legends

Fig. 1: Scatter plot of the first two axis scores (explaining 22.7% of variance) from a principle coordinate analysis on 25 informative AFLP loci for all 306 analysed skua individuals. Open, closed and grey symbols refer to South Polar Skua, Brown Skua and hybrids, respectively, according to the NewHybrids assignment. Larger symbols show samples from allopatric populations and dots within symbols indicate learning samples used in the final assignment procedure in NewHybrids.

Fig. 2: Exemplary AFLP based assignment results of five mixed pair families. Each set of bars represents one family with male, female and 2-4 chicks. The posterior probability of an individual being a South Polar Skua, a Brown Skua or a hybrid is represented by white, black and grey proportions of it’s bar. Family 1 is an example of pure parents and F1-hybrid chicks. Identification of hybrids (including backcrosses) is robust in many, but not all, cases if at least one parent has a higher than 0.8 probability of being a pure species individual (family 2-5).

Fig. 3: Assignment probability of all analysed individuals from sympatric populations at King George Island to South Polar Skua (white proportion of bar), Brown Skua (black) and hybrid (grey). Grouping into the three blocks is based on morphology (plumage, habitus) for adults and on ancestry (chicks from mixed pairs) for most hybrids

Fig. 4: Histogram of discriminant function scores based on mass and five morphometric measures from 38 South Polar Skuas (open bars) and 50 Brown Skuas (filled bars) from sympatry. Species assignment is based on informative AFLP markers and a higher than 0.8 assignment probability in NewHybrids. The maximum score for South Polar Skua was -1.26 and the minimum score for Brown Skua was 0.94.

Fig. 5: Discriminant function scores based on mass and five morphometric measures for 64 male (upper graph) and 69 female (lower graph) skuas with territorial map. The AFLP based grouping into South Polar Skua, Brown Skua or hybrid is based on a higher than 0.8 assignment probability in NewHybrids.

Tables and Figures

Table 1 Comparison of individual assignment based on morphology (plumage, habitus) during field work and on 25 informative AFLP loci.

	AFLP assignment			
Morphology	South Polar Skua	Brown Skua	Hybrid	Sum
South Polar Skua	**57**	4	60	121
Brown Skua	0	**39**	25	64
Hybrid	2	0	**6**	8
Sum	59	43	91	193

Table 2: Mean and standard deviation of mass (in g) and five morphological measurements (in mm) for male and female South Polar Skua and Brown Skuas from the hybrid zone on King George Island, Antarctica. Species determination is based on an AFLP based posterior assignment probability higher than 0.8 using NewHybrids. Unstandardized canonical discriminant function coefficients are given. The highest function score was -3.92 and -2.71 for South Polar Skua males and females, respectively and the lowest function score for Brown Skua males and females was 5.65 and 0.59, respectively

	Males					Females				
Trait	South Polar Skua Mean	±SD	Brown Skua Mean	±SD	Discriminant coefficients	South Polar Skua Mean	±SD	Brown Skua Mean	±SD	Discriminant coefficients
Mass	1096	± 63	1659	± 95	0,0101	1285	± 83	1853	± 146	0,0030
Head	106,5	± 2,9	118,6	± 2,0	0,0738	108,5	± 3,4	118,6	± 2,7	0,0448
Culmen	47,2	± 1,5	52,9	± 1,5	-0,0936	48,3	± 2,1	53,4	± 1,7	0,0009
Gonys	16,8	± 0,4	20,0	± 0,6	0,6921	17,4	± 0,6	20,4	± 0,8	0,1888
Wing	388,1	± 7,6	415,1	± 6,1	0,0153	404,2	± 9,3	426,6	± 6,9	0,0120
Tarsus	63,3	± 1,7	73,9	± 2,0	0,4012	66,0	± 1,9	77,4	± 2,1	0,2994
Constant					-62,8274					-41,0151
N	21		15			17		35		

Table 3 Standardized and unstandardized canonical discriminant function coefficients for species discrimination based on mass (in g) and five morphometric measurements (in mm). Morphological traits are sorted by their discriminatory power.

Morphological trait	Standardized coefficients	Unstandardized coefficients
Tarsus	0,5062	0,2052
Head	0,3729	0,1314
Gonys	0,3312	0,4741
Mass	0,3032	0,0021
Wing	-0,1745	-0,0177
Culmen	-0,0465	-0,0270
Constant		-33,1585

Table 4 Classification success of sexed South Polar Skua (SPS), Brown Skua (BS) and their hybrids by discriminant analysis based on mass and five morphometric measurements. An AFLP based genetic assignment with a higher than 0.8 assignment probability in NewHybrids was used as grouping reference.

	Morphometry assignment											
	Males (N=64)						Females (N=69)					
AFLP assign.	SPS		BS		Hybrid		SPS		BS		Hybrid	
SPS	**19**	**91%**	0	0%	2	9%	**16**	**94%**	0	0%	1	6%
BS	0	0%	**14**	**93%**	1	7%	0	0%	**34**	**97%**	1	3%
Hybrid	9	32%	9	32%	**10**	**36%**	6	35%	5	30%	**6**	**35%**

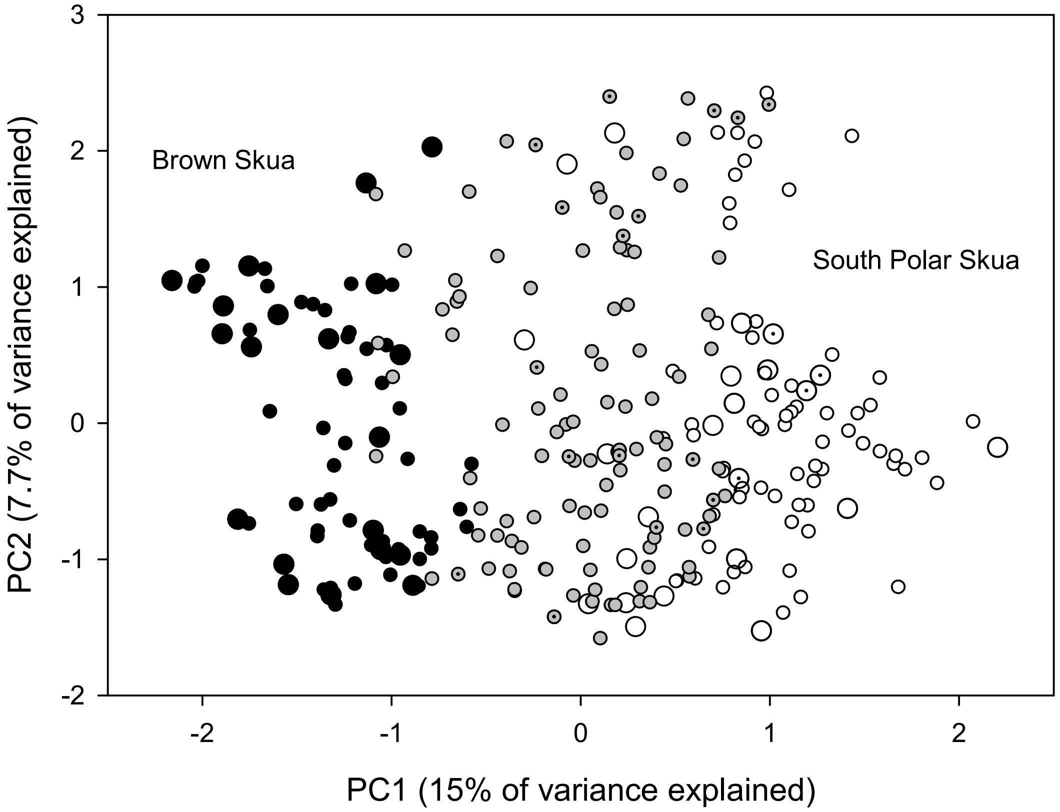

Brown Skua
South Polar Skua
PC2 (7.7% of variance explained)
PC1 (15% of variance explained)
3
2
1
0
-1
-2
-2
-1
0
1
2

