

Rhinoceros Auklet pair-mates migrate independently but synchronize their foraging activity during the pre-laying period

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Pair bonds are considered important for successful breeding in monogamous birds but their maintenance may be challenging for migratory species, as mates can be separated for months during the non-breeding period. To investigate whether mates of monogamous migratory seabirds stay together throughout the non-breeding period and how and when they start synchronizing their activity before breeding, we tracked seven pairs and 22 individuals of Rhinoceros Auklets *Cerorhinca monocerata* with geolocators and saltwater immersion loggers. Mates migrated across similar areas during the non-breeding period but with a sustained temporal shift, putting them an average of 377 km apart and resulting in an average difference of return date at the colony of 5.6 days, with no sex biases. These values did not differ significantly from those between ‘pairs’ of randomly selected, non-mated birds. Mates showed synchronized on-water/in-air at-sea activities once both birds returned and spent the first night together at the colony. The synchronization of activities was highest on the day following the nights when both mates visited the colony, and decreased with elapsed time. Mates then left the colony together for a pre-laying exodus of 8–9 days and males returned 2–4 days earlier than females before incubation started. Mates kept synchronizing at-sea activity during the early part of the exodus. We interpret this as the mates staying together at sea during the pre-laying period, increasing the males’ chances of copulation at sea. The patterns of mate association observed in Rhinoceros Auklets contrast with those of the Procellariiformes, presumably reflecting differences in the place and timing of copulation.

Keywords: alcid, geolocation, migration, monogamy, pair-bond, pre-laying exodus.

In long-lived monogamous bird species, pairs can maintain their bond for several years, which is important for successful breeding (Pyle *et al.* 2001, Sánchez-Macouzet *et al.* 2014). During the breeding season, coordinated activities between mates contribute to the maintenance of pair bonds and thus probably enhance breeding success (Davis 1988, Spoon *et al.* 2006, Mariette & Griffith 2012, Sánchez-Macouzet *et al.* 2014, Fayet *et al.* 2017). In sedentary species, it would be relatively easy to coordinate pair activities from the onset of breeding, as mates can stay together in their local home-ranges during the non-breeding period (e.g.

Newton & Wyllie 1996). Migratory birds move over thousands of kilometres after breeding, potentially becoming widely separated during migration, which would impede early breeding coordination. As the gap between mates’ arrival dates increases, pair bonds are more likely to break and an individual may seek a new partner or delay the onset of breeding (Ollason & Dunnet 1978, Olsson 1998, Gonzáles-Solís *et al.* 1999). Therefore, fine-tuning of the timing of arrival would be key to maintaining pair bonds in migratory species (Gunnarsson *et al.* 2004).

To synchronize the timing of arrival at the breeding site between mates of migratory species, moving together throughout the non-breeding period is one option. This is the case in geese and

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swans, which migrate in family groups (Ens *et al.* 1996, Rees *et al.* 1996), and ducks that mate on the wintering area (Savard 1985, Robertson *et al.* 1998). Surprisingly, in some species, paired birds achieve synchronized arrival at the breeding area even when mates spend the winter hundreds of kilometres apart and do not migrate together (for example, Black-tailed Godwit *Limosa limosa*: Gunnarsson *et al.* 2004). In other species, however, mates do not migrate together and arrive at the breeding site or colony asynchronously (Purple Martin *Progne subis*: Stutchbury *et al.* 2016, Scopoli's Shearwater *Calonectris diomedea*: Müller *et al.* 2015, Rockhopper Penguin *Eudyptes chrysolome*: Thiebot *et al.* 2015), yet in all cases, the mates cooperate to incubate and provision their chicks. How the latter group, which are typically monogamous, restores pair bonds at the onset of the breeding season is still not well understood.

For migratory species, synchronization or coordination of activity between mates after a return to the colony may facilitate their copulation and hence fertilization (Osorio-Beristain & Drummond 1998, Wojczulanis-Jakubas *et al.* 2014). In the Procellariiformes, both mates regularly visit the colony during the pre-laying period but then leave again for a pre-laying exodus that varies among species from a few days to nearly 2 months (Warham 1990). During this exodus, females presumably develop yolk and both sexes accumulate energy reserves needed for the upcoming incubation duties (e.g. Northern Fulmars *Fulmarus glacialis*: Mallory *et al.* 2009). Fertilization possibly occurs a couple of days before egg-laying (Gill 2007) but females of the Procellariiformes can potentially store sperm in storage glands (e.g. Northern Fulmars: Hatch 1983) and so the copulation that results in fertilization could occur before the exodus (Warham 1990). In Common Guillemots *Uria aalge* (Alcidae), females leave the colony within 4 days before egg-laying, but males do not (Birkhead & del Nevo 1987), and the frequency of copulation of a pair at the breeding site increases towards the start of exodus (Birkhead *et al.* 1985). In contrast, copulation takes place at the sea in burrow/crevice-nesting auklets and puffins (Gaston & Jones 1998). Thus, it is important for males of these burrow/crevice-nesting alcids to stay together with their females during the exodus to increase their chances of copulation at sea. Therefore, the frequency of copulation or the probability of effective copulation could vary

during the course of the pre-laying period depending on species. However, little information is available on nest attendance, exodus and opportunities for copulation in burrow/crevice-nesting alcids.

Rhinoceros Auklets *Cerorhinca monocerata* migrate up to 1470 km from the breeding colony (Takahashi *et al.* 2015). Thus, mates may not migrate together and may arrive in the colony asynchronously, but they are known to breed annually and to maintain pair bonds for consecutive years (Richardson 1961). They breed in burrows, forage by pursuit-diving mainly during daytime (Kuroki *et al.* 2003) and visit their colonies only during the night (Gaston & Jones 1998). Data collected by immersion sensors can thus give us information on colony attendance (long dry period during the night), incubation (long dry period during the day and night) and foraging/resting on water (wet) and flying (dry) activities at sea during daytime. Such data would give us an opportunity to analyse the synchronizations of colony attendance and at-sea activities between mates. We first determined whether the mates migrate separately and arrive at the colony asynchronously, as do some other monogamous seabird species (Müller *et al.* 2015, Thiebot *et al.* 2015). We then inspected the nest attendance patterns among males and females to determine synchronization of mates' colony visits, pre-laying exodus and at-sea activities during the period of high potential for effective copulations.

METHODS

Field study

The study was carried out on Teuri Island (44°24'N, 141°17'E), Hokkaido, Japan, in the 2010–2014 breeding seasons. Birds rearing chicks in artificial nest burrows were captured by hand at night and were fitted with a geolocator (MK3006, 14 × 16 × 6 mm, Biotrack Ltd, UK) attached to a plastic leg band with a cable-tie (total mass = 3.5 g). The loggers measure light intensity every minute and record the maximum value every 10 min. They also determine water immersion every 3 s and compile the proportion of immersions every 10 min. Seawater temperature was recorded after 20 min of continuous immersion with 0.5 °C precision. Bird sex was inferred from bill depth and length; the discriminant function correctly identifies 91% of the males and 100% of the females (Niizuma *et al.* 1999).

Of 70 birds captured in their burrows during the chick-rearing period, 48 were recaptured and their loggers retrieved during the incubation period in the following years (Table S1). Twelve loggers failed. Among the remaining 36 birds that gave accurate location data, we collected data from both mates of seven pairs (*true* pairs). The other 22 birds had no surveyed partner with data. Among the 36 birds with accurate location data, two did not have eggs at recapture and in two others, the loggers did not provide reliable activity data. Thus, we analysed nest attendance data for 32 birds. Immersion data at a 10-min interval of one of these 32 birds, however, were unreliable, possibly because foreign matter triggered the immersion sensor erroneously (bird 2011Af, see Fig. S1). Therefore, we excluded this pair from the detailed analysis of at-sea activity synchronization only. To examine whether mates migrated within a close distance, synchronized their timing of migration and synchronized their colony visits and foraging activities at sea after their arrival more than non-mated birds, we compared *true* pairs with all possible combinations of each paired bird and an individual of the opposite sex surveyed in the same year (*'pseudo pairs'*).

