

Observations of Heterospecific Courtship Behaviour in an Isolated Population of Ross's Gulls (*Rhodostethia rosea*)

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(Received 13 April 2016; accepted in revised form 27 June 2016)

ABSTRACT. Heterospecific sexual behaviour is notable because it should be strongly deterred by natural and sexual selection. Here we report observations of both male and female Ross's Gulls (*Rhodostethia rosea*) routinely engaging in sexual displays directed towards other species during the breeding season at a small, remote colony in the Canadian High Arctic. We suggest that in small, reproductively isolated populations, directing stereotyped courtship displays towards heterospecific partners may allow individuals to advertise fitness and experience to both male and female conspecifics and also accelerate hormonal development and readiness to mate during the brief and unpredictable High Arctic breeding season.

Key words: Ross's Gull; *Rhodostethia rosea*; courtship; Arctic; isolation; breeding

RÉSUMÉ. Le comportement sexuel hétérospécifique est remarquable, car celui-ci devrait être fortement dissuadé par la sélection naturelle et sexuelle. Ici, nous faisons mention d'observations de mouettes rosées mâles et femelles (*Rhodostethia rosea*) exhibant régulièrement des comportements sexuels envers d'autres espèces pendant la saison de reproduction dans une petite colonie éloignée de l'Extrême-Arctique canadien. Nous suggérons qu'au sein des petites populations reproductivement isolées, le fait d'axer la pariaade stéréotypée sur des partenaires hétérospécifiques pourrait permettre aux individus de faire état de leur forme physique et de leur expérience à leurs congénères mâles et femelles, en plus d'accélérer le développement hormonal et l'état de préparation à l'accouplement pendant la brève saison imprévisible de reproduction dans l'Extrême-Arctique.

Mots clés : mouette rosée; *Rhodostethia rosea*; pariaade; Arctique; isolement; reproduction

Traduit pour la revue *Arctic* par Nicole Giguère.

INTRODUCTION

Heterospecific courtship and mating are expected to be strongly deterred by both natural and sexual selection in free-living populations (Gröning and Hochkirch, 2008), but experiments across various taxa, including insects (Dukas, 2010; Costa-Schmidt and Machado, 2012), fish (Ryan and Wagner, 1987), and birds (Jones and Hunter, 1999), suggest that evolutionary biases in sexual preference can be accidentally or artificially exploited, and the manipulation of ambiguous chemical, morphological, or behavioural triggers can induce heterospecific courtship and even copulation. However, all such studies have either involved experimental modifications of anatomical or behavioural triggers or focused on very closely related species that are arguably still diverging and share a recent ancestral sensitivity to certain sensory triggers. Although heterospecific interactions and displays do occur rarely under incidental or accidental circumstances in natural populations, routine heterospecific courtship displays

unprovoked by ambiguous stimuli have never before been documented in a free-living species.

Here, we report observations of heterospecific courtship behaviour exhibited by Ross's Gulls (*Rhodostethia rosea*, a rare and poorly known Arctic seabird) at a breeding colony in the Canadian High Arctic. Although the local breeding population is very small here (or anywhere in North America; Maftai et al., 2012, 2015), we made extensive behavioural observations of Ross's Gulls to determine and describe the general ethology of this species. Remarkably, we frequently observed both male and female Ross's Gulls performing sexual displays directed towards a number of other species. We hypothesize that the limitations imposed by a brief and unpredictable breeding season at high latitudes may prompt Ross's Gulls in this small and isolated population to engage in heterospecific sexual display as a means of establishing reproductive dominance and advertising fitness and readiness to mate to conspecifics. This behaviour may also serve to accelerate hormonal development in individuals rapidly transitioning into breeding condition.

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METHODS

During the pre-breeding season in 2011–13, we observed Ross's Gulls on Nasaruaalik Island, Nunavut (75°49' N, 96°18' W). This island supports the largest and most stable breeding colony of this species in North America, and together with three nearby islands, comprises the only known breeding area currently used by this species in the Nearctic (Maftei et al., 2012).

We conducted focal observations of Ross's Gulls for a total of 244 h over three years. In 2011, we observed gulls for 125 h—an average of 7 h/day between 6 and 12 June, and thereafter opportunistically for approximately 1.5 h/day until 31 August. In 2012, we observed the gulls for 91 h—averaging 7 h/day between 9 and 15 June, and thereafter approximately 1.5 h/day until 13 August. In 2013, we observed the gulls for 28 h—an average of 3 h/day over nine days between 12 and 24 June. Ross's Gulls first laid eggs on 12 June in 2011 and on 16 June in 2012. In 2013, low temperatures and extensive snowpack prompted Ross's Gulls (and all other larids on Nasaruaalik Island) to defer breeding, although birds remained around the colony and engaged in pair-bonding behavior.