figure 1

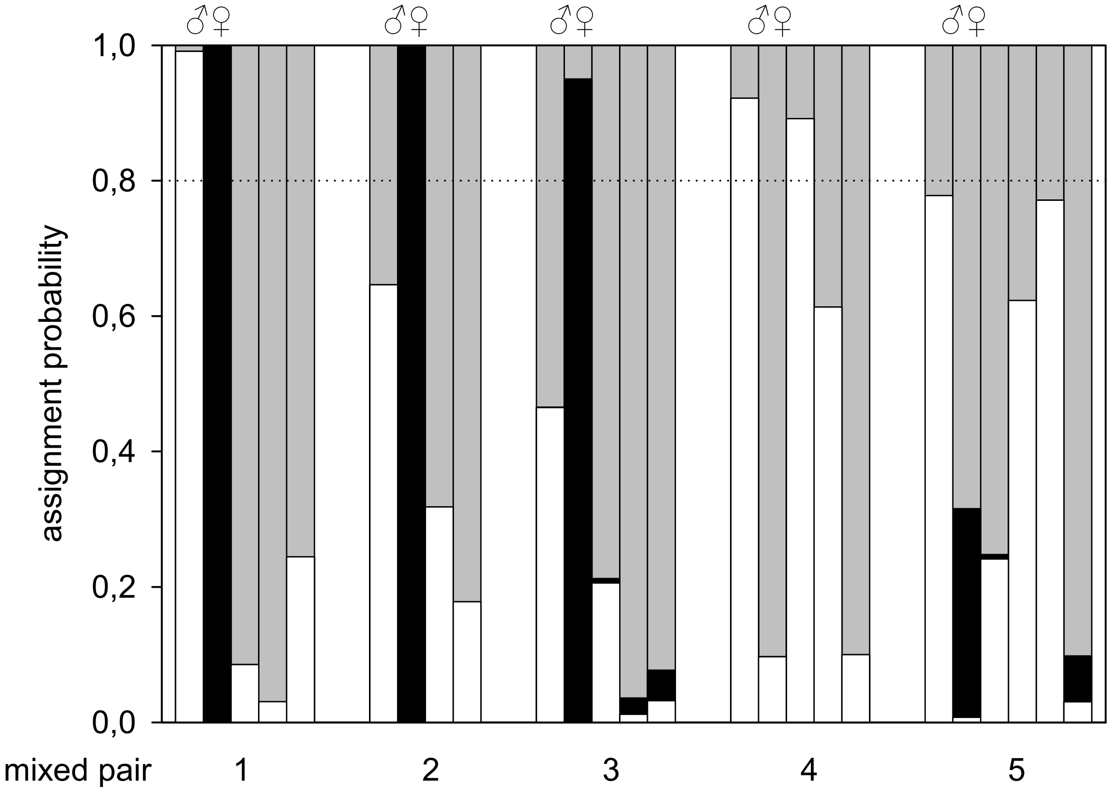


figure 2

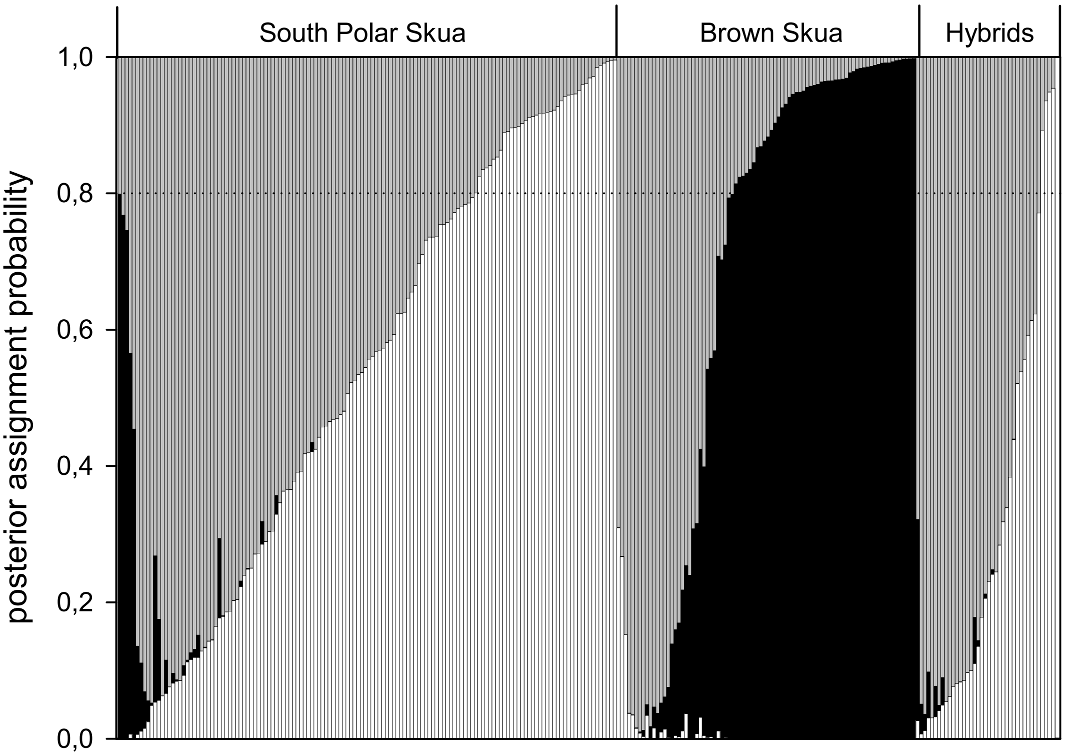

South Polar Skua
Brown Skua
Hybrids
posterior assignment probability
1,0
0,8
0,6
0,4
0,2
0,0

figure 3

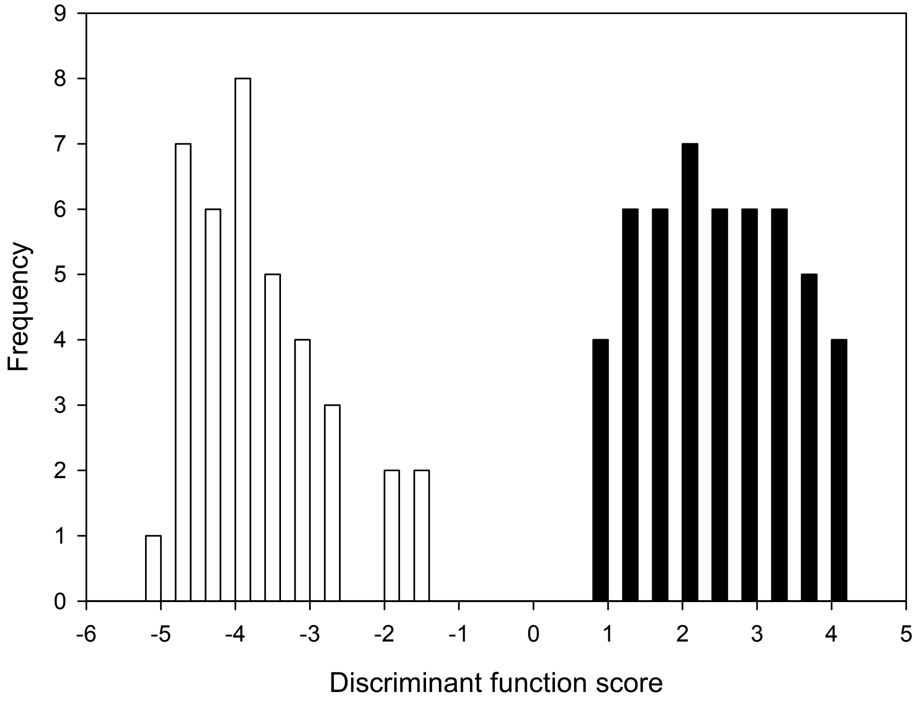
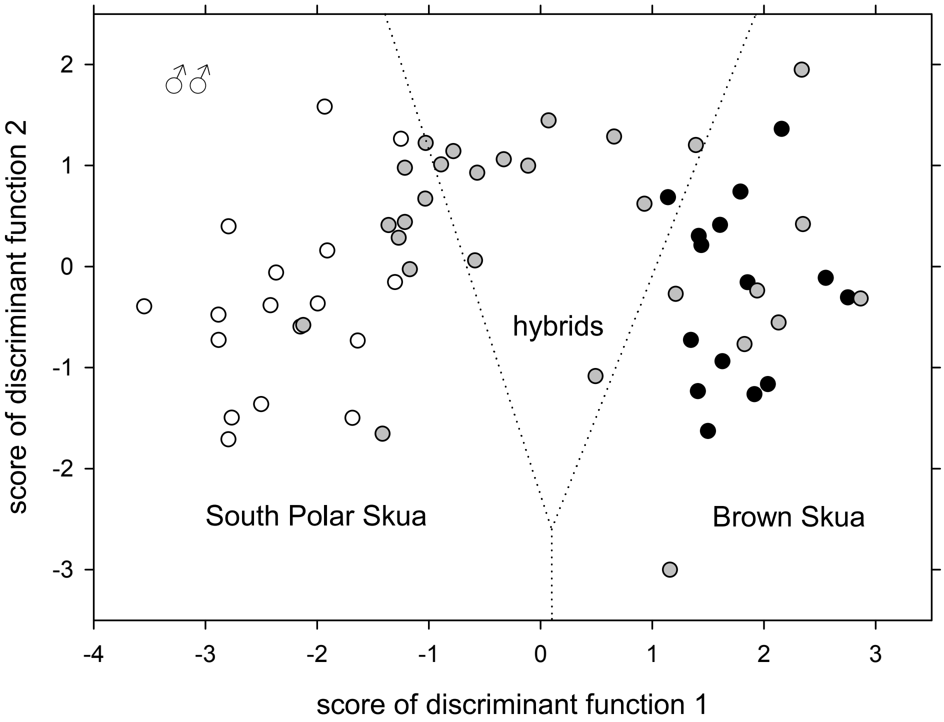

