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Supplementary Material for

Adaptive Sleep Loss in Polygynous Pectoral Sandpipers

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Published 9 August 2012 on *Science* Express
DOI: 10.1126/science.1220939

This PDF file includes:

Other Supplementary Material for this manuscript includes the following:
(available at www.sciencemag.org/cgi/content/full/science.1220939/DC1)

Movie S1
Audio S1
Database S1

Materials and Methods

General procedures

The study was conducted near Barrow (Alaska) on a 2 km^2 site consisting of tundra vegetation (*28*). Male and female pectoral sandpipers arriving on the breeding grounds between late May and mid-June were caught using mistnets. In 2004 – 2009 and 2011, we banded each bird with an aluminum U.S. Geological Survey band, a green plastic flag, and a unique combination of color bands. Color bands allowed us to follow the behavior of individual birds. Observations of male territorial behavior were performed from 2006 through 2009 every day during June by several observers (median four observers) who systematically walked through the entire study area. Once a male was identified, its position was recorded, using a handheld GPS, together with the observed behavior(s) of the focal individual. Male behavior was scored as territorial (vigilant watch, territorial advertisement flight, fight, including ritualized conflict), courtship (flight display, ground display, female guarding), feeding, preening or resting (see also table S4).

In 2008 and 2009, we also attached a 4 g interaction tag (iTag, e-obs GmbH, Gruenwald, Germany) on the back of all birds in the central study area using super glue. Tag dimensions were 26 mm x 9 mm x 15 mm with an 85 mm antenna sticking out at an angle of approximately 80° (fig. S2). We weighed each bird (Pesola balance, ± 0.5 g), measured culmen, total head and tarsus length (calipers, ± 0.1mm), and took a 200 – 300 µl blood sample.

We searched for nests on a daily basis and determined clutch initiation date in either one of two ways. If nests were found during laying, we calculated the date of the first egg assuming that females laid one egg per day. If nests were found with a full clutch (usually four, rarely three eggs), we estimated laying date by subtracting 22 days from the hatching date. Egg laying occurred between 6 – 27 June (date of first egg; 2008: 17 June ± 3.2 d (mean ± s.d.), n = 39 nests; 2009: 14 June ± 5.8 d, n = 17 nests). To avoid predation and to ensure that females continued incubation, we collected all complete clutches and replaced them with dummy eggs. We placed all collected eggs, marked with nest identity, in an incubator (Compact SA, Grumbach, Germany) until a few days before the expected hatching time, as determined by egg floating (*29*). We then moved the eggs to a hatcher with increased humidity until they hatched. We kept each clutch separate in the hatcher to allow unequivocal assignment of hatchlings to their putative mothers (incubating female caught on the nest). We banded each chick and took a small (± 50 µl) blood sample. Within a few hours after hatching, we brought groups of chicks back to the nest of an incubating female; all females accepted the chicks and continued caring for them. We also collected tissue from embryos of unhatched eggs as a source of DNA for paternity analysis.

Between 5 – 18 June 2011, we caught territorial males (101.5 ± 5.5 g, mean ± s.e.m., n = 29) with mistnets and transported them to the laboratory for surgery and EEG/EMG logger attachment (see below). Body mass of the selected males did not differ significantly from the body mass of males caught in previous years (table S1, Welch Two Sample t-test, $t_{33.48} = 1.615$, n control group = 714, $P = 0.12$).

Due to high male-male competition for territories, two people stayed on the territory of the male, defending it against male intruders by chasing them or by capturing and banding them until the return of the focal male.

All procedures were approved by the Max Planck Institute for Ornithology, the Alaska Department of Fish and Game (permit number 11-106) and the U.S. Fish and Wildlife Service (permit number MB210494-0).

Measurements of activity and male-female interactions

Virtually every male pectoral sandpiper that was resident on the study site and a representative sample of females was equipped with tags that recorded activity and male-female interactions during the 2008 and 2009 seasons. We deployed two types of iTags: each male obtained a receiving tag (R-iTag), whereas each female was equipped with a sending tag (S-iTag). All iTags had a unique ID. A Timing Transmitter Station (TTS) was set up in the center of the study site with an output radio power at 916 MHz of 1 Watt. We attached the omnidirectional TTS antenna at the top of a ≈ 20 m wooden pole. Every 4 s, each iTag recorded date, time and signal strength (in dBm) as transmitted from the TTS. Additionally, every 4 s, R-iTags (males) recorded the unique ID of each S-iTag (female) that was in the neighborhood (within ± 15 m), together with date, time and signal strength as transmitted from the S-iTag. We wirelessly downloaded the data from all deployed iTags to a memory card twice per 24-h day from a distance of approximately 50 m by walking through each male's territory with a handheld data receiver without disturbing the birds in their natural behavior.

Activity data were obtained based on variation in the strength of the signal received from the TTS. Signal strength did not vary appreciably when the transmitter was stationary (inactive bird), but fluctuated widely with changing location and orientation of the transmitter's antenna relative to the TTS antenna (active bird). We performed a field calibration using 41 tags which were placed at random locations within male territories throughout the study site. These tags recorded signal strength every 4 s for a total of 255 h. For each tag, we grouped signal strength by calculating means at 1 min intervals. We then applied a running coefficient of variance (CV = SD/mean) with a window of 10 min. To estimate the maximum level of variation in signal strength for an inactive bird, we used the 99% upper quantile of the CV as a threshold to distinguish between inactivity and activity (fig. S3).

For all deployed tags, we computed activity as the proportion of time an individual was active. We distinguished between two periods: (1) the fertile phase, i.e., the period during which fertile females were known to be present on the study site, estimated as the 95% upper quantile of incubation onset date; (2) the post-fertile phase, i.e., the period after the fertile phase.