The mass of devices attached on legs was 0.62% of the mean body mass of this species (Takahashi *et al.* 2015), lighter than the recommended maximum threshold in albatrosses and petrels (3%, Phillips *et al.* 2003). Individuals of this species carrying geolocators maintained body mass between initial capture and recapture (Takahashi *et al.* 2015).

Location and timing of migration

Estimates of daily location were performed according to Takahashi *et al.* (2015). Sunset and sunrise times were inferred from thresholds in the light curves. Latitude and longitude were then derived from day length and the time of local midday, respectively, and further corrected using remote-sensed sea surface temperature (8-day composite, resolution 9 km, measured by Aqua-MODIS, <https://oceancolor.gsfc.nasa.gov/data/aqua/>) and a Bayesian movement model (R package 'tripEstimation', Sumner *et al.* 2009; R Development Core Team 2015; script in Thiebot & Pinaud 2010), assuming a mean movement speed of 10 km/h over 24 h (Takahashi *et al.* 2015). This movement model calculates the

most probable location estimates along a bird's migration route, using Markov chain Monte Carlo and state-space modelling (Kalman filter). Model settings require that location estimates must (1) not occur on land, (2) start and end at the breeding colony (where the loggers were deployed and retrieved) and (3) conform to the specified animal's speed distribution. Using this model provided a realistic migration track for each of the surveyed birds, bypassing the need for a final subjective step to inspect visually and potentially discard location estimates.

Four timing variables were defined on the basis of the movement and/or activity of each individual outside the breeding period. Chronologically, the first variable was the date of departure from the colony based on immersion records from the loggers. Rhinoceros Auklets generally do not fly continuously for longer than 2.4 h and do not land on the ground in the daytime during the breeding period (Kato *et al.* 2003). Hence the birds were assumed to visit the colony during the night when the loggers had continuous dry records for > 5 h spanning midnight (Takahashi *et al.* 2015). We therefore assumed that a bird started its migration on the day following the last colony attendance at night before winter.

Secondly, during migration at sea, the date of arrival in the wintering area was determined for each individual as the first day when the distance to the colony reached a plateau. This change-point between movement and staging phases was objectively inferred using a 'broken stick' model based on optimized regression and maximum likelihood in R v.3.2.1 software (R Development Core Team 2015) (package 'betareg' package, Cribari-Neto & Zeileis 2010), following the script provided by Thiebot *et al.* (2014).

Thirdly, the date of departure of the bird from the wintering area was inferred using the same 'broken stick' model described above. In that case, the transition between staging and inbound migration movement was determined as the change-point between the plateau and a sharp decrease in the distance of the bird to the colony.

Fourthly, the first night spent ashore by the bird upon its return from the sea (arrival at the colony) was detected using the same approach based on continuous dry records for > 5 h spanning midnight time as for estimation of the departure date.

Colony attendance and synchronization of activity during the pre-laying period

Rhinoceros Auklets arrived at the colony in late February to late March for the pre-laying period, laid eggs in early April to early May, then raised chicks and departed from the colony in mid-July to early August, and spent the non-breeding period until they left the wintering area in mid-February to mid-March (Table S2). Day–night colony attendance was determined by the dry–wet pattern of birds. During the pre-laying period, we defined colony visits when the birds were continuously dry for > 5 h spanning midnight as we did in defining date of arrival at the colony. We estimated that birds started incubation when the logger from either the female or the male remained continuously dry for > 24 h, including daytime, and females laid eggs 1 day before the start of incubation (Table S3). The duration of an incubation stint was 1–4 days as reported (Wilson 1997 cited in Gaston & Jones 1998). We estimated that six females (2010Af, 2010Bf, 2011Af, 2011Bf, 2012Af, 2013Bf) of seven *true* pairs laid eggs at the end of the exodus. One female (2013Af) ended the exodus on 25 April, left the colony the next day and visited the colony with her partner on 26 April, when the male started incubation. We assumed that this female laid the egg on 25 or 26 April. Among these seven *true* pairs, six males and one female (2010Af) took the first incubation shift. Thus, for birds for which data of the partner were not collected, we estimated that the males took the first incubation stint and that the females laid eggs before the start of that stint. Thus, there might be a small inaccuracy (≤ 1 day) in our estimation of egg-laying date for these birds where data of the partner was not collected.

To assess the degree of synchronization in the at-sea activities between mates, we calculated Pearson's correlation coefficient (r) of the percentage of time spent on the water every 10 min between mates each day. The coefficient was greater on days when mates had near-identical timing of emersion/immersion (Fig. S2; see Takahashi *et al.* 2004 also) and was thus used as an index of mates' synchronization of on-water/in-air activities. It could be expected that if the mates did not synchronize their activity but still had the same percentage of time on the water every

10 min throughout the day, the index value would be high as well, especially when the percentage of time on water was large. However, our data revealed that this was not the case, as r did not depend on the male–female mean of percentage of time on water every 10 min (Fig. S3, $r = 0.05$, $n = 145$, NS). We excluded night-time data because the prolonged 'dry' or 'wet' periods measured at night while birds remained in the colony or rested on the water, respectively, would give large r even if mates did not synchronize the timing of on-water/in-air activities every 10 min. We thus calculated r for daytime only. We defined daytime as the period between 05:00 and 18:00 h local time (GMT + 9 h) to keep the sample size the same for each day. This was among the ranges of sunrise (04:46–05:44 h) and sunset (17:44–18:24 h) local times during the pre-laying period (mid-March to mid-April). The analysis was carried out in IGOR PRO v.6.3.7.2 software (1988–2014, Wave Metrics, Inc.).

To examine the factors affecting the synchronization of the on-water/in-air activities between males and females, we separated the pre-laying period into four phases. We defined the first three phases as (1) from the first day when both members of a pair left the wintering area to the first night spent at the colony by both members (*pre-meeting* phase), (2) from the first night spent at the colony by both members to the day when both members left for the exodus (*meeting* phase) and (3) from the day when both members left for the exodus until the night when either member visited the colony (*exodus* phase). We found that the males of all seven *true* pairs returned earlier from the exodus than the females (Tables S2 and S3), so we defined a further phase (4) from the day when males returned from the exodus to the day when females returned (*post-exodus* phase). As we had data of colony visits of all studied birds and had identified the nights when both males and females of *true* or *pseudo* pairs visited the colony on the same night, the phases were defined from the combination of the attendance pattern of each pair using the same criteria for both *true* and *pseudo* pairs. In *pseudo* pairs, some phases often could not be defined (Table S4), for example if one member of a *pseudo* pair returned from the exodus earlier than the start of the exodus of the other member.

Statistical analyses

To reduce the effects of the expected positioning error of geolocators (Phillips *et al.* 2004) on the variability of inter-bird distance calculations, we used the weekly averaged longitudes and latitudes to calculate distances between mates during the non-breeding period (August to March). We then compared distances from males to females between seven *true* and 71 *pseudo* pairs using a linear mixed model (LMM) with pair type (*true* vs. *pseudo*) and week (starting from 1 for 1–7 August) as fixed-effect factors and pair identity as a random-effect factor. Distance was log-transformed to hold normality. As birds were expected to be near the colony at the start and the end of the non-breeding period, and birds might then be close together, we also put week² to examine a non-linear effect. As a maximum of two *true* pairs were available for each year, year effects could not be separated from pair identity effects. Statistical analyses were performed using the *lmer* function of the 'lme4' package in R. Model selection was based on Akaike's information criteria (AIC) or AICc (AIC corrected for small sample size) in the MuMIn package of R. The single top model and multiple top models with ΔAIC or $\Delta\text{AICc} \leq 2.00$ were evaluated as the best model and equally supported models, respectively (Burnham & Anderson 2002).

