

Why do afternoon copulations mainly occur after the egg-laying peak date in a colony of Great Skuas on Skúvoy, Faroe Islands?

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(Med et dansk resumé: Hvorfor parrer Storkjoverne på Skúvoy, Færøerne, sig om eftermiddagen længe efter at æglægningen har kulmineret?)

Abstract In Great Skuas *Stercorarius skua*, copulations are often preceded by courtship feeding and occur in the morning and afternoon. We surveyed copulations in a colony of Great Skuas on Skúvoy, Faroe Islands during afternoons throughout the breeding season of 2013. The afternoon copulation frequency peaked 2.5 weeks after the peak in laying dates. This is unexpected because literature suggests that a pair copulates most frequently around a week before egg laying. As we were not able to link each copulation to a specific pair, several explanations are possible. First, if these afternoon copulations were pre-laying copulations, they were presumably mostly performed by pairs laying late in the season. A possible mechanism could be that young pairs and fish-eating pairs, which breed later in the season, make longer foraging trips and therefore feed their mate, and thus copulate, later in the day. These copulations may also reflect an increased copulation rate of young pairs, to strengthen the pair bond or compensate for low copulation success. Alternatively, if these copulations were post-laying copulations, they may be a response to mate feeding that continues during the incubation phase, and may strengthen the pair bond. We argue that potential individual and population differences should be taken into account when describing copulation behaviour at the species level.

Introduction

Copulations in birds serve to fertilise eggs and for the male to assure his paternity, but may also have other functions, such as strengthening the pair bond and 'rewarding' a food-provisioning mate, so that it will continue to bring food to the partner and eventually to chicks (Birkhead & Møller 1992). Copulation behaviour varies greatly among bird species. Hence, large variation exists in the number of copulations made per pair per clutch (ranging from just one to several hundreds), in the seasonal timing of the start of copulations (ranging from

over a month to several days before egg laying), and in the diurnal timing of copulations (rates peaking in the morning and/or evening, or no clear peak; Birkhead *et al.* 1987, Birkhead & Møller 1992). To what extent these characteristics vary within species has been little investigated (but see Petrie & Hunter 1993 for theoretical work). However, it is important to understand intraspecific variation in the rate and seasonal and diurnal timing of within-pair copulations (1) to allow us to validate whether the sample of populations or individuals used to characterise copulation behaviour of the species is

representative for the species, and (2) to give insight into possible intraspecific constraints to reproduction induced by copulation behaviour.

A way to explore whether all pairs in a population have a similar diurnal timing of copulations is to look at variation over the course of the breeding season. Birds of different age, quality, breeding experience, diet, or habitat, generally differ in egg laying date (Drent & Daan 1980). The Great Skua *Stercorarius skua*, a colonial predatory seabird, exhibits large variation in both laying date (1-1.5 months; Furness 1987) and diurnal timing of copulations. Catry & Furness (1997) surveyed copulations in the morning and early afternoon (P. Catry pers. com.), but copulations may also occur in the evening (this study). Copulations often follow food delivery by the male to the female after the male returns from a foraging trip (Perdeck 1960, Andersson 1976, see also Methods). The copulation rate is relatively high, at around 35 copulations per clutch, with a daily maximum per female of around 2.5 (Catry & Furness 1997, although Birkhead *et al.* 1987 report even 5-10).

Experienced breeding pairs in territories copulate more frequently than immature pairs on a club site (Glutz von Blotzheim & Bauer 1982). A pair may start copulating as early as one month before egg laying, while copulation rates peak 5-12 days before egg laying and thus already drop before eggs are laid (Catry & Furness 1997). After egg laying, the copulation rate is thought to be very low, at least in the mornings and early afternoons (P. Catry pers. com.). Because the male leaves the colony daily to forage for the pair during the pre-laying and incubation periods (Furness 1987), there is much opportunity for extra-pair copulations, but these rarely occur and make up only one percent of the total number of copulations (Catry & Furness 1997).

If all Great Skua pairs in a population behave according to the pattern described above, we would expect that the copulation frequency in the population peaks 5-12 days before the peak in egg laying date, both for copulations in the morning and in the afternoon. To test this prediction, we recorded afternoon copulations in a colony of breeding Great Skuas on the Faroe Islands throughout a breeding season. Originally, our fieldwork was designed to study feeding and breeding ecology (see Hammer 2017 and Methods) and the copulations were recorded as a side-activity.

