Breeding behavior and departure decisions of male pectoral sandpipers Calidris melanotos

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Contents

Introduction 2
Materials & Methods 4
  Study species and study site 4
  Catching 4
  Behavioral observation protocol 5
  Tenure 5
  Distance sampling 6
  Density estimation 7
  Statistical analyses 7
    Body weight and tenure 7
    Behavior 8
Results 8
  Movers and residents 8
  Seasonal changes in density and departure times 8
  Body weight 8
  Breeding behavior changes over time 9
  Foraging behavior and the interrelationship with breeding behavior 9
Discussion 12
References 13
Appendix 15

Introduction

Many shorebird species are long-distance migrants (van de Kam et al., 2004). Over the past decade studies have revealed secrets about various aspects of migration in this taxonomic family (e.g.: orientation (Alerstam et al., 2001), departure (Lank, 1989) and physiology (Piersma & Gill, 1998)). Others have linked migration distance to parental care behavior in an attempt to understand the evolution of these two traits in the sub-order Scolopaci (García-Peña et al., 2009; Gibson & Baker, 2012; Reynolds & Székely, 1997). The results of these studies are contradicting and limited in the sense that within species variation in the traits is not possible. For practical reasons, species are divided in discrete categories of traits (e.g. long or short distance migrants and polygamous or socially monogamous mating systems) while in some species multiple mating systems exist. For example, sanderlings *Calidris alba* and Kentish plovers *Charadrius alexandrinus* show multiple mating systems (Székely et al., 2006; Reneerkens et al., 2014;) and we have evidence for large variation in migration distance of pectoral sandpipers *Calidris melanotos* (unpubl. data). Pectoral sandpipers are migratory shorebirds with a polygynous mating system. In polygynous species, postzygotic paternal investment in young is absent (Lesku et al., 2012). Pectoral sandpiper males leave the breeding grounds when females start incubation in July. Breeding grounds are found in a large part of the circumpolar Arctic: from the Taimyr peninsula in Russia to Baffin Island in Canada (Fig. 1, BirdLife International, 2015).

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The mating system is not really a continuum: rather different mating systems (or strategies or tactics) are possible within a species.

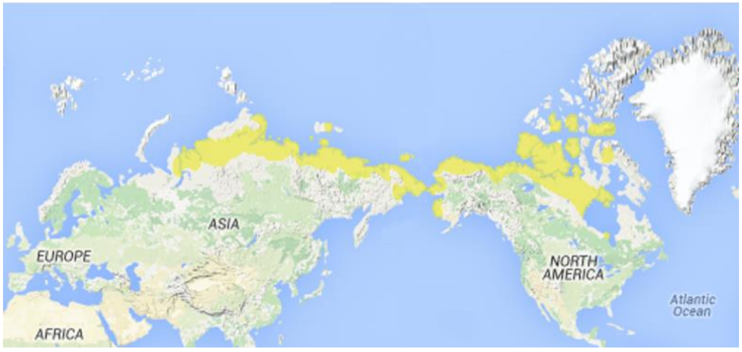

Fig. 1 Map of the breeding distribution of the pectoral sandpiper, indicated by the yellow highlighted areas, actual distribution is patchier than the map indicates. (BirdLife International, 2015).

Roughly in the middle, in Alaska, lays Barrow. During the breeding season, pectoral sandpiper males are highly territorial and are often involved in fierce fights with other males (Holmes & Pitelka, 1998). In the breeding season males have an inflatable throat sac that they use during display flights (Riede et al., 2015). Males perform a range of behaviors towards male and female conspecifics (Holmes & Pitelka, 1998) (as a matter of convenience from now on called: “breeding behavior”). If a male succeeds to obtain a territory, he will try to fertilize as many females as possible. In turn, females are very reluctant to mate and copulations have rarely been observed in the wild, despite around-the-clock observations (Lesku et al., 2012). In multiple years the birds have been banded, but the number of resightings between years was very low. Also, using radio-telemetry, many birds simply “disappeared” from the study area in the breeding season (B. Kempenaers, pers. comm.).