Frequency
9
8
7
6
5
4
3
2
1
0
-6
-5
-4
-3
-2
-1
0
1
2
3
4
5
Discriminant function score

figure 4


♂♂
hybrids
South Polar Skua
Brown Skua
score of discriminant function 2
score of discriminant function 1
2
1
0
-1
-2
-3
-4
-3
-2
-1
0
1
2
3

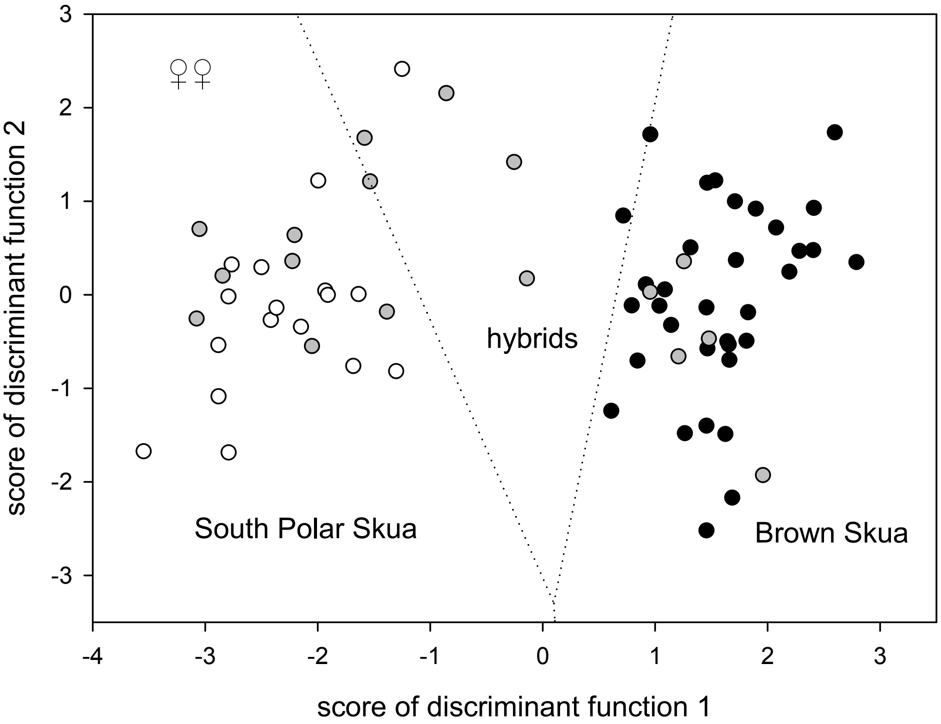

♀♀
hybrids
South Polar Skua
Brown Skua
score of discriminant function 2
score of discriminant function 1
3
2
1
0
-1
-2
-3
-4
-3
-2
-1
0
1
2
3

figure 5

Supplementary material:

Table S1 AFLP primer combinations used to discriminate between skua species and their hybrids. *Eco*RI primer 5'-GAC TGC GTA CCA ATT CNN N-3', *Mse*I primer 5'-GAT GAG TCC TGA GTA ANN N-3'.

Primer combination	*Eco*RI primer (NNN-3')	*Mse*I primer (NNN-3')	Informative loci
C2-C2	CAC	CAG	4
C2-C8	CAC	CTA	5
C3-C8	CAT	CTA	3
C4-C4	CCA	CCA	2
C7-C5	CGC	CCT	7
C7-C8	CGC	CTA	4

Table S2: Unstandardized canonical discriminant function coefficients for discrimination between species and hybrids based on mass (in g) and five morphometric measurements (in mm). An AFLP based genetic assignment with a higher than 0.8 assignment probability in NewHybrids was used as grouping reference.

	Males (N=64)		Females (N=69)	
	Function 1	Function 2	Function 1	Function 2
Mass	0,0033	-0,0057	0,0010	-0,0026
Head	-0,0188	-0,0112	-0,0088	-0,1772
Wing	0,0278	0,1120	0,0242	0,1205
Tarsus	0,1369	0,0726	0,2362	0,1047
Gonys	-0,3789	-0,2502	0,0241	-0,2084
Culmen	0,1104	0,0514	-0,0014	0,0202
Constant	-21,3747	-39,0434	-28,4026	-30,5854

DISCUSSION

Methods

Phylogeographic study (manuscript 1)

To investigate the phylogeography of southern hemisphere skua taxa, the hypervariable region 1 (*HVR I*) of the mitochondrial D-loop was sequenced for 270 individuals representing all five reported southern taxa and spanning the range of the two wider distributed taxa (South Polar Skua, Brown Skua). *HVR I* is known to be very variable and has been shown to evolve more than five times as fast as *cytochrom b* in larids (Liebers and Helbig 2002) and is therefore well suited for phylogenetic studies of recently emerged taxa. The southern hemisphere skua taxa were not resolved in a *cytochrom b + 12S* phylogeny and were supposed to have diverged within the last 500,000 years (Blechschmidt et al. 1993). In line with this, *HVR I* proved to be an adequate marker for this study with enough variation and no signs of saturation (Ritz et al. 2008). It could therefore be used to reveal the phylogeography and population genetic processes of the southern skua taxa.

There are good general reasons to use mitochondrial DNA for phylogeographic studies. It is maternally inherited and free of recombination (but see White et al. 2008). The resulting effective population size (N_e) is therefore four times smaller than for autosomal nuclear DNA with a resulting higher phylogenetic resolution for recent divergence events. The inheritance of mtDNA is also its drawback in phylogenetic studies (Ballard and Whitlock 2004) because the results represent only the female side of evolution. Especially in the case of unidirectional introgression, the evolutionary history of a species may differ from that of mtDNA (Helbig et al. 2001, Bensch et al. 2006). It is therefore advisable also to analyse nuclear markers to get a more complete picture of species' history. However, in practice, about 60% of phylogeographic studies published between 2001 and 2006 relied on mtDNA as the only marker set (Beheregaray 2008). Besides cost considerations for sequencing additional markers, it may often be difficult to find nuclear markers that provide the resolution needed if the patterns of interest involve the recent past. One may then be forced to, for example develop microsatellites for further population genetic analysis. In summary, mtDNA provides valuable information on species' histories but should be supplemented with nuclear marker information. However, most nuclear genes may turn out to evolve too slowly to be informative with respect to the very recent divergence of the southern skua taxa. Microsatellites have unfortunately not yet been developed for skuas. It may be worth trying AFLP as a next (inexpensive) step.

A serious pitfall in phylogenetics is the presence of pseudogenes. Amplification of numts instead of the targeted mitochondrial gene will nearly invariably lead to wrong inferences. Several procedures (long PCR fragment, different primer combinations, CsCl purification) confirmed the mitochondrial origin of the *HVRI* sequences in large gulls (Liebers et al. 2001). Skuas are close relatives of large gulls and it appears unlikely that numts of *HVRI* are present in skuas. Therefore, only the long template protocol was repeated as an assurance against numts in the phylogeographic study. No signs hinting at the presence of numts (e.g. double bands during sequencing, strongly diverged sequences) were encountered during the study.