Methods

The study was conducted in the Faroe Islands, on the island of Skúvoy (61°45'N, 6°48'W). On Skúvoy, the Great Skua has increased from 40-45 pairs in 1961 (Joensen 1963), 65 pairs in 2001 (Olsen 2003) to approximately

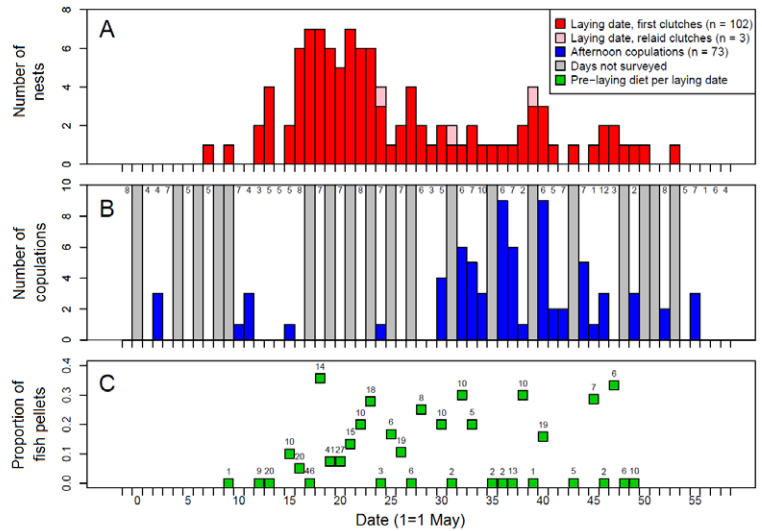
150 pairs in 2012 (Hammer 2017). For our study, we visited only the southwestern part of the island, i.e. Bergið, a sloping grass and peatland area of 0.6 km² where around 100 pairs of Great Skua breed annually (105 pairs in 2013).

From 29 April to 27 June 2013, the colony was visited on 41 days. On the other 19 days the colony was not surveyed because we were active elsewhere, or because very rainy weather prevented work in the colony due to the risk of egg chilling. We visited the colony in the late morning, afternoon, and evening, but not during the night or early morning. We spent on average 05:38 hours (\pm SD 02:14) in the colony per day from on average 14:09 to 19:47 (range 10:30 to 22:50). The time we spent in the colony per day was not biased over the season (linear regression model, $F(1,38) = 0.362$, $p = 0.8$). We collected data on copulation frequencies (see details below) throughout our presence in the colony. However, our main activities were monitoring territories, conducting a supplementary feeding experiment, following breeding phenology and success, ringing adults and chicks, and collecting pellets and prey remains (Hammer *et al.* 2015, Hammer 2017). For these activities, we visited the colony in the afternoons, because that is when more pairs are fully present in their territories. In the feeding experiment during the pre-laying month we supplemented every second pair with 200 g cat food on every second day, plus a chicken egg along with the first supplementation (Hammer 2017). The food was placed on a territory mound, the roosting place, and corresponded to 7.5% of the daily intake of a pair. The food was eaten quickly by the pairs, but also by other skuas that invaded the territories (up to 20 skuas at a time). No effect of supplementary feeding on egg volume or laying date was found (Hammer 2017), nor did we see copulations following the supplementary feeding, or regurgitation of our food by the male to the female. We therefore think that our experiment did not interfere with the natural copulation behaviour.

Pairs were mapped from spring arrival onwards, and nests were located by searching the territories of the pairs regularly (once every one to three days) and observing the colony from a high vantage point on a nearby hillside. Egg laying date was determined when the first egg appeared (when checked daily) or, if hatched, by subtracting 29 days from the hatching date (Perry 1948, Glutz von Blotzheim & Bauer 1982) or, in all other cases, calculated from a quadratic regression of egg density against incubation time, derived from eggs with known hatching date (Hammer 2017).

During these activities we were able to observe many copulations, as the far-reaching and distinctive sound of the male's copulation call alerted us to them.