In the summer of 2012 male pectoral sandpipers in Barrow were equipped with satellite-transmitters by a team of scientists of the Max Planck Institute for Ornithology (B. Kempenaers, pers. comm.). For the first time it was possible to follow movements of individuals during the breeding season. The data revealed that not only during spring and fall migration pectoral sandpipers fly long distances but also during the breeding season. Maximum distances of up to 15,000 km were recorded. Roughly, the first males to leave Barrow went East to Canada and later in the season they went West in to Russia. Along the way they made up to 19 stops. Some males only migrated shorter distances and stayed within the boundaries of Alaska. Aside from the distance migrated, there were also strong between-male differences in tenure (the number of days spent) in Barrow. Part of the males left Barrow at some point during the breeding season ("movers"), others stayed in Barrow during the entire breeding season.

The study was repeated in 2014 to verify the existence of the differences in tenure and to find out whether they are associated with differences in physiology and/or behavior. Such associations may indicate that different migration or breeding strategies within the species exist, whereby the movers could be males that use Barrow as stop-over site, whereas the residents could be males that try to breed locally.

The hypothesis that pectoral sandpiper males differ in their aim for staying in Barrow, leads to the following testable predictions.

Met opmerkingen [JM2]: You want to collect evidence that the residence time may indicate that different types of males exist. You do that by comparing them on the basis of 1) body mass, 2) breeding behavior and 3) foraging behavior. Thus no predictions. Your reasoning when you decide that they are different types is not yet clear to me.

1. *Body weight predicts tenure in Barrow*. Males that leave Barrow during the breeding season may not yet have a fully developed throat sac (consisting mostly of fat). Therefore, they may be lighter than residents. On the other hand, movers could be heavier than residents if they are fattening up for the next long flight. Alternatively, the decision to stay or leave may also depend on condition. For example, if there is strong local competition over access to females, only heavy males may be able to secure a territory.

Met opmerkingen [k3]: It is not clear what the testable prediction here is.

2. *Breeding behavior is either exclusively or more frequently observed in residents than in movers.* I assume that residents intend to breed in Barrow and that in order to do so, it is necessary for them to establish and defend a territory (and to display to females). Movers may either: **1)** not attempt to settle at all (no breeding behavior), **2)** attempt to settle briefly (but fail), **3)** or simply show some breeding behavior due to their hormonal breeding state and the presence of conspecifics. In this study it is not our aim to test the last two predictions but they will be taken into consideration in the discussion.

3. *The proportion of time spent foraging is higher in movers than in residents.* If movers use Barrow as a stop-over site, we expect them to fuel up for the next long flight and therefore we predict that they should spend most of their time foraging.

The aim of this study is to test whether movers and residents differ in behavior. Another way of stating this is that we aim to test whether differences in the occurrence or frequency of territorial behavior and the percentage of the time spent foraging can predict tenure in Barrow. To investigate this, we need to control for (a) date (breeding behavior may increase as the season progresses) and (b) local density (breeding behavior may increase with increasing local density). Daily variation in local density can also be related to the timing of departure of individuals. From previous years we know that pectoral sandpiper density in Barrow fluctuates over the breeding season. A secondary aim of this study was to link individual departure dates with data on general local density trends, i.e., we investigated whether individuals left on days when the local density declined. This would suggest that individual departures are part of larger group departures.

Materials & Methods

Study species and study site

In 2012 and 2014 pectoral sandpipers were studied in Barrow, Alaska (71°32' N, 156°65' W) from 27 May until 6 June and 24 May until 9 June respectively. The first birds generally arrived in the last week of May. Pectoral sandpipers are insectivorous and they mostly inhabit the wet tundra areas for foraging. After arrival males start defending territories: they seem to prefer drier tundra for territories and use tundra ridges for display. Females start incubation in the first week of July which is when resident males begin leaving Barrow. Females raise the chicks on their own and leave Barrow in late July to mid-August (Holmes & Pitelka, 1998). There is significant sexual dimorphism with males on average being 30% larger in body weight than females (Pitelka, 1959). The average body weight of males is 100 grams and females on average weigh 68 gram (Lesku et al., 2012).