We examined the sex differences in the dates of departure from the colony, arrival at and departure from the wintering area, and arrival at the colony, using a generalized linear model (GLM) with sex as a fixed-effect factor, using data of 18 males and 14 females. To examine the sex differences in the frequency of colony attendance during *pre-meeting* and *meeting* phases, we calculated the proportion of the number of nights when each bird visited the colony from the number of days from arrival at the colony to the start of the exodus. Absolute differences in these dates between a male and a female in a pair (gaps in days) were compared between seven *true* and 57 *pseudo* pairs using a GLM with pair type (*true* vs. *pseudo*) as a fixed-effect factor. To assess the synchrony of night-time colony visits by mates during the *meeting* phase, we compared the proportion of nights when a male and a female in a pair visited the colony simultaneously to the male–female mean of the number of nights of visits between *true* and *pseudo* pairs.

To examine factors influencing the synchronization of mates' on-water/in-air activities, we used an LMM with pair type (*true* vs. *pseudo*) and pre-laying phase (*pre-meeting*, *meeting*, *exodus* or *post-exodus*) as fixed-effect factors and pair identity as a random-effect factor for six *true* pairs and 52 *pseudo* pairs. In this analysis, we expected that synchronization would be highest immediately after the nights when mates met at the colony and would then decrease with time as the possibility of opportunistic separation increased. We also expected that the synchronization would be high during the day preceding night attendance at the colony because mates would by then have been using similar areas around the colony. Thus, the effects of elapsed time before (NDNB, the number of days before the simultaneous night-time colony visit by a male–female pair) and after the night when mates met at the colony (NDNA, the number of days after the simultaneous night-time colony visit by a male–female pair) were examined. From this analysis, we first examined the effects of pair type and phase, then we separately examined the effects of pair type, phase and NDNB and NDNA on the synchronization of the mates' on-water/in-air activities. The latter analysis was carried out only during the *meeting*, *exodus* and *post-exodus* phases, as, by definition, mates had not yet met at the colony during the *pre-meeting* phase.

For the analysis, we tested the autocorrelation in the percentage of time on water using 2 days of samples from each of the 12 birds of six *true* pairs. We found autocorrelation at the scale of 1–4 steps of 10 min (Fig. S4a). We thus re-sampled 10-min data every 30 min and used these values to calculate the index of synchronization of mates' on-water/in-air activities. Similarly, we found autocorrelation in the daily correlation coefficient values of r (index of synchronization) at around 1–3 steps (days) (Fig. S4b). We thus re-sampled these data every 2 days. There seemed to be a slight inflation of larger values (Pearson's $r > 0.9$) in the distribution of r (Fig. S5). However, the LMM residuals did not seriously deviate from the assumption of normality (Fig. S6).

RESULTS

The birds first migrated north during the non-breeding period, stayed around Sakhalin Island in autumn and then moved to the southern Sea of

Japan, where they spent the winter, before returning to the breeding colony in spring (Fig. 1). During their second survey year at least, all birds of the seven *true* pairs returned to the colony and maintained the same mates.

Non-breeding period

The average distance between mates among the seven pairs was 377 ± 320 km (mean \pm sd, $n = 245$ pair-weeks), whereas that between mates among the 71 *pseudo* pairs was 430 ± 352 km ($n = 2485$ pair-weeks). The best model explaining the inter-bird distances included week and week² as factors, but not pair type (Table 1). The positive parameter estimate for week and the negative parameter estimate for week² suggested that inter-bird distance increased in the early part, was greatest in mid-winter and decreased in the later part of the non-breeding period (Fig. S7).

The sexes did not differ in the timing of migration except that females departed from the wintering area and might arrive at the colony earlier than males. The null model best explained the dates of departure from the colony and arrival in the wintering area, whereas the sex model was the best at explaining departure from the wintering area (Table 2). The null model and the sex model were equally supported to explain the date of arrival at the colony (Table 2).

Nevertheless, substantial absolute differences in their timing of migration were found between

mates when they arrived at the colony. That, however, did not differ between pair types (Table 3). Similarly, the null model was best at explaining the absolute differences in timing between mates in arrival at the wintering area (Table 3). In contrast, the null model and the type model were equally supported to explain the absolute differences in timing between mates in departure from the colony and from the wintering area (Table 3), so mates of *true* pairs may depart from the colony and from the wintering area slightly more synchronously than mates of *pseudo* pairs.

Colony attendance during the pre-laying period

During the time from arrival at the colony to the start of the pre-laying exodus, males and females visited the colony with similar frequencies (Table 2), although a sex difference with males visiting more was not clearly rejected, as the sex model was equally supported. The proportion of nights when both mates visited the colony during the *meeting* phase did not substantially differ between *true* and *pseudo* pairs (Table 3), although a hypothesis that mates of a *true* pair arrived on the same night more than those of a *pseudo* pair was not clearly rejected, as the type model was equally supported. Males and females of *true* pairs started their pre-laying exodus on the same nights (Fig. 2a and 2b, Table S2) with females (absence of 3–17 days from the colony before the start of incubation) and males

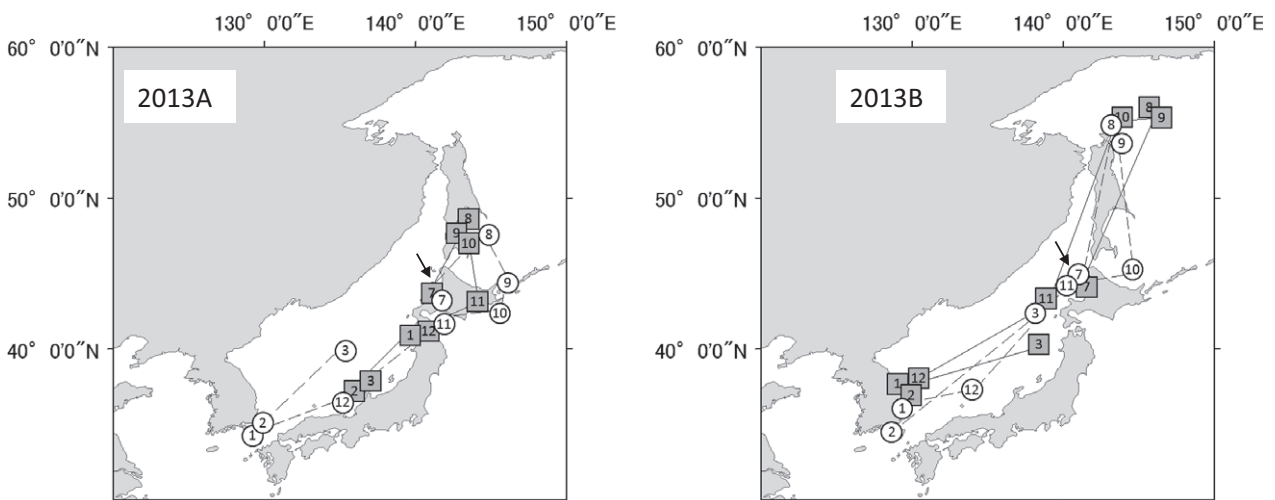


Figure 1. Migration routes of two typical pairs (2013A and 2013B) of Rhinoceros Auklets from Teuri Island (arrow). Symbols indicate monthly ('1'–'12') averaged locations: □ males, ○ females.