SNP between South Polar Skua and all other southern skuas (manuscript 2)

Samples used to test for the validity of the difference between South Polar Skua and all other southern hemisphere skuas at base 92 of the mitochondrial *12S* gene derive from the sympatric populations at King George Island. Therefore, the found absence of “C” at this site could, in theory, be the result of unidirectional introgression. Since mitochondrial DNA is maternally inherited and mixed pairs consist nearly always of a male South Polar Skua and a female Brown Skua (Parmelee 1988, Ritz et al. 2006a), F1-hybrids will carry a “T”. However, ten of the eleven selected individuals were genotyped for the informative AFLP loci and revealed an average hybrid probability of 0.10 (maximum 0.27). Therefore, the probability that these ten individuals are all hybrids, rather than South Polar Skuas, is less than 10^{-11}. Similar results were obtained if the morphological measurements of all eleven individuals are used to discriminate between the species and hybrids as described in manuscript 4. The mean probability of the individuals to be hybrids as revealed by the discriminant factor analysis was 0.11 with a maximum of 0.18. In conclusion, the supposed difference at base 92 of *12S* is not a diagnostic marker to distinguish between South Polar Skua and Brown Skua. Since only one South Polar Skua was sequenced for *12S* in the original study of Cohen et al. (1997), it is not clear whether this difference is still an informative SNP for some South Polar Skua populations, a rare point mutation or simply a sequencing/genotyping error. Clearly, single base pair differences are not suitable to distinguish taxa if not tested with many individuals and over the taxa's ranges. Such validations are even more important if the taxa are known to produce viable and fecund hybrids.

Hybrid zone description (manuscript 3)

Description of the hybrid zone relied on published and unpublished population censuses from the Antarctic Peninsula region. Because South Polar Skua and Brown Skua are morphologically similar, a potentially error source is the differing species identification ability of researchers. However, all included censuses were performed by researchers with several seasons worth of experience in Antarctica and can be expected to be accurate. A drawback of the study was the impossibility of identifying hybrids (apart from ringed offspring of mixed pairs) at the time of the study. With the hindsight from the AFLP study (manuscript 4), I can now say that hybrids are frequent in sympatric populations and are more often assigned to South Polar Skua than to Brown Skua in the field. Consequently, the proportion of South Polar Skua pairs in sympatric populations is most likely overestimated. The same holds true for the analysis of body size of breeding skuas at King George Island (figure 2 in manuscript 4). Hybrids could not be excluded and form a significant proportion of the individuals determined as South Polar Skua, and to a smaller extent, as Brown Skua. This blurred the differences between the species and the influence of hybrids on the analysis could be clarified using AFLP markers (manuscript 4).

AFLP hybrid assignment (manuscript 4)

Since the development of amplified fragment length polymorphism (Vos et al. 1995), the method has been shown to provide information on nearly every level of genetic variation, ranging from genera to within population variation and even parentage (Mueller and Wolfenbarger 1999, Questiau et al. 1999). Multiple tests confirmed that AFLP is highly repeatable and superior to various other methods (Lin et al. 1996, Powell et al. 1996, Jones et al. 1997). AFLP can be applied without any knowledge of the taxa's genomic background. Instead, the revealed markers can be assumed to be scattered over the whole genome of the individual. The "tuning" of the method to the resolution needed can be done by adjusting the number of selective primer nucleotides in the second PCR step and by choosing appropriate primer combinations. A disadvantage of AFLP is the markers' dominant nature which does not allow to distinguish between homo- and heterozygotes and require larger sample sizes for population genetic analyses. However, pedigree analysis can identify co-dominant AFLP markers which appear at frequencies of 4-15% (Waugh et al. 1997, Mueller and Wolfenbarger 1999). Further disadvantages are the lack of any sequence and hence functional information on markers and their potential homoplasy. However, although labour intensive, AFLP markers can be sequenced to get a co-dominant SNP or to identify the marker's location in the genome (Bensch et al. 2002a). In summary, AFLP is a fast, inexpensive and reliable method that can be used to answer a wide variety of questions. Despite these advantages, the technique has been neglected among animal scientists in contrast to botanists (Bensch and Akesson 2005).

AFLP was the method of choice to assign skua individuals to species and to identify hybrids in the sympatric populations at King George Island. The skua species were known to be very closely related (Blechschmidt et al. 1993, Cohen et al. 1997) and diagnostic sequence differences were not available. The one base pair difference in *12S* could, in theory, supplement the AFLP analysis but proved to be not valid (Votier et al. 2007).

A critical point is the choice of informative markers. This involves some subjectivity because markers that appear unreliably (i.e. faint bands, too close to another marker) have to be excluded. Furthermore, informative markers have to be selected based on their frequency difference if diagnostic markers are absent. To avoid subjectivity at this screening step, a marker was defined as being informative with respect to species identity if it was present in at least one eights and less than seven eights of the individuals and the frequency difference between species was at least 25%. Still, which individuals should represent the "true species" can be debated. Clearly, individuals from within the hybrid zone should not be the only reference. Even if morphologically distinct, such individuals may contain at least a small fraction of the other species' genome from repeated backcrossing. Comparably, individuals from allopatric populations close to the hybrid zone may be introgressed if gene flow occurs from the hybrid zone outwards or the hybrid zone was not at its current position in former times. On the other hand, individuals from very far away from the hybrid zone may already differ from pure species individuals close to or inside the hybrid zone due to isolation by distance effects. This dilemma is not easily solved. I decided to use an integrated approach with a step wise inclusion of individuals from distant allopatric populations, a population close to the hybrid zone (only for South Polar Skua) and of morphologically extreme individuals from sympatry.

It proved to be surprisingly complicated to extract informative AFLP loci for species discrimination. In fact, not a single diagnostic marker could be found and instead the whole assignment analysis relied on differences in allele frequency between South Polar Skua and Brown Skua. While this data set was sufficient to distinguish species and to identify hybrids it cannot be used to discriminate between various hybrid categories. Such analysis require large amounts of (diagnostic) markers (Boecklen and Howard 1997, Anderson 2008), such are unlikely to be found using AFLP considering that 98 primer combinations were screened already to extract 25 (non-diagnostic) loci. In summary, future studies which aim to identify F2-hybrids and backcrosses will have to identify markers of even higher resolution, like microsatellites and SNPs. However, the developed AFLP method can clearly be used to identify hybrids and thus allows more detailed analysis of hybridisation between South Polar Skua and Brown Skua.

Phylogeography of southern hemisphere skuas

Mitochondrial mutation rate

Timing of events in phylogeny (speciation) and population genetics (divergence, population size changes, range changes) require knowledge on the mutation rate of the marker used to reconstruct the events. Most studies use non-coding genes under the assumption that selection on these genes is absent or at least not changing and the genes evolve according to a "molecular clock". The clock-wise evolution of mitochondrial DNA with a mutation rate of around 2% per million years has been demonstrated in a large variety of organisms. It has been argued that mutation rate depends on body mass and temperature (Gillooly et al. 2005), is not universal among lineages (Pereira and Baker 2006) and real values estimated from fossil or geological calibrations may scatter considerably around this value (Lovette 2004). Even so, the 2%-rule is commonly used for bird studies (Fleischer et al. 1998, García-Moreno 2004). The ratio of *cytochrom b* vs. control region divergence showed large variation in 68 avian species but the control region was the most variable mitochondrial region in most cases (Ruokonen and Kvist 2002). The mutation rate of *HVRI* used for the phylogeographic study of southern skuas was adopted from gulls (*Laridae*) which are close relatives of skuas. Pair-wise comparison of *cytochrom b* and *HVRI* sequences in 63 gulls of the *Larus michahellies-cachinnans* group revealed on average 5.3 times higher divergence rates for *HVRI* (Liebers and Helbig 2002). Such a correlation in skuas is unfortunately impeded by the unresolved phylogenetic position of *C. skua* and *S. pomarinus*. Therefore, I have assumed that the pattern found in large gulls does also apply to skuas. In summary, although molecular clock-based timing estimates are on average good, they should be interpreted with caution if the mutation rate of the gene used cannot be confirmed with sub-fossil material, fossil records or geological events.