In all three years, we observed a group of 6–12 Ross's Gulls that spent the vast majority of the breeding season in a small polynya off the southern point of Nasaruaalik Island. Virtually the entire polynya and the entire area of the island used by nesting Ross's Gulls were visible from our elevated vantage point at the southern end of the island (Polynya Colada Point). Birds were observed with the naked eye, 8× binoculars, or a 20–60× zoom spotting scope, as conditions dictated.

We recorded three categories of courtship behaviour in all three years of the study: synchronized chase flights, tail displays (tail-raising displays and landing displays), and copulation attempts (key behavioural postures shown in Fig. 1a–f). In 2011 and 2012, we were not able to identify individual birds or quantify observed behaviours on an individual basis, but we recorded the frequencies of particular courtship display behaviours. In 2013, we were able to identify most of the birds present on the island by way of unique colour band combinations, and we conducted detailed observations of individual birds, which were followed during regularly scheduled time periods. Banded birds were sexed through DNA testing, and we were able to determine the sex of all marked individuals retroactively.

All research was conducted after obtaining animal care committee approval for Canadian Wildlife Service Banding Permit number 10694, as well as annual renewals of Canadian Wildlife Service Scientific Permit NUN-SCI-09-01 and Nunavut Wildlife Research License WL2010-042.

RESULTS

In all three years of study, Ross's Gulls arrived on Nasaruaalik Island between 6 and 13 June and were

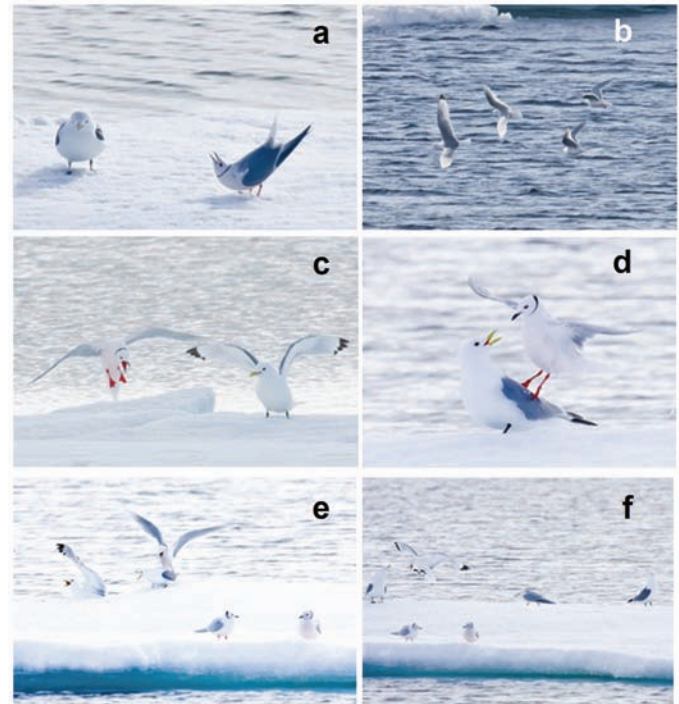


FIG. 1. Photographs of heterospecific courtship behaviours by Ross's Gulls. a) A male Ross's Gull performing a tail-raising display towards a black-legged kittiwake; b) Three male Ross's Gulls pursuing a Black-legged Kittiwake over the polynya off the south point of Nasaruaalik Island; c) A male Ross's Gull performing a landing display beside a Black-legged Kittiwake after engaging in a prolonged synchronized pursuit; d) A male Ross's Gull mounting a Black-legged Kittiwake before attempting to force copulation; e) A male Ross's Gull attempting to force copulation with a Black-legged Kittiwake; f) A male Ross's Gull (rear) defends a Black-legged Kittiwake (right) by charging another kittiwake (in flight) in an aggressive display.

observed displaying to other species immediately upon arrival. During our observation periods, the gulls spent almost all of their time within sight of each other in the restricted area of open water adjacent to the island, an area that rarely exceeded 3 km².