Table 1. Factors affecting the distance between weekly averaged positions of mates.

Response variable and factors	Parameter estimate \pm se or variance \pm sd	Models	df	LogLik	AIC	Δ AIC	wi
Week	0.020 \pm 0.003***	Week + Week²	5	-1504.47	3018.9	0	0.925
Week ²	-0.001 \pm 0.000***	Week + Week ² + Type	6	-1506.034	3024.1	5.13	0.071
Random factor	0.019 \pm 0.139	Week + Week ² + Type + Type \times Week	7	-1507.999	3030	11.06	0.004
		Week + Week ² + Type + Week ² \times Type	7	-1512.119	3038.2	19.3	0
		Week ²	4	-1518.481	3045	26.02	0

Pair type (*true* vs. *pseudo*), week (from 1 August), week² and their interactions were explanatory factors, and pair ID was a random factor. A linear mixed model was applied to seven *true* and 71 *pseudo* pairs. Models including all possible combinations of factors and interactions were generated (13 models). Selection of models was carried out based on AIC and the top five models are shown. The best model (Δ AIC \leq 2) is in bold. The parameter estimates \pm se with *** P < 0.001, and the estimated value of variance \pm sd of random intercept (pair ID) of the best models are shown. AIC weights (wi) and log likelihood (LogLik) are shown also.

Table 2. Timing of departure from the colony, arrival at the wintering area, departure from the wintering area and arrival at the colony in males ($n = 18$) and females ($n = 14$) shown as average \pm sd of date (month/day).

Response variables	Males	Females	Parameter estimate \pm se Sex (Male)	Model	df	LogLik	AICc	Δ AICc	wi
Departure from the colony	7/26 \pm 4.3	7/24 \pm 5.6		Null	2	-96.294	197	0	0.764
				Sex	3	-96.249	199.4	2.35	0.236
Arrival at the wintering area	12/11 \pm 10.1	12/10 \pm 12.9		Null	2	-123.379	251.2	0	0.771
				Sex	3	-123.372	253.6	2.43	0.229
Departure from the wintering area	3/2 \pm 11.1	2/22 \pm 10.2	8.341 \pm 3.935*	Sex	3	-121.233	249.3	0	0.733
				Null	2	-123.465	251.3	2.02	0.267
Arrival at the colony	3/18 \pm 7.0	3/16 \pm 5.2		Null	2	-104.872	214.2	0	0.636
			1.603 \pm 2.312	Sex	3	-104.21	215.3	1.12	0.364
Duration of exodus	8.1 \pm 4.1	9.1 \pm 4.0		Null	2	-90.737	185.9	0	0.727
			-1.016 \pm 1.506	Sex	3	-90.497	187.9	1.96	0.273
Proportion of nights when birds visited the colony	0.45 \pm 0.10	0.42 \pm 0.13		Null	2	23.256	-42.1	0	0.731
			0.028 \pm 0.043	Sex	3	23.477	-40.1	2	0.269

Duration of exodus (average \pm sd in days) and the proportion of nights when males and females visited the colony during the period between arrival at the colony and the start of exodus are also shown. Effects of sex were examined using a generalized linear model with sex as the explanatory factor. Selection of models was carried out based on AICc. The best models and equally supported models (Δ AICc \leq 2) are in bold. Parameter estimates \pm se for the best and equally supported models are shown with * P < 0.05.

(absence of 2–17 days) being absent for a similar time (Table 2), although we could not fully reject a sex difference with males making a longer exodus than females, as the sex model was equally supported. In fact, using data of the seven *true* pairs where colony visits were determined in both male and female members, males returned from the exodus to the colony 3.9 ± 1.9 days earlier than females. During this *post-exodus* phase, males visited the colony on $95 \pm 13\%$ ($n = 18$ males) of nights until the start of incubation, while females continued their exodus.

Synchronization of on-water/in-air activity during daytime

Among the models explaining the synchronization of mates' on-water/in-air activities, the best model included pair type, phase and their interaction (Table 4). The correlation coefficients were highest during the *meeting* phase and were significant for *true* pairs only during the *meeting* and *exodus* phases and were never significant for *pseudo* pairs (Fig. 3). In other words, *true* pairs had synchronized on-water/in-air activities only after they had

Table 3. Absolute differences between a male and a female in a pair (gaps in days) in the timing of departure from the colony, arrival at the wintering area, departure from the wintering area and arrival at the colony in *true* pairs ($n = 7$) and *pseudo* pairs ($n = 57$) shown as average \pm sd (days).

Response variables	<i>True</i> pair	<i>Pseudo</i> pair	Parameter estimate \pm se Pair type (<i>True</i>)	Model	df	logLik	AICc	Δ AICc	wi
Departure from the colony	4.1 \pm 4.2	4.8 \pm 3.5	-0.664 \pm 1.438	Null	2	-171.735	347.7	0	0.729
				Type	3	-171.625	349.6	1.98	0.271
Arrival at the wintering area	10.4 \pm 9.0	12.1 \pm 10.6	-5.216 \pm 3.637	Null	2	-240.323	484.8	0	0.735
				Type	3	-240.239	486.9	2.04	0.265
Departure from the wintering area	5.7 \pm 4.1	10.9 \pm 9.5	-0.118 \pm 0.060	Null	2	-232.038	468.3	0	0.514
				Type	3	-230.994	468.4	0.12	0.486
Arrival at the colony	5.6 \pm 4.7	5.2 \pm 4.4	0.118 \pm 0.060	Null	2	-185.41	375	0	0.745
				Type	3	-185.382	377.2	2.15	0.255
Proportion of nights when both males and females visited colony	0.77 \pm 0.18	0.66 \pm 0.15	0.118 \pm 0.060	Type	3	31.168	-55.9	0	0.698
				Null	2	29.223	-54.2	1.68	0.302

The proportion of nights when both males and females visited the colony (no. of nights both visit)/(male–female average of no. of visits) during the *meeting* phase is shown as average \pm sd. Effects of pair type (*true* vs. *pseudo*) were examined using a generalized linear model where pair type was an explanatory factor. Selection of models was carried out based on AICc. The best models and equally supported models (Δ AICc ≤ 2) are in bold. Parameter estimates \pm se of the best or equally supported models are shown.

met at the colony, whereas *pseudo* pairs did not show synchronization at any point.

We further examined the effects of pair type, phase and elapsed time (NDNB and NDNA) on mates' synchronization of on-water/in-air activities. The model including pair type, NDNA, phase, type \times NDNA and type \times phase, and that including type, NDNA and type \times NDNA were equally supported (Table 4). There was no effect of NDNB. The correlation coefficients were higher in *true* pairs and decreased with NDNA but were never significant in *pseudo* pairs, suggesting no synchronized activities in *pseudo* pairs (Fig. 4). The supported models did not include interactions for NDNA and phase (Table 4), indicating that mates' synchronization decreased with NDNA similarly across the *meeting*, *exodus* and *post-exodus* phases.

DISCUSSION

We found that males and females of *true* pairs of Rhinoceros Auklets did not migrate closer to each other and might not arrive at the colony more synchronously than *pseudo* pairs. However, we could not exclude the possibility of slightly higher synchronization for *true* pairs than *pseudo* pairs in departure from the colony and from the wintering area. Moreover, males and females of *true* pairs synchronized on-water/in-air activity at sea more

than *pseudo* pairs once the later-returning bird spent the first night at the colony. This activity synchronization was highest in the day following the nights when both mates visited the colony, and decreased with elapsed time.