Colonisation of the southern hemisphere

Relying on the larid mutation rate, the southern hemisphere was colonised by skuas before around 220,000yBP. Exact dating of this event is difficult because this requires a firm sister taxon of the southern taxa. This in turn is complicated by the enigmatic position of *C. skua* and/or *S. pomarinus* in the skua phylogeny. Both taxa could potentially be sister to the southern skua complex as will be discussed below. However, the most parsimonious colonisation time is shortly before this time from other considerations. Firstly, it appears unlikely that a founder population colonised the southern hemisphere much earlier and did not spread and diverge until ca. 220,000yBP. Although skuas are philopatric (Parmelee and Pietz 1987 for South Polar Skua) they are migratory and flexible, opportunistic predators and should be able to quickly occupy new breeding grounds. This assumption is corroborated by the range expansion of the Great Skua (*C. skua*) towards Spitzbergen and Norway during the last decades (Furness 1987). A range expansion is even more likely if the species can occupy an ecological niche that is not yet filled by another organism. This is the case for skuas at the southern hemisphere, as skuas are sometimes called the ‘birds of prey’ of the southern oceans. Consequently, skuas have nowadays occupied all possible areas around Antarctica including southern South America. Secondly, glaciation history also points at a colonisation timing of 250,000 – 220,000yBP. Large parts of the polar region were covered by ice during this glacial maximum (Oerlemans 2005, Jouzel et al. 2007) and biotopes and species’ ranges were shifted towards the equator. This should have facilitated a ‘jump over the equator’ and subsequent breeding of skuas at the southern hemisphere.

Diversification of the southern skua complex

The southern taxa first diverged into current South Polar Skua and Brown Skua. The South Polar Skua is a homogenous taxon what can be explained by its distribution around continental Antarctica. Although South Polar Skua populations are often isolated from each other by large glaciated, inhabitable areas, especially in East Antarctica, gene flow along the coast occurs regularly. In contrast, the Brown Skua which inhabits sub-antarctic islands is considerably differentiated across its range. The explained fraction of variance between groups in an AMOVA on the *HVRI* data tripled when Brown Skua populations were grouped by ocean basins. Brown Skuas stay south of the equator during migration (Phillips et al. 2007) or winter close to the breeding grounds (Furness 1987, Hemmings 1990) which may limit latitudinal gene flow (Friesen et al. 2007). An alternative hypothesis to a differentiation of the Brown Skua according to ocean basins is a continuous genetic cline over the species' vast range in accordance with an isolation by distance model. Samples from geographically intermediate populations (e.g. South Sandwich Islands, Bouvet Island, Kerguelen Islands and Amsterdam Island) would be needed to resolve this question.

Atlantic Brown Skua populations were the source for founders of the Tristan Skua population. The remote location of the Tristan archipelago on the Atlantic ridge and small population sizes favoured the genetic and morphological differentiation (Swales 1965, Votier et al. 2004) into the current sub-species.

The Tristan Skua is most likely the ancestor of the Chilean Skua and populated South America via a long-distance colonisation event. This finding can be debated because Chilean Skua individuals also share a very common haplotype with Brown Skuas and South Polar Skuas (Ritz et al. 2008 figure 2). In addition, a colonisation of South America from considerably closer sub-antarctic islands (e.g. South Georgia, Signy Island) appears intuitively more likely. However, time to most recent common ancestor (TMRCA) estimates are higher for these two populations than for Tristan Skua and Chilean Skua. The common haplotype can easily be explained by hybridisation between the three taxa whereas the position of Chilean Skua haplotypes at tips of the network and connected to a private Tristan Skua haplotype should more reliably represent the actual colonisation history.

Reconstruction of the colonisation scenario of the Falkland Skua is least reliable. Sample sizes were only five and seven for the South American and Falkland populations, respectively, hindering statistical analyses. Falkland skuas could have emerged from every other southern skua taxon due to the central position of the Falkland Islands in relation to skua taxa ranges. Furthermore, extensive hybridisation with neighbouring taxa may have erased the genetic trace of colonisation and the Falkland Skua could be a 'melting pot' taxon. Additional samples will hopefully allow a more detailed look into the past of the Falkland Skua.

Glaciation and skua diversification

The role of glaciation for skua speciation is compelling because all divergence events fall into the one but last glacial period. The southern skua ancestor most likely colonised Antarctica and sub-antarctic islands during the warm period around 200,000yBP and diverged into South Polar Skua and Brown Skua. With a drop in temperature and increasing ice sheets, these taxa were "pushed off" Antarctica and colonised lower latitude islands and South America. South Polar Skuas most likely survived the glacial in refuges which still provided food (other seabirds and penguins, fish) and ice free ground for nesting.

Speciation mode

The reconstructed modes and patterns of differentiation in the southern skua complex is most consistent with ongoing allopatric speciation. Skuas expanded their ranges and spread around the southern hemisphere. They differentiated when gene flow between populations decreased due to geographical barriers (open water) and high philopatry. However, divergence is not complete with ongoing gene flow between most taxa. Therefore, the final speciation step could theoretically be achieved in sympatry in the future. Though, selection against hybrids seems to be very weak and any further differentiation is more likely to happen under geographic isolation. From the current perspective, further mixing of at least South Polar Skua and Brown Skua due to warming of Antarctica (Vaughan et al. 2003) and a possible expansion of Brown Skuas southwards appears likely.

Educated guesses concerning the skua enigma

An interesting feature in the phylogeographic study was the position of the northern hemisphere skua species in the mitochondrial haplotype network. *C. skua* and *S. pomarinus* haplotypes were eight mutational steps away from the southern skua complex ingroup and connected to New Zealand Brown Skuas (Ritz et al. 2008 figure 2). In contrast, the two jeager species *S. longicaudus* and *S. parasiticus* were 38 steps away and connected to the opposite side of the network. Thirteen more mutational steps would be required to connect all northern hemisphere species. This is also true for the original unresolved (ambiguous) network. Although network rooting is difficult and especially unreliable if outgroups are far away from the ingroup (Castelloe and Templeton 1994, Tarrio et al. 2000, Cassens et al. 2003), this argues for an involvement of the southern hemisphere during evolution of *C. skua* and *S. pomarinus*. A possible scenario might be:

1. Colonisation of the southern hemisphere by a jeager;
2. Shift to the *Catharacta* morphotype in morphology (larger size, brownish plumage) and behaviour (long call complex) in the founder population;
3. Spread and diversification of this morphotype around the southern hemisphere;
4. Re-colonisation of the northern hemisphere with…
5. extensive hybridisation of the *C. skua* ancestor with a jeager in a small founder population.

To me this appears no less likely than the emergence of the *Catharacta* morphotype in the northern hemisphere (via allopatric speciation in a glacial refuge?), colonisation of the southern hemisphere by individuals from this morphotype and hybridisation of *C. skua* with a jeager at the northern hemisphere. A critical point with the second scenario is that hybridisation between *C. skua* and a jeager must have occurred at a rather small population size to result in the fixation of the presently seen genetic and morphological patterns. Such a small (*C. skua*) population would then have given rise to all southern taxa and a new, or at least strongly modified, jeager species at the northern hemisphere. Though not impossible, such would be a rather unique pattern in avian evolution.

However, multiple alternative scenarios do exist (Andersson 1973, Cohen et al. 1997, Braun and Brumfield 1998, Andersson 1999a, Andersson 1999b). All have their pro and cons and with our current knowledge we cannot eliminate any of them. The phylogenetic position of *C. skua* and *S. pomarinus* remains enigmatic and further work on it is highly desirable.

Hybridisation between South Polar Skua and Brown Skua

Hybrid zone characterisation

As earlier mentioned, hybridisation between South Polar Skua and Brown Skua was already recorded at the beginning of the last century (Bennet 1920, Watson 1975) with the start of a more detailed scientific exploration of Antarctica. It appears reasonable to assume that the hybrid zone also existed in the centuries before human influence in Antarctica when seal populations were much higher and formed a reliable food resource for Brown Skuas. This species depends much more on terrestrial food than the South Polar Skua which can also reproduce successfully feeding on marine food (Pietz 1987, Peter et al. 1990, Young 1994, Reinhardt 1997, Phillips et al. 2004). The approximate age of the hybrid zone can only be guessed. The South Polar Skua inhabits continental Antarctica and most likely colonised the area of the Antarctic Peninsula region shortly after the divergence from the Brown Skua (Ritz et al. 2008). Mitochondrial control region data suggest that the two taxa differentiated in allopatry but gene flow between them never (?) completely ceased. Whether historic gene flow occurred via the hybrid zone at the Antarctic Peninsula or via occasional migration between continental Antarctica and sub-antarctic islands can hardly be reconstructed due to minimal intra-specific structure of the South Polar Skua. It is hypothesized that the Brown Skua expanded its range southwards into the Antarctic Peninsula region in the warm period with its Holocene climatic fluctuations (Clapperton 1990) following the last glacial maximum (15,000yBP).