Fig. 1. Distribution of egg laying dates (A) and observed afternoon copulations (B) in the Great Skua colony in Bergið, Skúvoy, in the 2013 season, and the pre-laying diet (C) of pairs starting egg laying at a certain date. For the latter, we divided the number of regurgitated pellets consisting of only fish remains by the total number of prey remains found at these territories. Numbers in B indicate number of hours surveyed per day; numbers in C are numbers of prey remains examined. *Fordeling af datoer for æglægning (A) og eftermiddagsparring (B) hos storkjove i Bergið på Skúvoy i ynglesæsonen 2013, og før-æglægningens kosten (C) for de par, hvor vi kender æglægningens dato. For de sidstnævnte dividerede vi det antal gylpbolde, der indeholdt fisk, med det totale antal gylpbolde, som blev fundet ved hvert territorie. Tallene i B indikerer timer, som kolonien blev observeret pr. dag, og C er antallet af gylpbolde, som blev undersøgt.*



At closer range, the female could also be heard to utter soft purring sounds. This call is used by the female to beg the male for food after a foraging flight by the male and stimulates the male during copulation (Perdeck 1960, Andersson 1976). According to Perdeck (1960) copulations are always preceded by the male's copulation call, but only 32.6% of the copulation calls are followed by a copulation. However, Perdeck's (1960) study was performed at a club site (a place where immature non-breeding individuals reside) and he makes the point that courtship behaviour on a club site differs from that on breeding territories. On breeding territories, the male feeds the begging female more readily, and a copulation always follows once the female has assumed the willing posture, something that happens in only half of the cases on club territories. In our colony we also had the impression that a male's copulation call is almost always followed by a copulation, although we did not record this systematically. A copulation call lasted several tens of seconds to a few minutes before and during a copulation, which allowed us to locate its place in the colony and to confirm that it concerned a pair preparing for or performing a copulation. Linking the copulating pairs to territories proved difficult, as territories were not marked in the field. We restrict our study therefore to the colony level.

The weather in April-June 2013 was quite typical for Faroese spring, with changeable weather and average temperatures from approximately 4.2 °C in April to 9.1 °C in June, with four and two days of freezing tempera-

tures in April and May, respectively (Statistics Faroe Islands 2018). Average wind speed went from 8.7 m/s in April to 6.6 in June, and total precipitation went from 146.5 mm in April to 69.7 mm in June (Statistics Faroe Islands 2018). We think that only severe wind and rain may interfere with the copulation frequency, as the male needs to balance on top of the female. It may also have been more difficult for us to notice a copulation in windy weather because the sound of the calls is carried away. Even though we did see copulations in windy circumstances (with the male jumping on and off the female repeatedly) and also even far across the colony, we probably did not detect all copulations in the whole colony during our visits. Therefore our results are likely to represent only a part of the copulations.

Statistical tests were carried out in R software (R Core Team 2017).

Results

In total, 108 clutches were found in the Bergið colony, of which three were replacement clutches (Fig. 1A). On average, the laying date was 25 May (range 7 May to 22 June; $n = 105$, three cases unknown). A clear peak occurred around 19 May, and a smaller peak around the second week of June. The laying dates were observed directly for six nests, determined from hatching for 94 nests, and from egg density regression for five nests.

The average clutch size was 1.68 (28×1 egg, 80×2 eggs), and before hatching, three nests were depredat-

ed (by other Great Skuas). In all three territories that lost their first clutch, a replacement clutch was produced.

In total, 73 afternoon copulations were recorded, with an average date of 4 June (range 2 May to 24 June, Fig. 1B). A clear peak was found around 6 June, and possibly a smaller peak around the first week of May. Copulations were seen across the whole Bergið colony.

The afternoon copulations occurred significantly later than the egg laying dates in the population (Kruskal-Wallis Rank sum test, $\text{Chi}^2 = 32.2$, $\text{df} = 1$, $p < 0.001$). Before the laying peak, i.e. during 29 April – 19 May, only eight afternoon copulations were noticed in the colony (0.57 per day, 0.11 per hour). After the laying peak, i.e. during 20 May – 27 June, the afternoon copulation rate in the colony was about four times higher, with 65 copulations during 27 days (2.41 per day, 0.42 per hour).