Over the three years, we observed 372 pre-breeding courtship displays performed by Ross's Gulls, 62% of which were directed towards heterospecific partners. These included Glaucous Gulls (*Larus hyperboreus*), Sabine's Gulls (*Xema sabini*), Arctic Terns (*Sterna paradisaea*) and, most commonly, Black-legged Kittiwakes (*Rissa tridactyla*). Chases were the most common displays, followed by ground displays and copulation attempts (Fig. 2). In 2011 and 2012, approximately half of the observed pre-breeding courtship displays were directed towards heterospecifics (51% of 109 displays in 2011; 50% of 113 displays in 2012; Fisher Exact test, $p = 0.69$). In 2013, the proportion was even higher: more than three-quarters of displays (77% of 150; $p < 0.001$) were directed towards heterospecifics.

The suite of sexual displays that Ross's Gulls directed towards other species was also observed directed towards other Ross's Gulls. We frequently observed several Ross's Gulls chasing each other, as well as individuals of other species, in group chases. However, once Ross's Gulls settled into pairs, they no longer participated in or disrupted

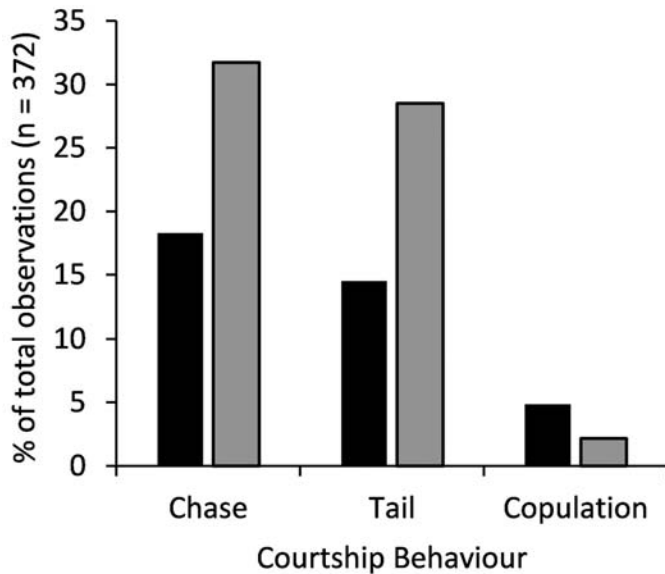


FIG. 2. Percent of total 372 observations for each type of pre-breeding courtship display directed by Ross's Gulls toward their conspecifics (black bars) or other marine bird species (gray bars) over the three-year study period (2011–13).

the displays of unpaired conspecifics, and only rarely were they disturbed by other unpaired individuals, even though they remained close by the polynya for several days until the snow melted enough to make nesting sites accessible. During this period, mated pairs were observed copulating and actively prospecting for nest sites within the colony.

DISCUSSION

At high latitudes, the brief and unpredictable summer places many constraints on the behaviours of Arctic birds and prompts adaptations that effectively compress the breeding cycle (Silverin, 1995; Martin and Wiebe, 2004; Mallory and Forbes, 2007). This is especially true for altricial species such as Ross's Gulls that have a longer developmental period. The rapid establishment or reformation of pair bonds during the pre-breeding season is an important aspect of the breeding cycle for virtually all Arctic nesting species. Because of the narrow window in which incubation and chick-rearing must take place, pre-breeding displays and other pair formation activities at breeding sites are constrained to the brief period between first arrival at breeding sites and the earliest time that egg-laying is possible (Hahn et al., 1995).

Many typical elements of courtship in monogamous species, such as the establishment and defense of desirable nesting territories by males, are impractical during the High Arctic spring, when nesting sites are covered in snow and highly localized access to food concentrates individuals of both sexes into indefensible neutral territories. This situation results in (and even places an emphasis on) courtship displays that are better indications of individual fitness rather than about the relative quality of nesting territories

(Lanctot and Weatherhead, 1997; Lanctot et al., 1998; Lovvorn et al., 2012; Vézina et al., 2012). The limited availability of mates in small and highly isolated populations would also negate many of the advantages conferred by experience and dominance if males dispersed to display on territories across a wide area where female encounter rates would be minimal. For most High Arctic breeding seabirds, limited access to open water in the early spring restricts individuals to relatively isolated areas of foraging habitat within recurring polynyas or leads (Stirling, 1997; Maftai et al., 2015). By congregating at a resource-rich site during the pre-breeding season, both males and females can also maximize their chances of encountering potential mates. Congregation during the pre-breeding season may actually allow more experienced birds to pair with a mate and initiate breeding faster despite the presence of competitors nearby (Jehl, 2006).