A few breeding pairs of South Polar Skua have been reported at Signy Island in the 1980s (Hemmings 1984), an island approximately 600km north of the species' so far northernmost breeding site at King George Island. Whilst breeding pair numbers have declined since then and the South Polar Skua is again absent from Signy Island in recent years (BAS unpublished data), this episodic range expansion was accompanied by an increase in breeding pair numbers at King George Island (Hahn et al. 2003). Since most of the hybrids are assigned by field workers to South Polar Skua (manuscript 4) this increase could, at least in part, actually be an increase in hybrid numbers. Since 2003, a Brown Skua lives at the British station at Rothera Island 350km south of Anvers Island, the southernmost breeding location of Brown Skuas. Rather than taking this as evidence for a southwards range expansion by the Brown Skua triggered by global warming, this is most likely an artefact of human presence in Antarctica since Brown Skuas are regularly fed by station personal.

In conclusion, the hybrid zone between South Polar Skua and Brown Skua in the Antarctic Peninsula region is a secondary hybrid zone, which is mostly stable but may have changed its dimensions and borders since its emergence in response to range expansions and population size changes of both species.

Preliminary fitness aspects

Although a detailed analysis of hybrid fitness still needs to be done, some aspects are already clear. Haldane's rule (Haldane 1922) does apply to well differentiated species and could not be observed in hybrids between South Polar Skua and Brown Skua. F1-hybrid females are viable, fertile and produce viable offspring. Also, there are no signs for an F2-breakdown, since F1-hybrids identified by the AFLP study reproduced and fledged chicks in our study populations. Hence, based on the current knowledge, skuas do not appear to suffer from fitness loss if mating with heterospecifics or hybrids.

Degree of admixture and direction of introgression

The degree of admixture between South Polar Skua and Brown Skua in the sympatric populations at King George Island was found to be higher than previously assumed. Nearly half of the individuals had a >50% probability of being of hybrid origin (manuscript 4). This argues for a long lasting hybridisation with no severe fitness loss for hybrids. In consequence, nearly all individuals in this population are expected to have at least a small proportion of introgressed genes from the other species. In fact, skuas at King George could be seen as hybrid swarm with pure species individuals still existing but most of the individuals showing various degrees of introgression.

Interestingly, a higher proportion of South Polar Skuas than Brown Skuas was found to actually be of hybrid origin. Species identification during field work was based on plumage and general appearance and it can be hypothesised that genes controlling for these traits are inherited unequally to F1-hybrids or that South Polar Skua alleles are dominant. Since such quantitative traits are most likely under polygenic control, both scenarios appear not very likely. Concerning colouration, darkness of the mantle has been demonstrated to depend on the number of copies of a single gene, *MC1R*, in *Stercorarius parasiticus* (Mundy et al. 2004) but not in *Catharacta* species (Janssen and Mundy 2007). Furthermore, the few birds, whose hybrid origin could be verified by pedigree, were reported to closely resemble Brown Skuas instead of South Polar Skuas (Parmelee 1988). Different hybrid categories could not be distinguished in the present AFLP study and a far more plausible explanation is a higher rate of backcrossing with South Polar Skuas than Brown Skuas. Mixed pairs consist nearly always of a South Polar Skua male and a Brown Skua female (Parmelee 1988, Ritz et al. 2006a) and this unidirectional maternal gene flow from Brown Skua into South Polar Skua was even recovered in populations outside the hybrid zone (Ritz et al. 2008). To also find biased gene flow in nuclear DNA, F1-hybrids of at least one sex would have to mate preferably with South Polar Skua. This hypothesis can now be tested independent from ringing pedigrees with sufficient sample size using the AFLP based assignment.

Mate choice in skuas

The pairing behaviour of hybrids raises questions about mechanisms of mate choice in skuas. Skuas of the genus *Catharacta* are uniformly brownish without conspicuous traits that could signal individual quality, at least from a human perspective. Information on individual quality is therefore likely to be conveyed by behaviour. The most conspicuous behaviour of both skua species is the long call complex – a loud rhythmic sound emission accompanied by raising of the wing and the display of the white wing patch. The long call complex is displayed in situations when individuals interact - during courtship, to greet mates, during fights over food or nesting territories. In Brown Skuas, parameters of the long call were shown to be indices of reproductive success in males but not in females (Janicke et al. 2008). The two species differ in their long calls (Pietz 1985) but it remains to be investigated whether parameters signalling individual quality differ between species. Theoretically, the choosy sex could be confronted with a conflict between choosing a high quality mate and choosing a mate of its own species. This would be the case if call parameters in South Polar Skua males would be similar, or even superior, to parameters of high quality Brown Skua males. The area of the white wing patch has been shown to correlate with bird age up to 12 years in Brown Skuas (Hahn and Peter 2003). Age is correlated with reproductive success (Furness 1984, Hamer and Furness 1991, Forslund and Pärt 1995) but there is considerably residual variation in wing patch size and it appears unlikely that age is the only information emitted via this signal. Hence, the long call complex is most likely involved in mate choice but its potential contribution to the formation of mixed pairs needs further investigation.

Body size or body condition is mostly positively correlated with reproductive success in seabirds (Chastel et al. 1995, Barbraud 2000). It may thus be used by individuals to asses the quality of potential mates. Yet, whilst Parasitic jaegers (*S. parasiticus*) mate assortatively with respect to body size (Catry et al. 1999), such a correlation is absent in Brown and South Polar Skuas (Phillips et al. 2002, own unpublished data). South Polar Skuas are smaller than Brown Skuas and the species can be distinguished based on the combination of several morphometric measurements (Peter et al. 1990, manuscript 4). Therefore, skua individuals could use body size as an index of species identity rather than quality. In agreement with this view, South Polar Skua males in mixed pairs were found to be larger than males in South Polar Skua pairs (Hahn et al. 2003). However, this finding has to be retracted because the AFLP study revealed that the larger size of these individuals was caused by the misidentification of male hybrids as South Polar Skuas.

Since the two skua species separated relatively recently and selection against hybrids appears to be minimal (or zero), pre-zygotic isolating mechanisms may be weak or absent. The observed lower than (under the assumption of random mating) expected frequency of mixed pairs (Parmelee 1988, Ritz et al. 2006a) may then simply be the result of different arrival times at the breeding grounds. Brown Skuas were observed to arrive on average nearly one week ahead of South Polar Skuas in the Palmer station area (Neilson 1983). Protandrous arrival is common in migratory birds (Morbey and Ydenberg 2001) and male South Polar Skuas arrive one week earlier than females (Neilson 1983). As a result, Brown Skua females that are still unpaired at the end of the arrival period may mate with recently arrived South Polar Skua males and ‘make the best of a bad job’. This strategy even works when South Polar Skua females are around because the larger and heavier Brown Skua is dominant in intra-sexual competition.

Further classification of the hybrid zone has to await detailed data on hybrid fitness. At present, the hybrid zone does neither comply to the bounded hybrid superiority hypothesis nor is selection against hybrids detectable. Therefore, the neutral diffusion hypothesis may best describe the investigated skua hybrid zone. Strong barriers to gene flow were not detected between taxa and character clines across the Antarctic Peninsula may be wide compared to the mean dispersal distance. This could be verified by sampling along a transect across the Antarctic Peninsula.

Taxonomic status of southern skuas

Evidence for historical and actual gene flow between all currently recognised southern skua species argues against their classification as species following a strict interpretation of the Biological Species Concept (BSC; Dobzhansky 1937, Mayr 1942). However, a strict interpretation of the BSC in ornithology would deny species status to many well-differentiated groups of taxa (e.g. ducks) as birds loose the ability to produce fertile hybrids comparably late (Price and Bouvier 2002, Lijtmaer et al. 2003). Therefore, the Comprehensive Biological Species Concept (CBSP; Johnson et al. 1999) extends the BSC and allows for gene flow between species as long as the species discreteness is retained. The three southern skua species show differences in plumage, morphology and behaviour and even extensive hybridisation between South Polar Skua and Brown Skua in a limited area compared to both species ranges has not (yet) decreased inter-specific differences.