Catching

Between 27 May and 6 June 2012 and 25 May and 7 June 2014 60 males were caught on the study site near Barrow and equipped with transmitters, so that individuals could be tracked during the breeding season up until autumn migration when molt starts (Holmes & Pitelka, 1998). They were caught using a mist net that was operated by two people. We caught most males in an area located next to the laboratory in which we subsequently processed them. Each bird was weighed (with a Pesola balance, ± 0.5 g), and culmen, total head and tarsus length were measured (with calipers, ± 0.1mm), and a 200 – 300 µl blood sample was taken. We banded each bird with an aluminum U.S. Geological Survey band, and a unique combination of 3 color bands. A 5 g transmitter (Solar ARGOS - PTT-100; Microwave Telemetry Inc., Columbia, MD, USA) was attached on the back of all males using superglue. In 2012 we glued the transmitter directly to the back of the bird. In 2014 the transmitter was first glued to a piece of prepared goat skin; this increased the attachment area and enhanced the connection between the bird and the transmitter. Transmitter dimensions were 26 mm x 9 mm x 15 mm with an 85 mm antenna sticking out at an angle of approximately 80° (Fig. 2).

Fig. 2 Pectoral sandpiper male with transmitter glued on its back (Photo: D. Werner).

Behavioral observation protocol

Birds in the Arctic are in general less alarmed by humans than in other regions. Therefore, it was possible to approach the males for observations with no or minimal disturbance. Behavioral observations were performed in 2014 on male pectoral sandpipers with transmitters only. The most recently caught males got first priority to get observations on as many different males as possible. An observation ideally lasted 20 minutes. Approximate locations of males were available from the data provided by the transmitters. Observers would go to such a location and start looking for tagged males. When a male was found he was identified by the combination of the aluminum and plastic colored rings and his location was recorded using a handheld GPS. After each minute, we recorded the behavior the male was involved in at that particular moment (Table 1). If the male moved more than approximately 15 meters the observer followed and recorded a new location using the handheld GPS. For the analysis we distinguished breeding and non-breeding types of behaviors (see Table 1 and Fig. 3).

Table 1 Scored behaviors during focal observations.

Behavior	Breeding behavior	Note
Foraging	No	foraging, head down
foraging interaction	No	non-breeding interaction
long flight	No	>15m
short flight	No	<15m
not available	No	>30s out of sight during the last minute
Preening	No	bathing, cleaning feathers etc.
Resting	No	head in feathers/eyes closed
Standing	No	standing watching, not displaying/territorial on a pingo
Walking	No	
aerial chase	Yes	follows or being followed by other PESA in the air
Hooting	Yes	flying, throat sac inflated, making hooting sounds
male female interaction	Yes	on the ground
male male interaction	Yes	on the ground
standing territorial	Yes	displaying/pingo sitting
territorial flight	Yes	flying around, moving up and down

Tenure

Tenure was defined as the number of days spent in Barrow, and calculated as departure date from Barrow minus capture date. A bird was defined as a resident if he stayed within 7 km of the location where it was released (near the laboratory building). We used the data from the transmitters to determine departure dates. This was done manually using Google Earth (Google Earth version 7.1.2.2041). Locations received by the transmitters come in 7 categories (0, 1, 2, 3, A, B, Z) that are of different accuracy (Roshier & Asmus, 2009; CLS, 2015). We only used the locations that had the highest signal quality (type 1,2 and 3). We excluded all birds for which a departure date could not be determined (2012: n=8, 2014: n=6), either because the male died, lost the tag or stayed in Barrow until the end of the season.