Independent migration of mates during the non-breeding period

Among *true* pairs, the inter-mate distance averaged 377 km over the non-breeding period, greater than the assumed accuracy of our geolocator (~ 200 km, Phillips *et al.* 2004), and did not differ from that of *pseudo* pairs. This suggests that Rhinoceros Auklet mates did not migrate closer to each other than non-mated pairs, although more precise measurements of the movements of a larger number of birds would be needed to exclude fully the possibility of flocking effects at sea. It therefore seems that as for other migratory seabirds (Müller *et al.* 2015, Thiebot *et al.* 2015), Rhinoceros Auklet mates become incidentally separated during long periods at sea, as individual birds move over featureless ocean, depending on their own movement timing, body condition, flight performance and genetic characteristics. Our analyses further indicated that inter-mate distance tended to be shorter when mates were approaching the colony at the end of migration. Thus, proximity to the colony might explain the change of inter-pair

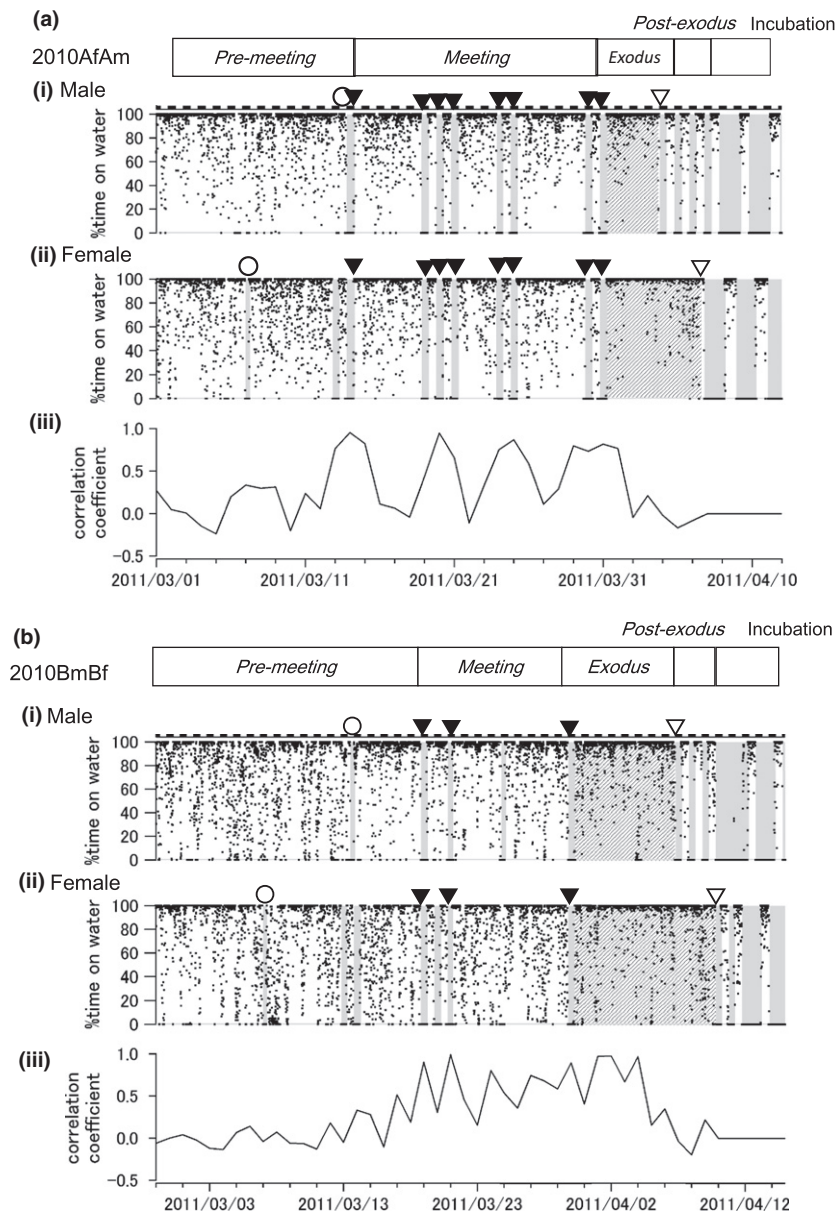


Figure 2. Percentage of time spent on the water every 10 min by (i) male and (ii) female of two Rhinoceros Auklet pairs (a, pair 2010A; b, pair 2010B) between the date of the male's departure from wintering area and early incubation. Night-time is indicated by the short horizontal line at the top of (i). In (i) and (ii), the vertical grey bars show colony attendance of each bird at night, the open circles indicate the night of first arrival at the colony, the closed triangles show the nights when both mates visited the colony simultaneously, and the open triangles indicate the end of exodus. The hatched areas indicate the periods of exodus. In (iii) daily Pearson's r between mates during daytime (index of synchronization of on-water/in-air activities between mates) are shown. Egg-laying probably occurred between the night when females ended exodus and the date when one of the parents began continuous colony attendance during day and night, reflecting incubation. Similar patterns of visits to the colony were observed in the other pairs with some variations (Table S1).

distance across weeks, as well as separation of mates with time.

Males generally arrive at the colony earlier than females in the Procellariiformes (Warham 1990)

and penguins (Warham 1975), and slightly earlier in alcids (Gaston & Jones 1998). However, males did not arrive at the colony earlier than females for Rhinoceros Auklets and the absolute difference

Table 4. Factors affecting the index of synchronization of on-water/in-air activities between mates (Pearson's *r* of percentage of time on water every 10 min each day between mates).

Factors	Parameter estimate \pm se	Models	df	LogLik	AIC	Δ AIC	wi
Effects of pair type and phase (best model)							
Type (<i>True</i>)	0.409 \pm 0.060***	Type + Phase + Type \times Phase	10	-57.45	134.9	0	1
Phase (<i>Pre-meeting</i>)	0.017 \pm 0.032	Type + Phase	7	-72.766	159.5	24.63	0
Phase (<i>Meeting</i>)	0.086 \pm 0.032**	Type	4	-87.253	182.5	47.6	0
Phase (<i>Post-exodus</i>)	0.012 \pm 0.071	Phase	6	-93.614	199.2	64.33	0
Type (<i>True</i>) \times Phase (<i>Pre-meeting</i>)	-0.287 \pm 0.67***	Null	3	-109.764	225.5	90.63	0
Type (<i>True</i>) \times Phase (<i>Meeting</i>)	-0.046 \pm 0.066						
Type (<i>True</i>) \times Phase (<i>Post-exodus</i>)	-0.492 \pm 0.123***						
	0.002 \pm 0.045						
Random factor (Variance \pm sd)							
Effects of pair type, phase and elapsed time (best model)							
Type (<i>True</i>)	0.684 \pm 0.061***	NDNA + Phase + Type + NDNA \times Type + Phase \times Type	10	-113.87	247.7	0	0.669
NDNA	-0.008 \pm 0.002**	NDNA + Type + NDNA \times Type	6	-118.666	249.3	1.59	0.302
Phase (<i>Meeting</i>)	0.064 \pm 0.027*	NDNA + NDNB + Phase + Type + NDNA \times Type + NDNB \times Type + Phase \times Type	12	-115.51	255	7.28	0.018
Phase (<i>Post-exodus</i>)	0.055 \pm 0.052	NDNA + NDNB + Phase + Type + NDNA \times Type + Phase \times Type	11	-117.721	257.4	9.7	0.005
Type (<i>True</i>) \times NDNA	-0.033 \pm 0.006***	NDNA + Phase + Type + NDNA \times Type	8	-121.408	258.8	11.08	0.003
Type (<i>True</i>) \times Phase (<i>Meeting</i>)	-0.158 \pm 0.052**						
Type (<i>True</i>) \times Phase (<i>Post-exodus</i>)	-0.403 \pm 0.092***						
Random factor (variance \pm SD)	0.002 \pm 0.048						
Effects of pair type, phase and elapsed time (2nd best model)							
Type (<i>True</i>)	0.568 \pm 0.039***						
NDNA	-0.010 \pm 0.002***						
Type (<i>True</i>) \times NDNA	-0.039 \pm 0.005***						
Random factor (Variance \pm sd)	0.002 \pm 0.046						