The afternoon copulations were observed from 14:30 to 21:15 and on average at 18:08 (\pm SD 1:35, $n = 69$, four cases unknown; Fig. 2). When modelled as a non-linear regression with a Gaussian curve (function 'nls' in R software), the copulation rate appeared to peak around 18:57 with 0.53 copulations per hour in the colony (Fig. 2).

Discussion

In the Bergið colony, the frequency of afternoon copulations peaked 2.5 weeks later than the frequency of egg laying dates. This is unexpected because the copulation rate of a pair of Great Skua typically peaks 5-12 days be-

fore egg laying, as shown by Catry & Furness (1997) in Shetland.

As we were not able to link each copulation to a specific breeding pair, several explanations for our results are possible. First, we may assume that the observed copulations were pre-laying copulations. In that case, our results suggest that not all pairs are equally likely to copulate in the afternoon; pairs that lay eggs later in the season would copulate more often or be more likely to do so in the afternoons. According to literature from Shetland, younger birds generally breed later in the season (Furness 1987, Catry & Furness 1999), and fish specialists breed later than bird specialists (Votier *et al.* 2004). In Shetland, fish-eating skuas make longer foraging trips (approximately five hours, roaming far out at sea) than bird-eating skuas (approximately two hours, roaming the nearby cliffs; Votier *et al.* 2004). Also, younger skuas spend more time foraging, probably because of lower efficiency (Catry & Furness 1999). As Great Skuas start foraging trips mostly in the early morning (Shetland: Perry 1948 p.123, Votier *et al.* 2004; Faroes: Bayes *et al.* 1964), variation in the duration of foraging trips can cause younger skuas and fish-eating skuas to return to the colony later during the day (i.e. afternoon) than older or bird-eating skuas (i.e. morning) and thus also copulate later on the day. At midday, there is a lull in activity on the territories, even though both partners may be present (Bayes *et al.* 1964).

The above explanation is quite speculative, because it mainly builds on information from Shetland or from decades ago, and the relevance for present-day Faroese skuas is not evident. The only assumption that we can verify is that pairs breeding later in the season have a higher proportion of fish in their pre-laying diet. This was indeed the case in our colony. On 76 out of 105 territories that started egg-laying, we found 383 prey remains (pellets, regurgitated food or plucked birds) in the pre-laying period of each pair. On average, five such remains were found per territory (range 1-20), on average 16 days before egg laying by that territory's pair (range 0-51 days), spanning the period of 21 April to 15 June 2013. Identified fish species in the diet were Norway pout *Trisopterus esmarkii*, blue whiting *Micromesistius poutassou*, haddock *Melanogrammus aeglefinus*, redfish *Sebastes* sp., and mackerel *Scomber scombrus* (see Hammer 2017 for further details). In the later half of the nests (laying date \geq 23. May), the pre-laying diet showed a higher proportion of pellets that consisted of only fish remains (15.5%) than the first half of the nests (6.9%, laying date \leq 22 May, Fig. 1C). Difference tested with a general linear model (GLM) with a binomial error structure: $z = 2.641$, $\text{df} = 381$, $p = 0.008$). Nevertheless, there were also some late territories at which we found no fish pellets.

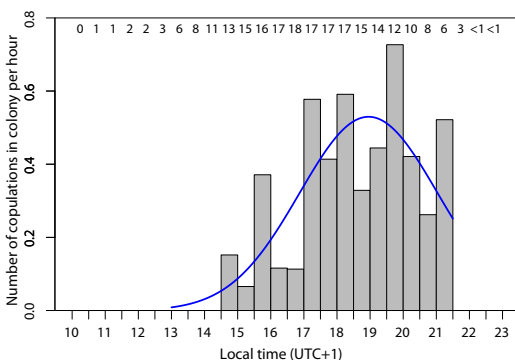


Fig. 2. Diurnal timing of observed afternoon copulations in the Great Skua colony in Bergið, Skúvoy, 2013. Numbers indicate the number of days on which the time slot was surveyed. The blue line indicates the best fit for a Gaussian curve (modelled with 'nls' function in R Software).

Dagrytmen af observerede eftermiddagsparringer for storkjove i Bergið, Skúvoy, i ynglesæsongen 2013. Tallene indikerer antal dage, hvor det angivne tidsrum blev holdt under observation. Den blå linje indikerer en tilpasset Gaussisk-kurve (modelleret med 'nls' funktionen i R programmet).