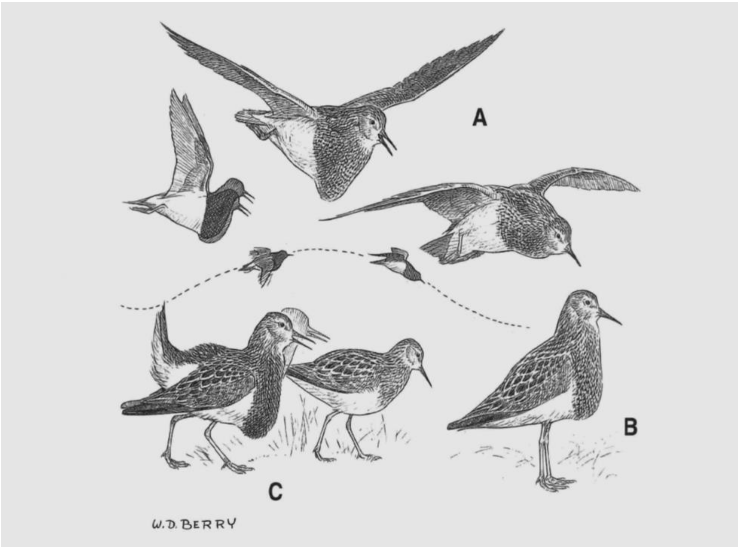

Fig. 3 Illustrations of some pectoral sandpiper breeding behaviors. A. Flight display of male, expanded and pulsating throat sac, also undulating flight. B. Sentinel posture of territorial male, often assumed when standing on lookout or mound. C. Courtship display, with male following female. (Drawings by William D. Berry in Holmes & Pitelka, 1998)

Distance sampling

A point count is a type of distance sampling in which the observer counts all objects of some kind in all directions. This is a well-established method for estimating population density (Thomas et al., 2013). Every morning and evening all pectoral sandpipers were counted for 10 minutes at 5 count locations in the study area (Table 2). During a count, the radial distance from the observer to each encountered bird was recorded. There are 5 basic assumptions:

(i) Birds that are very close to the observer will always be detected.
(ii) There is no movement of birds in response to the observer (attraction or repulsion) and none are counted twice.
(iii) All distances are measured without error.
(iv) Sightings of different birds are independent events.
(v) Count locations are placed randomly or in a systematic random pattern

The first 3 days the morning and evening counts were performed by 2 observers to make sure they followed the same protocol. The next 15 days, the counts were always performed by one observer. Assumption (v) was not met as count locations were not placed randomly in the study area. However, the distance between locations was such that the chance of counting the same bird more than once during a counting session was minimized. Instead of measuring radial distance from the observer to the bird (iii), each bird that was encountered was assigned to one of 3 predetermined distance categories (0-50m, 50-100m, 100-200m). Measuring distance is predicted to be less precise for increasing distance, therefore the use of distance categories was chosen over measuring radial distances. The same distance categories were used for all observations. The distance at first detection was registered when a bird moved between distance categories.

Table 2 Point count locations and GPS coordinates.

Location	Degrees Latitude	Degrees Longitude
Radar	71.32703	-156.642
Lab Corner	71.32381	-156.674
Browerville	71.29801	-156.698
Gas Station	71.27401	-156.643
Cake Eater	71.28877	-156.665

Density estimation

The results of the point counts were analyzed using Distance 6.2 Release 1 (Thomas et al. 2010). First, histograms are plotted, then curves are fitted over the histograms. These curves are detection functions that describe the probability of detecting a bird at radial distance r (Fig. 4). Detection probability is negatively related to radial distance, based on the simple assumption that the probability that an object is detected is 1 at distance 0 and decreases with distance. In Distance the user can choose the shape of the detection function with a key function (e.g. half-normal) and a series expansion (e.g. cosine adjustment) to find the model that best fits the data based on the lowest AIC value. The Distance software can then be used to calculate the density (for details on the method see Buckland et al., 1993; Rizzi, 2011 and Thomas et al., 2013).