First, the effects of pair type (*true* vs. *pseudo*), phase (*pre-meeting*, period before the night when mates met at the colony; *meeting*, period between first meeting and departure for prolonged trip before egg-laying; *exodus*, period when both males and females were absent for prolonged period before egg-laying; *post-exodus*, period between end of male exodus and end of female exodus) and their interaction (Type \times Phase) were examined. Secondly, the effects of pair type, phase and elapsed time (days) after each night when both mates visited the colony (NDNA) and the elapsed time (days) before that date (NDNB) and their interactions (Type \times NDNA, Type \times NDNB, Phase \times NDNA, Phase \times NDNB) were examined. *Pre-meeting* phase was excluded, as meeting at the colony was not observed during this phase. A linear mixed model was applied to six *true* and 52 *pseudo* pairs. Models including all possible combinations of factors and interactions were generated where Pair ID was a random factor. Five and 72 models were generated for the first test of the effects of pair type and phase and for the second test of the effects of pair type, phase and elapsed time, respectively. Selection of models was carried out based on AIC and the top five models are shown. The best models and equally supported models (Δ AIC \leq 2) are in bold. Parameter estimates \pm sd with ** P < 0.01, *** P < 0.001 and estimated value of variance \pm sd of random intercept (Pair ID) of the best and equally supported models are shown.

in arrival dates between mates did not differ between *true* and *pseudo* pairs. Therefore, mates did not actively synchronize their timing of arrival, which is believed to be important for maintaining pair bonds in other migratory bird species

(Gunnarsson *et al.* 2004). Nevertheless, the absolute differences in the timing of arrival at the colony averaged \leq 6 days, even between individuals of *pseudo* pairs. In other seabird species, when mates' arrival dates differ substantially, pair bonds

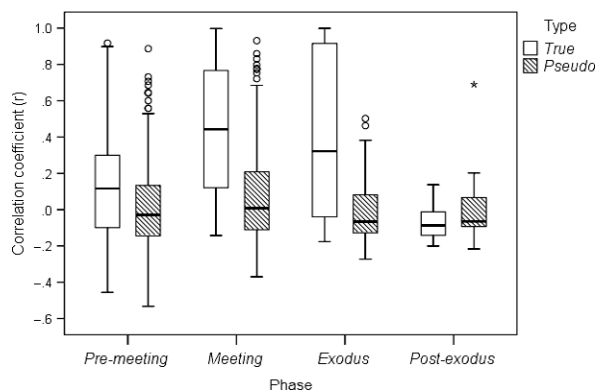


Figure 3. Pearson's r of the percentage of time spent on the water every 10 min each day between mates during the *pre-meeting*, *meeting*, *exodus* and *post-exodus* phases in *true* vs. *pseudo* pairs. Boxes indicate median and 1 exponent and 3 exponent quartiles. Whiskers indicate minimum and maximum values, excluding outliers (O and * are outliers showing values > 1.5 and $> 3.0 \times$ interquartile range, respectively). Values of $r > 0.38$ are significant ($P < 0.05$, $n = 27$).

are more likely to break up and an individual may then seek a new partner (Ollason & Dunnet 1978, Olsson 1998, Gonz  les-Sol  s *et al.* 1999). We suggest that Rhinoceros Auklets adjust their migratory movements to the highly seasonal availability of prey within their migratory ranges (Takahashi *et al.* 2015) and that this could produce relatively high synchronicity of arrival dates within a given year. As all of the *true* pairs maintained their mates during at least two consecutive years, this range of differences in arrival dates between mates appears small enough not to cause divorce in this species. As in many seabird species (Bried & Jouventin 2002), most pairs of Rhinoceros Auklets nest at the same location during successive years (Richardson 1961). Nest-site fidelity also may thus facilitate re-mating even when the partners do not migrate together and do not synchronize their arrival at the colony.

Colony attendance during the pre-laying period

We did not have strong evidence that the proportion of nights when both mates visited the colony during the *meeting* phase was greater for *true* than for *pseudo* pairs. This indicates that mates of *true* pairs did not actively synchronize their visits to the colony even after they first met at the colony. Although the number of birds visiting the colony each night varied greatly, sometimes all our sample birds visited the

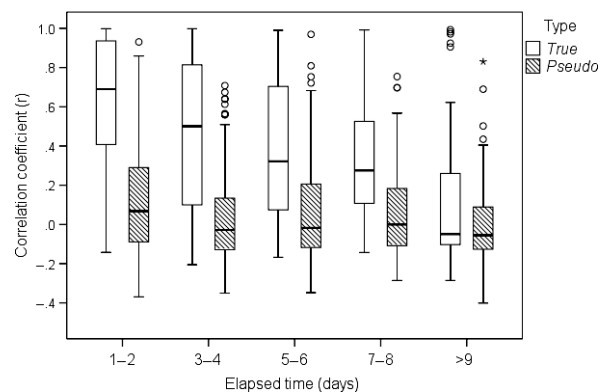


Figure 4. Pearson's r of the percentage of time spent on the water every 10 min each day between mates over the elapsed time since both mates visited the colony, in *true* vs. *pseudo* pairs. Symbols are the same as in Figure 3.

colony on the same night. Thus, colony-wide synchrony of night attendance may occur infrequently. Hence we could not preclude the possibility that colony-wide synchrony of colony visits might result in the synchronous visits by mates.

How mates depart the colony together for the exodus is unclear. As the departure for the exodus ranged over a month within each year, colony-level synchronization of the departure for exodus was unlikely. Another possibility may be that mates copulate in the colony on the night before leaving for the exodus, as in the Procellariiformes (Warham 1990), facilitating synchronous departure for the exodus. However, copulation takes place at sea, in offshore gathering areas, in auklets and puffins (*Aethia* spp., *Cyclorrhynchus* spp., *Fratercula* spp.) (Gaston & Jones 1998). Although the time and place of copulation by Rhinoceros Auklets have not been clearly determined previously, we occasionally observed copulation offshore of Teuri Island in early April (M. Aotuska pers. comm., Y. Watanuki pers. obs.). Therefore, copulation at the nest-site on the night before the exodus is unlikely. The synchronization of departure for the exodus may suggest that either females or males convey signals of undertaking their exodus to their partner when they depart for exodus or when mates are in the colony together the previous night.

Synchronized on-water/in-air activities

Synchronization of the on-water/in-air activities of mates was highest the day following the nights

when both mates visited the colony, and decreased with elapsed time. Meeting at the nest-site during the night might facilitate the synchronization of the on-water/in-air activities between mates at sea the following day.