In a breeding colony of Great Skuas on Skúvoy, the frequency of afternoon copulations peaked 2.5 weeks after the peak in egg laying dates. This pair is displaying after attacking the authors, who were measuring their chick, Bergið, 27 June 2013.

Photo: Kees Schreven.

I storkjovekolonien på Skúvoy er hyppigheden af eftermiddagsparringer på sit højeste 2,5 uger senere end kulminationen på æglægningen. Dette par udfører territorial display efter et angreb på forfatterne, der var i gang med at måle deres unge, Bergið 27. juni 2013.

Alternatively, the occurrence of afternoon copulations may reflect an increased copulation activity of young pairs. Since their relationship has lasted only a short time, young partners may have a higher chance of losing their mate, and can therefore be expected to solicit copulations more often to strengthen the pair bond or because copulations are less successful (Birkhead & Lessels 1988, Petrie & Hunter 1993). However, Glutz von Blotzheim & Bauer (1982) state that young Great Skuas (i.e. on club site territories) copulate less frequently than older birds (i.e. on breeding territories).

Second, we may assume that the observed afternoon copulations were post-laying copulations. Catry & Furness (1997) do not report copulations after egg-laying, but according to P. Catry (pers. com.) they probably hardly occurred at all. Birkhead *et al.* (1987) show for other species (ibises, hawks, rails, gulls, passerines) that post-laying copulations do occur, but up to a maximum of 1–1.5 weeks after laying. The function of post-

laying copulations, if they serve a function at all, may be to strengthen the pair bond, and may occur as a response to mate feeding during incubation. This may stimulate the male to continue bringing food to the female. In Great Skuas, both parents incubate (female 60% of the time), and although the female also makes her own foraging trips when the male is incubating, the male does most of the foraging for the pair (Perry 1948, Furness 1987).

Based on data in Catry & Furness (1997), the 73 copulations observed in this study are a small fraction (9%) of the total number of copulations expected to occur in this colony during our observation time. We think that we indeed missed a fraction of the copulations but also that the copulation rate is lower in the afternoons on Skúvoy than in the mornings and early afternoons in the study by Catry & Furness (1997) in Shetland.

This study of afternoon copulations of Great Skuas on Skúvoy shows that either (1) these copulations have

a different timing in the breeding cycle of a pair than copulations in the morning and early afternoon that are reported from Shetland by Catry & Furness (1997) or (2) are not made by all pairs to the same extent, which may relate to the age, breeding experience, or diet of the pair. It is therefore important to take such potential individual or population differences into account when describing the copulation behaviour of a species.

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Resumé

Hvorfor parrer Storkjoverne på Skúvoy, Færøerne, sig om eftermiddagen længe efter at æglægningen har kulmineret?

Storkjove *Stercorarius skua* 'frier' ofte før selve parringen med mad, og dette sker om morgenen og eftermiddagen. Vi overvågede parringen i en storkjovekoloni på Skúvoy på Færøerne om eftermiddagen i hele ynglesæsonen 2013. Eftermiddagsparringerne toppede 2,5 uger senere end kulminationen af æglægningen i kolonien. Dette gik imod vores forventning, idet literaturen siger, at parringen mest foregår omkring en uge før æglægningen. Da det ikke var muligt i vores studie at forbinde parring til individuelle par, er der flere mulige forklaringer. Den første er, at hvis disse parringen er før-æglægningsparringen, kunne det tyde på, at parringerne hovedsageligt foregik blandt de fugle, der ynglede relativt sent. En mulig mekanisme for dette kunne være, at unge par og fiske-ædende par yngler senere på sæsonen, og fodrer magen (og dermed parrer sig) senere på dagen, da de tager på længere forageringstogter. Parringerne kan også reflektere en højere parringshyppighed blandt yngre par for at styrke parbåndet og kompensere for en lav parringseffektivitet. Alternativt, hvis parringerne foregik efter æglægningen, må det antages, at de tjener en anden funktion end befrugtning af æggene. De kan eventuelt være en respons på den magedodring, som også foregår i rugetiden, og kan styrke et pars sociale bånd. Vi foreslår dermed, at mulige individuelle og populationsforskelle bør tages i betragtning, når man beskriver en arts parringsadfærd.

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