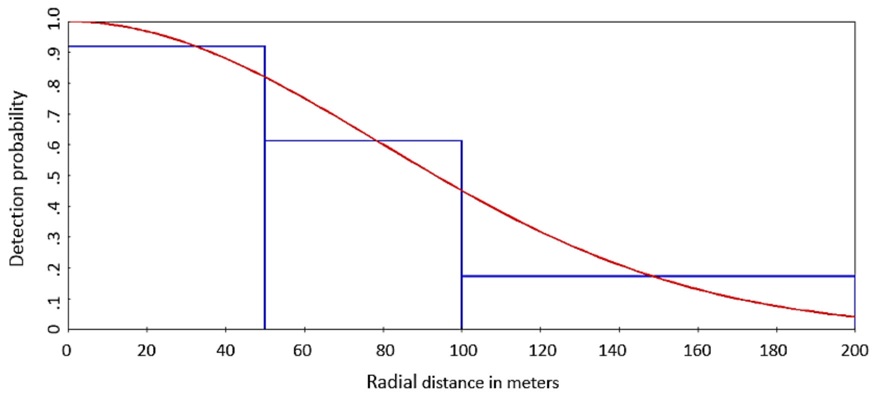

Fig. 4 Example of a detection function fitted (by Distance) over the point count data of 9 June 2014. The detection function decreases with distance. We used three distance bins, showed by the three bars.

Statistical analyses

All statistical analyses were carried out using R in R Studio (Version 0.98.1087) and models were built using the lme4 package.

Body weight and tenure

Since we excluded birds without a departure date from the study area, none of the 2012 birds could be classified as resident. Therefore, we could only test if body weight predicts tenure for the year 2014. Tenure was the response variable and body weight was used as a predictor.

Behavior
We used a GLMM to test whether breeding behavior increased over the season within and between individuals. The response variable was the number of breeding behaviors shown per observation. Day was used as a fixed effect and also as a random effect. Pectoral sandpiper density and male identity were used as random effects and we corrected for variation in the length of observations. We used the fitted intercept per individual as a measure for the amount of performed breeding behavior per individual, and tested its effect on tenure in Barrow using a generalized linear model (glm). We followed the same procedure to test whether foraging behavior can predict tenure in Barrow. First, we used a GLMM to get an individual estimate for the amount of performed foraging behavior per observed male, controlling for seasonal changes and density. Then, this individual estimate was used as a predictor for tenure in a glm. We expected breeding behavior and foraging to be inversely correlated, such that birds that show more breeding behavior should be less often observed foraging. We tested this using a linear model.

Results

Variation in tenure
Despite improved attachment, the tracks did not cover a significantly longer period of time in 2014 than in 2012 (Welch Two Sample t-test, $t_{97.05} = -1.471$, $P = 0.145$)). In 2012, none of the birds could be classified as a stayer (Fig. 5, left panel), probably because birds lost their tags (or died) before departure from Barrow. In 2014, we found 6 residents (Fig. 5, right panel) of which the first part of their southward migration was covered. A summary of the catching results and tagging results can be found in the Appendix Fig. 8.

Seasonal changes in density and departure times
Pectoral sandpiper density in the study area fluctuated over the season (Fig. 6, black line). The density estimates include females and untagged males. Tagged males departing from Barrow followed a similar seasonal pattern (Fig. 6, red line). A high departure rate of tagged birds that coincides with a density peak is often followed by a drop in density the next day. This suggests that the tagged birds that left were part of larger groups of departing birds.

Body weight
The average body weight of the tagged males in 2012 was 101.4 g and in 2014 99.8 g, but this year-difference was not significant (Welch Two Sample t-test, $t_{102.051}=0.92$, $P = 0.36$). Body weight did not predict tenure (Table 3), even when residents were removed from the sample ($R^2 = 0.00047$, $F_{1,46} = 0.022$, $P = 0.88$).