Rhinoceros Auklets fly when they move substantial distances. Thus, males and females should show high synchronization of on-water/in-air activity if they move together. Therefore, when mates of *true* pairs showed higher synchronization of the on-water/in-air activities compared with *pseudo* pairs, we interpreted this as their being within sight range and moving together or staying in a similar area doing similar activities during the *meeting* phase and possibly the *exodus* phase. If we assume that the synchronization of the on-water/in-air activities indicated proximity between mates, then a change of the degree of the synchronization across phases might be related to the potential for copulation and the need for mate-guarding. Our study females possibly laid their egg soon after they returned from the 9-day exodus. Female alcids take 7–15 days to develop yolk in the ovary fully before ovulating and a further 3–5 days to accumulate albumen and eggshell while the ovum is passing through the oviduct (Astheimer 1986, Birkhead & del Nevo 1987). Therefore, the duration of the exodus in Rhinoceros Auklets seems to be slightly shorter than the period of egg formation. In birds, eggs are generally fertilized while they are in the anterior end of the oviduct (Gill 2007). Thus, in alcids, fertilization might occur 3–5 days before egg-laying. As described above, puffins and auklets copulate at sea, so effective copulation of Rhinoceros Auklets might occur at sea during the *exodus* phase. In effect, the synchronization of on-water/in-air activity seemed to be high for the first 3–4 days of the exodus as well as the *meeting* phase, perhaps as long as the pre-fertilization time window. However, Horned Puffins *Fratercula corniculata*, a species closely related to Rhinoceros Auklets, have sperm storage glands (Hatch 1983), so effective copulation in Rhinoceros Auklets may occur also during the *meeting* phase when the synchronization of on-water/in-air activity was highest.

Whether male alcids guard their mates at sea to prevent extra-pair copulation is unclear. Extra-pair fertilization is not common in alcids (Anker-Nilsen *et al.* 2010), as in other seabird families (Quillfeldt *et al.* 2012), but extra-pair copulation has been observed often in alcids (Birkhead *et al.*

1985, Wojczulanis-Jakubas *et al.* 2014). Thus, there is a potential risk of extra-pair fertilization for males. Males of Rhinoceros Auklets may not know when their mates have started egg development or have already stored sperm. Thus, males would increase their chances of effective copulation by staying close to the females throughout the *meeting* and *exodus* phases. In addition, males might be able to gain information about expected date of egg-laying by staying together with their females throughout the exodus. However, our results do not support the latter interpretation. Mates did not synchronize on-water/in-air activity in the later part of the *exodus* and males returned earlier than females and visited the colony almost every night until females returned and possibly laid eggs. Thus males might not have contact with females in the later part of the exodus even if the female's fertile window may not be closed. Instead, males might prepare to be at the nest almost every night during the *post-exodus* phase in time for the start of incubation.

To conclude, although our sample size was small, this study provides the first description of colony attendance, exodus and mate's synchronization of activities at sea in a burrow/crevice-nesting alcid. Males of shearwaters visit their colonies more often than females before leaving for the exodus (Yamamoto *et al.* 2011, Hedd *et al.* 2014) and use different foraging habitats from females during exodus (Pinet *et al.* 2012, Hedd *et al.* 2014). In contrast, males of Rhinoceros Auklets may not visit the colony more often than females, and mates appeared to stay together at sea in the early part of the exodus. Effective copulation occurs in the colony before the exodus in the Procellariiformes but at sea in puffins and auklets. Thus, for males of Rhinoceros Auklets, staying together with mates at sea might be critical for successful copulation and mate-guarding. Our results suggest that the nest attendance patterns and the proximities of mates might be associated with the site and timing of copulation.

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REFERENCES

- Anker-Nilssen, T., Kleven, O., Aarvak, T. & Lifjeld, J.T. 2010. Low or no occurrence of extra-pair paternity in the Black Guillemot *Cepphus grylle*. *J. Ornithol.* **151**: 247–250.
- Astheimer, L.B. 1986. Egg formation in Cassin's Auklet. *Auk* **103**: 682–693.
- Birkhead, T.R. & del Nevo, A.J. 1987. Egg formation and pre-laying period of the Common Guillemot *Uria aalge*. *J. Zool.* **211**: 83–88.
- Birkhead, T.R., Johnson, S.D. & Nettleship, D.N. 1985. Extra-pair matings and mate guarding in the Common Murre *Uria aalge*. *Anim. Behav.* **33**: 608–619.
- Bried, J. & Jouventin, P. 2002. Site and mate choice in seabirds: an evolutionary approach. In Schreiber, E.A. & Burger, J. (eds) *Biology of Marine Birds*: 264–318. London: Academic Press.
- Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodel Inference: a Practical Information-theoretic Approach*, 2nd edn. New York: Springer.
- Cribari-Neto, L. & Zeileis, A. 2010. Beta regression in R. *J. Stat. Softw.* **34**: 1–24.
- Davis, L.S. 1988. Coordination of incubation routines and mate choice in Adélie Penguins (*Pygoscelis adeliae*). *Auk* **105**: 428–432.
- Ens, B.J., Choudhury, S. & Black, J.M. 1996. Mate fidelity and divorce in monogamous birds. In Black, M.J. (ed.) *Partnerships in Birds*: 44–401. Oxford: Oxford University Press.
- Fayet, A.L., Shoji, A., Freeman, R., Perrins, C.M. & Guilford, T. 2017. Within-pair similarity in migration route and female winter foraging effort predict pair breeding performance in a monogamous seabird. *Mar. Ecol. Prog. Ser.* **569**: 243–252.
- Gaston, A.J. & Jones, I.L. 1998. *The Auks*. New York: Oxford University Press.
- Gill, F.B. 2007. *Ornithology*, 3rd edn. New York: W. H. Freeman and Company.
- González-Solís, J., Becker, P.H. & Wendeln, H. 1999. Divorce and asynchronous arrival in Common Terns, *Sterna hirundo*. *Anim. Behav.* **58**: 1123–1129.
- Gunnarsson, T.G., Gill, J.A., Sigurbjörnsson, T. & Sutherland, W.J. 2004. Pair bonds: arrival synchrony in migratory birds. *Nature* **431**: 646.
- Hatch, S.A. 1983. Mechanism and ecological significance of sperm storage in the Northern Fulmar with reference to its occurrence in other birds. *Auk* **100**: 593–600.
- Hedd, A., Montevecchi, W.A., Phillips, R.A. & Fifield, D.A. 2014. Seasonal sexual segregation by monomorphic Sooty Shearwaters *Puffinus griseus* reflects different reproductive roles during the pre-laying period. *PLoS ONE* **9**: e85572.
- Kato, A., Watanuki, Y. & Naito, Y. 2003. Foraging behaviour of chick-rearing rhinoceros auklets at Teuri Island, Japan, determined by acceleration-depth recording micro data loggers. *J. Avian Biol.* **34**: 282–287.
- Kuroki, M., Kato, A., Watanuki, Y., Niizuma, Y., Takahashi, A. & Naito, Y. 2003. Diving behavior of an epipelagically feeding alcid, the Rhinoceros Auklet (*Cerorhinca monoceratae*). *Can. J. Zool.* **81**: 1249–1256.
- Mallory, M.L., Forbes, M.R., Ankney, C.D. & Alisauskas, R.T. 2009. Nutrient dynamics and constraints on the pre-laying exodus of High Arctic Northern Fulmars. *Aquat. Biol.* **4**: 211–223.
- Mariette, M.M. & Griffith, S.C. 2012. Nest visit synchrony is high and correlates with reproductive success in the wild Zebra Finch *Taeniopygia guttata*. *J. Avian Biol.* **43**: 131–140.
- Müller, M.S., Massa, B., Phillips, R.A. & Dell'Omo, G. 2015. Seabirds mated for life migrate separately to the same places: behavioural coordination or shared proximate causes? *Anim. Behav.* **102**: 267–276.
- Newton, I. & Wyllie, I. 1996. Monogamy in the Sparrowhawk. In Black, M.J. (ed.) *Partnerships in Birds*: 249–267. Oxford: Oxford University Press.
- Niizuma, Y., Takahashi, A., Kuroki, M. & Watanuki, Y. 1999. Sexing by external measurements of adult Rhinoceros Auklets breeding on Teuri Island. *Jpn. J. Ornithol.* **48**: 145–150.
- Ollason, J. & Dunnet, G.M. 1978. Age, experience and other factors affecting the breeding success of the Fulmar, *Fulmarus glacialis*, in Orkney. *J. Anim. Ecol.* **47**: 961–976.
- Olsson, O. 1998. Divorce in King Penguins: asynchrony, expensive fat storing and ideal free mate choice. *Oikos* **83**: 574–581.
- Osorio-Beristain, M. & Drummond, H. 1998. Non-aggressive mate guarding by the Blue-footed Booby: a balance of female and male control. *Behav. Ecol. Sociobiol.* **43**: 307–315.
- Phillips, R.A., Xavier, J.C. & Croxall, J.P. 2003. Effects of satellite transmitters on albatrosses and petrels. *Auk* **120**: 1082–1090.
- Phillips, R.A., Silk, J.R.D., Croxall, J.P., Afanasyev, V. & Briggs, D.R. 2004. Accuracy of geolocation estimates for flying seabirds. *Mar. Ecol. Prog. Ser.* **266**: 265–272.
- Pinet, P., Jaquemet, S., Phillips, R.A. & Le Corre, M. 2012. Sex-specific foraging strategies throughout the breeding season in a tropical, sexually monomorphic small petrel. *Anim. Behav.* **84**: 979–989.
- Pyle, P., Sydeman, W.J. & Hester, M. 2001. Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's Auklets. *J. Anim. Ecol.* **70**: 1088–1097.
- Quillfeldt, P., Masello, J.F. & Segelbacher, G. 2012. Extra-pair paternity in seabirds: a review and case study of Thin-billed Prions *Pachyptila belcheri*. *J. Ornithol.* **153**: 367–373.
- R Development Core Team. 2015. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Rees, E.C., Lievesley, P., Pettifor, A.R. & Perrins, C. 1996. Mate fidelity in swans: an interspecific comparison. In Black, M.J. (ed.) *Partnerships in Birds*: 118–137. Oxford: Oxford University Press.
- Richardson, F. 1961. Breeding biology of the Rhinoceros Auklet on Protection Island, Washington. *Condor* **63**: 456–473.