Ross's Gulls engage in extensive and highly stereotyped courtship behavior, which can be interpreted as conspicuous and costly displays of fitness directed towards conspecifics of both sexes. Although the primary function of sexual courtship is to advertise fitness to prospective mates (Andersson, 1994), conspicuous displays can also serve to establish a dominance hierarchy among individuals of the same sex (Mateos and Carranza, 1999; Parker and Ligon, 2002; Vergara and Martinez-Padilla, 2012). In this context, courtship behaviours directed towards unsuitable mates (such as heterospecific partners) may still increase the quality or quantity of an individual's mating opportunities by reducing subsequent intrasexual conflict once a suitable mate is attracted. Male-male forced copulation, for example, has been well documented in several monogamous Arctic birds, including Common Murres (*Uria aalge*) (Birkhead et al., 1985) and Ivory Gulls (Mallory et al., 2008; Kylin, 2011), and it has been correlated with increased extra-pair copulations in dominant males in at least one species, the Razorbill (*Alca torda*) (Wagner, 1992, 1996). We speculate that the heterospecific courtship displays of Ross's Gulls may also function to help establish dominance hierarchies, but additional data on marked birds are clearly required to address this possibility.

Another theory, not mutually exclusive with advertising fitness, could explain the heterospecific displays we observed in Ross's Gulls: individuals arriving at breeding sites with very limited time in which to attract and secure a mate and initiate breeding may benefit from accelerating their hormonal development through behavioral stimulation. Since both males and females rely on hormonal changes to reach a state of breeding readiness (Ball and Balthazart, 2009), engaging in courtship displays as a means of triggering or elevating such readiness could be advantageous for both sexes even in the pre-breeding season, particularly under ecological constraints that favour the shortest possible gap between pair-bonding and egg-laying (Hahn et al., 1995; Wingfield and Silverin, 2009). Such a hormonal priming mechanism has been reported in Spectacled Eiders (*Somateria fischeri*) (Lovvorn et al.,

2012), which also make a very rapid transition into breeding condition in a harsh and unpredictable Arctic climate. A lack of conspecific partners at small, High Arctic Ross's Gull breeding colonies would make heterospecific or even homosexual partners a serviceable alternative for individuals of both sexes priming themselves for breeding. The type of behaviour observed in Spectacled Eiders, in which the primary motivation appears to be self-stimulation as opposed to partner attraction (Lovvorn et al., 2012), is similar to that which we observed in Ross's Gulls, in that individual birds appear to perform sexual displays directed towards multiple, apparently random partners.

We caution that empirical testing of any hypothesis explaining the behaviors observed is hampered by the limited sample of birds present, as well as the tendency of this species to defer breeding regularly (Maftei, 2014). While a similar number of individuals (6–12) have been present on Nasaruaalik Island in each of our study years (2007–14), observations of colour-banded individuals revealed a pattern of irregular annual attendance at the colony. Regional surveys (Maftei et al., 2012, 2015) indicated that the total population of Ross's Gulls in Queens Channel is likely fewer than 30 individuals. Moreover, we recognize that at least some of our observations represent replicates of the same individuals (i.e., all data were pooled). However, we were consistently able to observe multiple individuals simultaneously, and the tendency of Ross's Gulls to remain within a very restricted area around the polynya during the pre-breeding season when observations were conducted permitted us to follow most if not all of the birds present at the colony daily in each year. Thus, while we are unable to analyze the frequency of particular displays for each individual present, we are confident that our pooled data accurately reflect the general behavior within this population over all three years of study. In the case of the Ross's Gulls on Nasaruaalik Island, a small breeding population could limit opportunities to display solely to conspecifics but the presence of suitable heterospecific partners such as Black-legged Kittiwakes may prompt and sustain this highly unusual strategy. Interestingly, Ross's Gulls have also been reported displaying to Bonaparte's Gulls (*Chroicocephalus philadelphia*) and Black-headed Gulls (*C. ridibundus*) (Densley, 1999) in the Palearctic, at locations remote from polynyas (but possibly still very limited in available breeding habitats and partners). These reports suggest that the heterospecific displays we observed were not isolated or extraordinary, but may be part of the regular breeding behaviour of this species.

ACKNOWLEDGEMENTS

We thank T. Sailor and I. Pratte for their assistance in conducting observations. We also thank the Canadian Wildlife Service (Environment and Climate Change Canada), the Canadian Wildlife Federation, the Polar Continental Shelf Program (Natural Resources Canada), the Northern Scientific

Training Program (Aboriginal Affairs and Northern Development Canada), and Canada Goose, Inc. for providing financial and logistical support for this research. Reviews from E. Miller, V. Johnston, I. Jones, C. Walsh, and an anonymous reviewer greatly improved the manuscript.

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