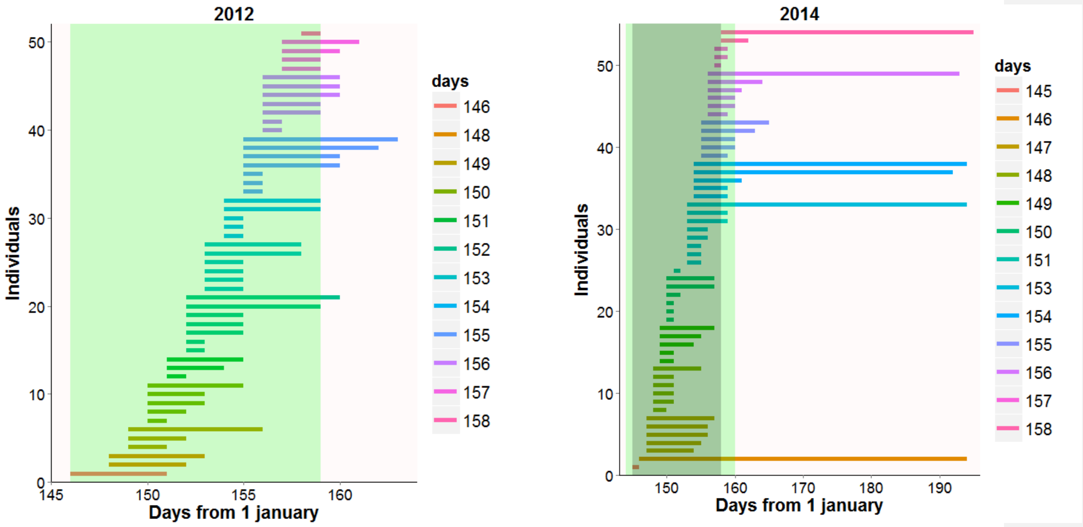

Fig. 5 Figure showing the capture and departure day of tagged pectoral sandpipers in the study area. Each bar represents a bird. The colors of the bar indicate the day on which the bird was caught. In the left panel (2012), the highlighted green area is the period in which birds were caught in Barrow. In the right panel (2014), the highlighted dark-green area is the period in which birds were caught in the study area; the light green area indicates the period during which observations and point counts were carried out.

Breeding behavior changes over time

After excluding males without a departure date (see Methods section), the dataset consisted of 29 individual males of which 17 had been observed on at least 2 days (mean number of observations: 2 days, sd: 1.2 days). In total 65 observations were carried out with a total observation duration of 1232 minutes (mean observation length: 19 min, sd: 3 min). Twenty-three out of 29 males (79 %) showed breeding behavior. Breeding behavior was observed both in movers and residents (80% of movers (n=25), 75% of residents (n=4)). Figure 7 shows the increase in breeding behavior as the season progressed (linear model controlling for length of observation: $R^2 = 0.12$, $F_{1,63}= 8.355$, P = 0.005, (Table 3)).

Density did not have an effect on the likelihood of observing breeding behavior, so it was excluded from the mixed model (P= 0.44). The individual measure for breeding behavior could not predict tenure, as is showed by the result of the glm (P = 0.15, Table 3). Males that showed more breeding behavior did not have a longer tenure in Barrow.

Foraging behavior and the interrelationship with breeding behavior

The proportion of foraging behavior observed during observations decreased over the season (linear model controlling for length of observation: R2 = 0.091, F1,63= 6.312, P = 0.001, see Fig. 8). Day as a random factor had no effect on foraging behavior so we excluded it from the model (Variance= 0.00, S.d.=0.00). The individual measure of foraging behavior predicted tenure (Table 3): males that showed more foraging behavior stayed shorter in Barrow. Finally, breeding behavior and foraging behavior are inversely correlated, as expected.