All described southern taxa deserve to be treated as Evolutionary Significant Units (ESU; Ryder 1986, Crandall et al. 2000). The species and the described sub-species as well are genetically differentiated from each other and show adaptations that are likely to prohibit ecological exchangeability. Whether the genetic differentiation between populations of Brown Skua coincides with significant local adaptations or whether isolation by distance is responsible for the observed pattern, needs further investigation.

Whichever route one wishes to follow, the southern skua taxa are still in an early phase of speciation with obviously limited barriers to gene flow (figure 2). Still, mating is not random in sympatry arguing for some degree of reproductive isolation although the actual pre-zygotic barrier(s) has still to be identified. The absence of intrinsic post-zygotic barriers (Haldane's rule), at least between South Polar Skua and Brown Skua, is in agreement with the recent divergence of southern skuas. Emergence of pre-zygotic barriers usually predates post-zygotic barriers although the relative contribution of both forms to speciation is still debated (Coyne and Orr 2004). Time to reach complete hybrid inviability is especially long in birds compared to other taxonomic groups and realised at a *cytochrom b* sequence divergence greater 10% (Price and Bouvier 2002, Lijtmaer et al. 2003) corresponding to more than 5 my. In contrast, taxa of the southern skua complex do not differ in *cytochrom b* (Cohen et al. 1997, Votier et al. 2007) and diverged less than 200,000 yBP (Ritz et al. 2008).

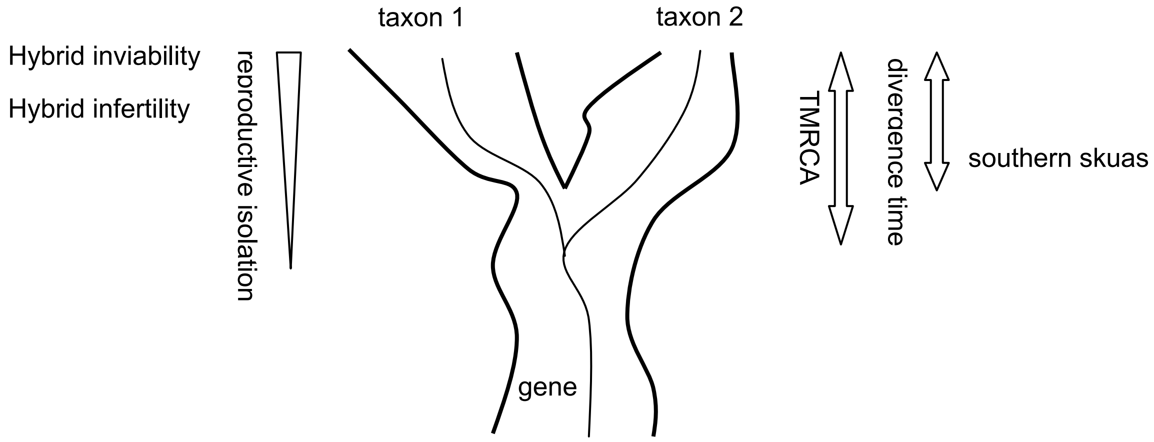


Figure 2: Schematic evolution of two hypothetic taxa and a gene. Breadth of the branches indicates changing effective population size. Divergence estimates, reproductive barriers and

the likely position of southern skuas are indicated. TMRCA = time to most recent common ancestor

OPEN QUESTIONS, ONGOING PROJECTS

Sequencing of *12S* mitochondrial DNA led to a retraction of the first record of a Brown Skua at the northern Atlantic (Votier et al. 2007). Diagnostic differences between the southern taxa were absent in this gene. Although analysis of *HVRI* did also not reveal abundant private haplotypes for South Polar Skua or Brown Skua, some haplotypes were much more frequent in one species than the other (Ritz et al. 2008). Reanalysis of DNA from the mystic birds found in the northern Atlantic for *HVRI* may thus shift evidence towards one species or identify the population of origin at the best.

The most pressing analysis to be performed concerning hybridisation between South Polar Skua and Brown Skua is an evaluation of long-term reproductive success of mixed pairs and hybrids in comparison to pure species pairs. Reproductive success of skuas in Antarctica varies greatly depending on environmental conditions (Ritz et al. 2006a, Hahn et al. 2007). Evaluation of fitness, in terms of reproductive success, will thus have to be done over several seasons to provide reliable estimates. Furthermore, such an evaluation definitely has to consider the high degree of admixture in the sympatric populations at King George Island and find a way to account for the presence of several hybrid categories.

Understanding mate choice in skuas is essential to understand how mixed pairs are formed. Future research may analyse aspects of the long call complex and potentially find its involvement in inter-specific matings. Recording individual arrival times at the breeding grounds over several seasons will possibly show whether arrival is correlated between years and whether Brown Skua females in mixed pairs arrive late.

Mate fidelity could be higher in pure species pairs if mating heterospecifically is a ‘making the best of a bad job’ strategy. Individuals could try to find a mate of their own species and dismiss their mixed pair partner if successful. But divorce induces costs in terms of no reproduction, delayed clutch initiation and lower reproductive success in the season of mate change (Catry et al. 1997).

Because the immune system of species is adapted to the environmental conditions under which the species live, inter-specific hybrids may suffer from a maladaptive intermediate immune system. This can be investigated in chicks of mixed pairs and identified hybrids compared to pure species pairs and adults.

Since South Polar Skuas migrate every winter to the Arctic and Brown Skuas stay south of the equator (Parmelee 1992, Phillips et al. 2007) it is of especial interest to discover where hybrids overwinter. Hybrid birds show intermediate migration behaviour (Helbig 1991) and hybrid skuas could thus be expected to winter in the warm and food poor tropics. After fledging, skuas spend 2-4 years at sea before returning to the breeding grounds. Staying in an unsuitable habitat for such a long time should result in reduced survival until first breeding. Such could be an extrinsic post-zygotic isolation barrier in the absence of strong intrinsic (hybrid inviability or sterility) barriers. However, the migration behaviour of one species may be dominant (Veen et al. 2007) and hybrids may actually show the migration behaviour of South Polar Skuas (Koeppen and Scheil 2001).

SUMMARY

This study investigated the evolution of southern hemisphere skua taxa (*Catharacta* spp.) and revealed the modes and patterns of speciation in this group of seabirds. A hybrid zone between two species was investigated in more detail using AFLP to discriminate between species and their hybrids. This assignment could be used to uncover the degree of admixture and patterns of gene flow between both taxa.

Skuas colonised the southern hemisphere before 220,000yBP, probably around the glaciation maximum at 250,000yBP. Diversification was rapid between 210,000 – 150,000yBP and coincided with a glacial period spanning 230,000 – 150,000yBP. The oldest taxon is most likely the South Polar Skua (*Catharacta maccormicki*), of which the Brown Skua (*C. a. lonnbergi*) split off first. The Tristan Skua (*C. antacrtica hamiltoni*) diverged from Atlantic populations of Brown Skuas and the Chilean Skua (C. *chilensis*) most likely originated from long-distance colonisation by Tristan Skuas to South America. The origin of the Falkland Skua (*C. antarctica antarctica*) is the least well defined of the southern taxa and the taxon may be the result of immigration from surrounding populations of several taxa.

All taxa and many populations were significantly differentiated from each other. The South Polar Skua is the most homogenous taxon, while the Brown Skuas shows strong phylogeographic structure across its circum-Antarctic range. Evidence for gene flow was detected between most neighbouring population pairs of different taxa. This agrees with actual observations of limited hybridisation between Chilean Skua and Falkland Skua, South Polar Skua and Chilean Skua and extensive hybridisation between South Polar Skua and Brown Skua. The southern taxa do not deserve species status after the strict application of the Biological Species Concept but can be treated as species following the Comprehensive Biological Species Concept. Even so, the strong mitochondrial differentiation of the Brown Skua is not reflected by its current taxonomy.