- Robertson, G.J., Cooke, F., Goudie, R.I. & Boyd, W.S. 1998. The timing of pair formation in Harlequin Ducks. *Condor* **100**: 551–555.
- Sánchez-Macouzet, O., Rodríguez, C. & Drummond, H. 2014. Better stay together: pair duration increases individual fitness independent of age-related variation. *Proc. R. Soc. B* **281**: 20132843.
- Savard, J.P.L. 1985. Evidence of long-term pair bonds in Barrow's Goldeneye (*Bucephala islandica*). *Auk* **102**: 389–391.
- Spoon, T.R., Millam, J.R. & Owings, D.H. 2006. The importance of mate behavioural compatibility in parenting and reproductive success by Cockatiels, *Nymphicus hollandicus*. *Anim. Behav.* **71**: 315–326.
- Stutchbury, B.J., Fraser, K.C., Silverio, C., Kramer, P., Aepli, B., Mickle, N., Pearman, M., Savage, A. & Mejeur, J. 2016. Tracking mated pairs in a long-distant migratory song bird: migration schedule are not synchronized within pairs. *Anim. Behav.* **114**: 63–68.
- Sumner, M.D., Wotherspoon, S.J. & Hindell, M.A. 2009. Bayesian estimation of animal movement from archival and satellite tags. *PLoS ONE* **4**: e7324.
- Takahashi, A., Ito, M., Suzuki, Y., Watanuki, Y., Thiebot, J.B., Yamanoto, T., Iida, T., Trathan, P.N., Niizuma, Y. & Kuwae, T. 2015. Migratory movements of Rhinoceros Auklets in the northwestern Pacific: connecting seasonal productivities. *Mar. Ecol. Prog. Ser.* **525**: 229–243.
- Takahashi, A., Sato, K., Nishikawa, J., Watanuki, Y. & Naito, Y. 2004. Synchronous diving behavior of Adélie Penguins. *J. Ethol.* **22**: 5–11.
- Thiebot, J.B. & Pinaud, D. 2010. Quantitative method to estimate species habitat use from light-based geolocation data. *Endangered Species Res.* **10**: 341–353.
- Thiebot, J.B., Authier, M., Trathan, P.N. & Bost, C.A. 2014. Gentlemen first? 'Broken stick' modelling reveals sex-related homing decision date in migrating seabirds. *J. Zool.* **292**: 25–30.
- Thiebot, J.B., Bost, C.A., Dehnhard, N., Demongin, L., Eens, M., Lepoint, G., Cherel, Y. & Poisbleau, M. 2015. Mates but not sexes differ in migratory niche in a monogamous penguin species. *Biol. Lett.* **11**: 20150429.
- Warham, J. 1975. The Crested Penguins. In Stonehouse, B. (ed.) *The Biology of Penguins*: 189–269. London: Macmillan.
- Warham, J. 1990. *The Petrels: Their Ecology and Breeding Systems*: 440. San Diego: Academic Press.
- Wilson, U.W. 1997. *A study of the biology of the Rhinoceros Auklet on Protection Island, Washington*. Master's thesis, University of Washington, Seattle.
- Wojczulanis-Jakubas, K., Jakubas, D. & Chastel, O. 2014. Different tactics, one goal: initial reproductive investments of male and females in a small Arctic seabird. *Behav. Ecol. Sociobiol.* **68**: 1521–1530.
- Yamamoto, T., Takahashi, A., Oka, N., Iida, T., Katsumata, N., Sato, K. & Trathan, P.N. 2011. Foraging areas of Streaked Shearwaters in relation to seasonal changes in the marine environment of the Northwestern Pacific: inter-colony and sex-related differences. *Mar. Ecol. Prog. Ser.* **424**: 191–204.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Percentage of time spent on the water every 10 min by (a, b) bird 2011Am and (c, d) bird 2011Af, (a, c) between their departure from the colony (2011/7/26) and the start of incubation behaviour the following year (2012/4/16) and (b, d) during the pre-laying period.

Figure S2. (a) Example of synchronized on-water/in-air activities of male and female of a Rhinoceros Auklet pair (2010A) on 20 March 2011 and (b) relationships between the mates in percentage of time on water.

Figure S3. Relationship between percentage of time on water each day (average values of males and females of *true* pairs) and Pearson's correlation coefficient of percentage of time on water between mates of *true* pairs.

Figure S4. (a) Average \pm sd of autocorrelation in percentage of time on water every 10 min during 05:00–18:00 h from 2-day samples of 12 birds (26 bird-days) and (b) average \pm sd of autocorrelation in percentage of time on water between mates of six *true* pairs across days during pre-laying period.

Figure S5. Distribution of the correlation coefficients of percentage of time on water in 10 min every 30 min between mates in each day.

Figure S6. Distribution of residuals of linear mixed model for analysis of the effects of phase and pair type on the index of synchronization of on-water/in-air activities between mates.

Figure S7. Inter-mate distances calculated from the weekly averaged locations from *true* and *pseudo* pairs against number of weeks from 1 August.

Table S1. List of sample birds showing year when geolocators were attached, sex and pair ID.

Table S2. Chronology of events during the non-breeding period (departure from the colony, arrival at the wintering area, departure from the wintering area, and arrival at the colony) and those during the pre-laying period (start and end of exodus, estimated date of egg laying) for each bird.

Table S3. Day–night colony attendance of birds, determined by dry–wet patterns in the data.

Table S4. Differences between males and females in the timing (days) of movements (departure from the colony, arrival at the wintering area, departure from the wintering area, and arrival at the colony) in *true* and *pseudo* pairs.