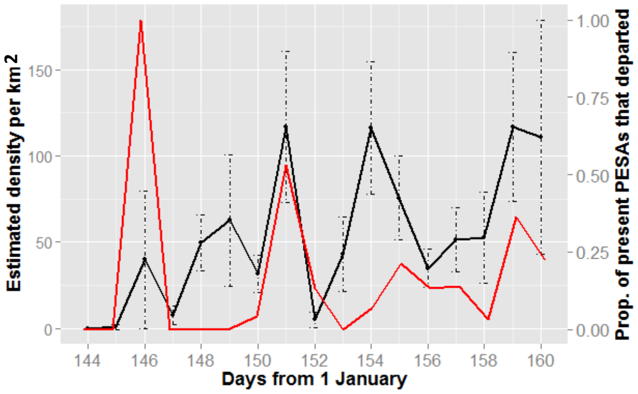

Fig. 6 Pectoral sandpiper density in- and departures of tagged males from Barrow per day during the field season. Pectoral sandpiper density is on the left y-axis and indicated by the *black* line, dashed bars indicate the 95% confidence interval. The proportion of tagged pectoral sandpipers that departed on a given day is shown on the right y-axis and is indicated by the *red* line.

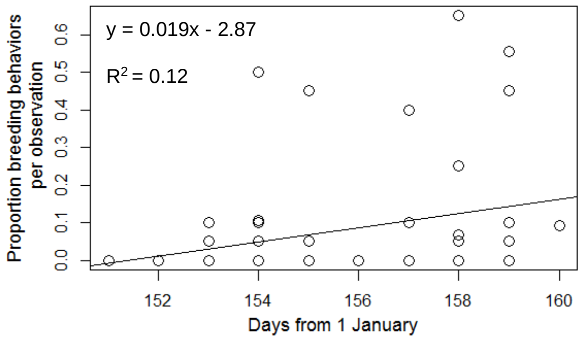

Fig. 7 The increase in breeding behavior over the season. We controlled for the length of an observation by using the proportion of breeding behaviors (sum of breeding behavior divided by the length of the observation).

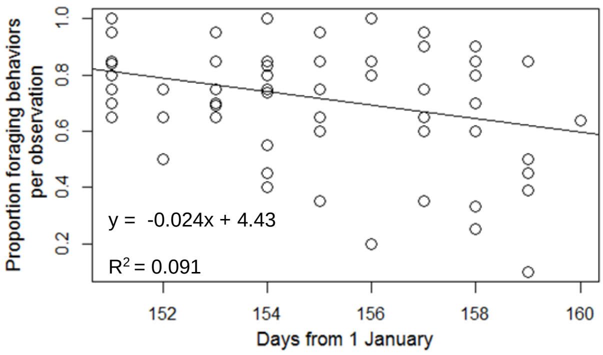

Fig. 8 The decrease of foraging behavior over the season. Length was controlled for by using the proportion of foraging behaviors (sum of foraging behavior divided by the length of the observation).

Table 3 Summary of the results of the statistical analyses. The table is divided in 3 sections indicated by colors: GLMMs (purple) on the effect of season (day) on breeding and foraging behavior, GLMs (red) where we used the intercepts of the GLMMs as an individual measure for behavior independent of day to predict tenure, and LMs (orange) to test if body weight predicts tenure and if breeding behavior is inversely correlated with foraging behavior. Significant effects are denoted in bold face.

GLMM	***Breeding behavior***				
	Fixed effects	Estimate	s.e.	z-value	P-value
	Intercept	-4.86	0.65	-7.49	**< .001**
	Day	1.71	0.49	3.46	**< .001**
	Random effects	Variance	s.d.		
	Bird identity	3.04	1.74		
	Day	0.60	0.77		
	Sample size	65 observations		29 birds	
	Foraging behavior				
	Fixed effects	Estimate	s.e.	z-value	P-value
	Intercept	-0.34	0.05	-7.51	**< .001**
	Day	-0.10	0.04	-2.28	**0.02**
	Random effects	Variance	s.d.		
	Bird identity	0.02	0.15		
	Sample size	65 observations		29 birds	
GLM	***Tenure ~ Breeding behavior***				
		Estimate	s.e.	z-value	P-value
	Intercept	2.61	0.21	12.64	**< .001**
	Breeding behavior	0.06	0.04	1.43	0.15
	Sample size	29 birds			
	Tenure ~ Foraging behavior				
		Estimate	s.e.	z-value	P-value
	Intercept	1.82	0.23	8.08	**< .001**
	Foraging behavior	-1.44	0.61	-2.34	**0.02**
	Sample size	29 birds			
LM	***Tenure ~ Body weight***				
		Estimate	s.e.	t-value	P-value
	Intercept	10.85	9.86	1.10	0.27
	Body weight	-0.05	0.10	-0.50	0.62
	Sample size	52 birds			
	Foraging behavior ~ Breeding behavior				
		Estimate	s.e.	t-value	P-value
	Intercept	-7.68	0.74	-10.34	**< .001**
	Breeding behavior	-8.77	2.10	-4.17	**< .001**
	Sample size	29			