Extensive unidirectional hybridisation between male South Polar Skuas and female Brown Skuas in the Antarctic Peninsula region and subsequent backcrossing of hybrids with presumably preferentially South Polar Skua has led to a high degree of admixture, especially in South Polar Skuas. Hybrids are viable and fertile and Haldane's rule does not apply. Likewise, F1-hybrids reproduce and fledge viable F2-offspring. Selection against

hybridisation appears to be weak or absent but more detailed analyses are needed. The hybrid zone is best explained with the neutral diffusion hypothesis and appears to be relatively stable. The borders and width of the hybrid zone may change quickly as a reaction on climatic conditions or food supply.

As shown, the southern skua complex clearly serves as useful model system for recently diverged taxa with (still) limited barriers to gene flow. Application of the developed AFLP method can be used to get detailed insights into reproductive isolation barriers at this early stage of speciation.

ZUSAMMENFASSUNG

In der vorliegenden Arbeit wurde die Evolution der südlichen Skuas (*Catharacta* spp.) untersucht und die Art und Weise der Besiedlung der Südhalbkugel rekonstruiert. Hybridisierung zwischen zwei der untersuchten Arten konnte durch die Entwicklung einer AFLP-Methode zur Unterscheidung der Arten und ihrer Hybriden detailliert untersucht werden. Dies ermöglichte eine Beschreibung der Stärke der Introgression und des Genflusses zwischen den Arten.

Skuas kolonisierten die Südhalbkugel vor mehr als 220.000 Jahren, wahrscheinlich zur Zeit des Maximums der Vergletscherung um 250.000 Jahren. Die Diversifizierung erfolgte sehr schnell zwischen 210.000 – 150.000 Jahren v.u.Z. und fällt mit einer Eiszeit von 230.000 – 150.000 Jahren v.u.Z. zusammen. Das älteste Taxon ist wahrscheinlich die Südpolarskua (*Catharacta maccormicki*) von welcher sich zuerst die Braune Skua (*C. antarctica lonnbergi*) abspaltete. Die Tristan-Skua (*C. antarctica hamiltoni*) entstand aus Gründern von atlantischen Populationen der Braunen Skua und die Chileskua (*C. chilensis*) geht wahrscheinlich auf eine Weitstrecken-Besiedlung von Südamerika durch Tristan-Skuas zurück. Der Ursprung der Falklandskua (*C. antarctica antarctica*) ist am unsichersten und das Taxon kann das Ergebnis von vielfältiger Immigration von Individuen der umgebenden Populationen verschiedener Taxa sein.

Alle Taxa und viele Populationen sind genetisch signifikant voneinander verschieden. Die Südpolarskua ist das homogenste Taxon während die Braune Skua eine starke phylogeographische Strukturierung über ihr circum-antarktisches Verbreitungsgebiet aufweist. Genfluss konnte zwischen den meisten Nachbarpopulationen verschiedener Taxa nachgewiesen werden. Dieses Ergebnis ist in Übereinstimmung mit Beobachtungen von begrenzter Hybridisierung zwischen Chileskua und Falklandskua, Südpolarskua und Chileskua und intensiver Hybridisierung zwischen Südpolarskua und Brauner Skua. Die südlichen Skuataxa sind bei einer strikten Handhabung des biologischen Artkonzeptes nicht als Arten zu betrachten aber können nach dem „Comprehensive Biological Species Concept“ als Arten eingestuft werden. Die starke mitochondriale Differenzierung der Braunen Skua wird durch die gegenwärtige Systematik nicht widergespiegelt.

Ausgiebige einseitige Hybridisierung zwischen männlichen Südpolarskuas und weiblichen Braunen Skuas und nachfolgende Rückkreuzungen haben im Bereich der Antarktischen Halbinsel zu einer starken Introgression besonders in Südpolarskuas geführt. Hybriden sind lebensfähig und fertil und „Haldane's rule“ ist nicht nachweisbar. Ebenso produzieren F1-Hybriden lebensfähigen F2-Nachwuchs. Selektion gegen Hybridisierung erscheint zu fehlen oder schwach zu sein aber für genaue Aussagen sind weitere Analysen notwendig. Die Hybridzone lässt sich am besten mit der „neutral diffusion hypothesis“ beschreiben und erscheint relativ stabil. Allerdings kann sich die Ausdehnung und Lage der Hybridzone schnell als Reaktion auf klimatische Bedingungen und die Nahrungsverfügbarkeit verändern.

Aufgrund der gezeigten Ergebnisse kann der Komplex der südlichen Skuas als nützliches Modelsystem für die Untersuchung von sehr jungen Arten mit eingeschränkten Barrieren für Genfluss angesehen werden. Die Anwendung der entwickelten AFLP-Methode ermöglicht weitere detaillierte Einblicke in diese frühe Phase der Artbildung.

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CURRICULUM VITAE

Birthday/place: 17.08.1976 in Dresden, Saxony, GDR, married, two daughters
Work address: Institute of Ecology, Friedrich-Schiller University Jena,
Dornburger Str. 159, 07743 Jena, Germany
Private address: Wenigenjenaer Ufer 5, 07749 Jena, Germany
E-mail: markus.ritz@web.de

Education

2006-	Position at the Chair of Genetics at F.-Schiller University Jena, Germany, "Evolution of interacting MADS-box genes"
2003-2008	PhD on "Speciation and hybridisation in skuas (*Catharacta* spp.)" at the Institute of Ecology at F.-Schiller University Jena, Germany
1998-2002	Diplom-Biology course at F.-Schiller University Jena, Germany
1996-1998	Diplom-Biology course at Technical University Dresden, Germany
1995-1996	Civilian service in National Park Saxonian Switzerland, Germany
1991-1995	A-Levels at M.A. Nexö Special Gymnasium Dresden, Germany
1991	O-Levels at A. Saefkow POS Dresden, Germany

Scientific experience

2000-2006	Field work during five austral summers at the South Shetland Islands, Antarctica (Patterns and consequences of hybridisation in skuas)
2005-	Lab manager of the molecular laboratory at the Institute of Ecology, F.-Schiller University Jena
2001	Practical course at MPI Seewiesen, "Behavioural ecophysiology of a phaneropterine bushcricket", supervisor D. v. Helversen
2000	Project (2 months) on invertebrate behavioural ecophysiology at ISU, Normal, Illinois, USA, supervisor S.K. Sakaluk
1999-2000	Project assistance at the Institute of Ecology of the University of Jena (Bird Ecology Group)
1998	Stay (2 weeks) at ringing station Col de Bretole, Switzerland
1998	Project assistance in the limnological institute of TU Dresden
1997	Practical course (4 weeks) at the "Museum der Westlausitz Kamenz", supervisor O. Zinke
1996	Practical course (3 weeks) at the Zoological Museum Dresden, supervisor S. Eck

PUBLICATIONS

Publications in international refereed journals

12. **Ritz, M.S.**, Millar, C., Miller, G.D., Phillips, R.A., Ryan, P., Sternkopf, V., Liebers-Helbig, D. & Peter, H-U. (2008) Phylogeography of the southern skua complex – rapid colonization of the southern hemisphere during a glacial period and reticulate evolution. *Molecular Phylogenetics and Evolution* 49: 292-303

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EHRENWÖRTLICHE ERKLÄRUNG

Hiermit erkläre ich ehrenwörtlich, dass mir die geltende Promotionsordnung der Biologisch-Pharmazeutischen Fakultät der Friedrich-Schiller-Universität Jena bekannt ist und ich die vorliegende Arbeit selbst angefertigt habe. Alle von mir benutzten Hilfsmittel, persönlichen Mitteilungen und Quellen habe ich in meiner Arbeit angegeben. Mein Anteil an den Manuskripten ist den den Manuskripten vorangestellten Erklärungen zu entnehmen. Bei der Auswertung des Materials sowie bei der Herstellung des Manuskriptes haben mich die in den Danksagungen genannten Personen unterstützt. Ferner erkläre ich ehrenwörtlich, für die Anfertigung der Arbeit keinen Promotionsberater in Anspruch genommen zu haben, und dass Dritte weder unmittelbar noch mittelbar geldwerte Leistungen von mir für Arbeiten erhalten haben, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen. Die Dissertation habe ich bisher nicht als Prüfungsarbeit für eine staatliche oder andere wissenschaftliche Prüfung vorgelegt. Auch habe ich weder diese Dissertation noch eine in wesentlichen Teilen ähnliche oder eine andere Abhandlung bei einer anderen Hochschule als Dissertation eingereicht.

Jena, den 3. Dezember 2008

Markus Ritz