Discussion

We tested the hypothesis that there are strong differences in tenure in male pectoral sandpipers and looked for differences in behavior and physiology that could be related to tenure. There was no relationship between body weight or the performance of breeding behavior and tenure. The data also showed that males with the longest tenure foraged the least. At first, that seems incoherent with the absence of an effect on body weight. One would expect to find an effect on body weight if movers forage more. Since body weight was measured at catching there could have been an effect but that may have been measurable only later in time.

In this study we looked for behavioral and physiological differences that could be related to tenure but we did not look into the underlying mechanism that could drive the differences. It remains unknown whether males decide to stay in Barrow before arrival (migration distance is an inflexible trait) or whether they test their chances to obtain a territory after arrival (migration distance is a flexible trait). In the first case we would expect bimodality in behavior and physiology and it would mean that there are two types of males, leavers that only use the study area as a stopover and residents that intend to breed locally. Breeding behavior performed by leavers in the study area would then be a by-product of high testosterone levels state (Wingfield & Hunt, 2002). Following the alternative hypothesis, we would expect a more continuous distribution of tenures. All males try to establish a territory and breed locally. First they evaluate the area and subsequently they decide to leave or not. This evaluation could be influenced by for example the number of females present, the number and strength of competitors.

Do our findings point to either one of the mechanisms? Following our results, we would predict that all males try to establish a territory in the study site. After all, almost all birds were observed performing breeding behavior regardless of type. It points to the idea that all males attempt to settle when they arrive in the study area. We determined the amount of breeding behavior that they showed, because we assumed it would be a measure to estimate their chance to obtain a territory and stay in Barrow. However, it turned out breeding behavior is unimportant in explaining tenure at the study site. So even though most males showed breeding behavior we do not know what is the factor that determines if they stay in Barrow or not.

Met opmerkingen [JM4]: reformulate

The result that most males showed breeding behavior but did not breed in Barrow could be non-adaptive. It may be caused by their hormonal breeding state (Wingfield & Hunt, 2002) and the presence of conspecifics. The hormone-part of the hypothesis could be tested by experimentally increasing hormone levels and see if they develop breeding behavior afterwards. In 2006 Steiger et al. measured hormone levels in pectoral sandpipers (Steiger et al., 2006). As expected, hormone levels were much higher in males than in females. Even though the strongest difference was found between the sexes, there were still some males with low hormone levels. The males were not divided in groups of residents and leavers in that study. With today's knowledge, it would be interesting to know if those low-hormone-level males are the ones that leave Barrow or not.

The estimated pectoral sandpiper density in the study area fluctuated and breeding behavior increased over time. Also, we observed many groups of males foraging together with breeding behavior being absent. Therefore, the presence of conspecifics does not seem to be the main cause for males showing breeding behavior. It would have been informative to separate male and female density per day to see if sex-specific density fluctuations exist. However, females are more cryptic so the relevant data cannot easily be collected. For future studies we would recommend focusing specifically on females for this purpose. We did observe male behavior when females were present but the sample size was too small.

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Appendix

Fig. 9 A summary of the movements of tagged males in the study area during the field seasons of 2012 and 2014. The figures show (1) the cumulative increase of caught males over time, (2) number of tagged males that left the study area, (3) number of tagged males still present in the study area and (4) the proportion of males departed from the study area corrected for the number of tagged males present. Note that the x-axis is the same for all graphs. Males departed earlier from the study area in 2014.