For the analyses on reproductive success, we only included males with at least 48 h of continuous recordings during the fertile phase (median = 271 h, range = 48 – 662 h, n = 30 males in 2008, n = 43 in 2009) and nesting females (n = 20 in 2008 and n = 17 in 2009). The total recording time equaled 22,937 h. The total time during which at least one interaction was recorded during the fertile phase equals 42.5 h, i.e., females interacted with a male during 0.45% of the total recording time. In total we recorded 2,713 distinct interaction bouts during the period when fertile females were present on the

study site, and 829 (328 in 2008, and 501 in 2009) distinct male-female interactions, amounting to 54.7% (2008) and 68.5% (2009) of all possible male-female interactions.

Parentage analysis

We extracted DNA from blood samples stored in lysis buffer with the GFX Genomic Blood DNA Purification Kit (GE Healthcare Europe, Freiburg, Germany) or from tissue stored in ethanol using the DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany). We used 13 microsatellite markers: *Clk*polyQ (*30*); Cme1-3, 5, 7, 9, 10, 12 (*31*); R1, R6, R50 (*32*); Sru24c (*33*). Products were sized on an ABI 3100 Genetic Analyzer (Applied Biosystems, Darmstadt, Germany) and alleles were determined manually using GeneMapper software v4.0.

We conducted parentage analysis using Cervus 3.0 (*34*). Among all adult individuals sampled in 2008 and 2009, the 13 microsatellites had on average 15.2 alleles per locus (range: 4 – 22); allele frequencies did not deviate from Hardy-Weinberg equilibrium at any of the loci, and the estimated frequency of null alleles was < 0.03 for all loci. The combined probability of falsely assigning the father, given a known mother, was 2.7×10^{-7}. Paternity of offspring was determined for each year separately by including the incubating female caught on the nest as the known mother, and all adult males caught in 2008 (n = 185) or 2009 (n = 84) as candidate fathers. Note that many of these males were not territorial and had left the study area after 0 – 2 d. Among 207 genotyped offspring (2008: 141, 2009: 66) from 53 broods (2008: 36, 2009: 17) only one showed a single mismatch with the putative mother, probably due to a mutation. For the simulation of paternity, we used the following parameters: proportion of loci typed: 0.99, proportion of loci mistyped: 0.01, proportion of candidate males sampled: 0.80. We accepted a male as the father of an offspring when he either showed no mismatches with the offspring (taking the maternal alleles into account; n = 124) or when he showed one mismatch but had fathered the other offspring in the same nest (with zero mismatches; n = 5). In all cases, males were assigned at the 95% confidence interval. In total, 74 offspring (36%) were not assigned to any male (2008: 53 or 38%, 2009: 21 or 32%). However, most unassigned offspring were from nests found at the edge of the study site, where trapping effort had not been as intense.

Electrophysiological recording and analysis

To determine the relationship between inactivity and sleep, in 2011, males underwent a surgery to attach EEG and EMG electrodes using standard techniques (*14*). Briefly, we anesthetized the birds with isoflurane (induction at 5%, maintenance at 1 – 2%) vaporized in 100% oxygen and then made a midline incision (10 mm length) to expose the cranium. We drilled four holes (0.5 mm diameter) into the cranium to the level of the dura, with one hole over the anterior and posterior hyperpallia (4 mm apart and 2 mm lateral of the midline) to constitute a bipolar EEG derivation for each hemisphere. The hyperpallium can be identified visually through the cranium, as the bone overlying this structure is particularly thin. A fifth hole, over the left hemisphere, housed the ground. We placed a fine medical-grade stainless steel wire electrode (AS 631, Cooner Wire, Inc., USA) in each hole and attached the wire to the cranium with superglue. In addition, we placed two stainless steel wire electrodes over the nuchal (neck) muscle to record the EMG and then closed the incision with a topical skin

adhesive (Hystoacryl®, Aesculap AG, Germany). All electrode wires were thread through a flexible silicon tube (1.8 mm outside diameter, 7.5 cm length), and glued down the back of the neck between the feathers using a non-toxic, flexible, skin adhesive (Manfred Sauer GmbH, Germany). The wires connected to a miniature, lightweight (5 g, battery included) data logger (www.vyssotski.ch/neurologger2) used in other studies of sleep and wakefulness (*13*). The logger was glued on the upper back between the wings with super glue and skin adhesive (movie S1).

Each bird came out of anesthesia quickly, and was typically fully alert within 10 min. We returned the birds to their territory 20 – 30 min thereafter. All birds either maintained their territory or departed the study site; however, the frequency of departures was comparable to that observed following leg banding alone in previous years (41% of the 29 EEG males departed within 24 h vs 35% males first caught and only color banded in previous seasons; $n = 421$, Fisher Exact Test, $P = 0.55$), and was therefore not related to the surgery *per se*. In one exceptional case, the focal male was challenged by an intruder within minutes of its release. The males engaged in posturing displays, parallel walks, charging, and a 3.3 min high-altitude competitive flight; the male with the EEG/EMG logger maintained his territory. In a separate instance, another instrumented bird was filmed courting and attempting to copulate (perhaps successfully) with a female less than 1.5 d after surgery (movie S1). Furthermore, in June 2012, we recaptured two males on the study site (behaving as residents) that had undergone the surgical procedure in 2011, suggesting that long-term effects of the surgery are minimal.

We recaptured the birds after 4 – 5 d in the tundra (i.e., batteries maintained a sufficient charge for, at most, 5 d). We either removed or refurbished the equipment for an additional recording and then released the birds back onto their territories. Weight loss during this interval was 5.4 ± 1.2 g (mean ± s.e.m.) and did not differ from that in control birds caught in previous years (3.8 ± 1.9 g, $n = 24$) (mean ± s.e.m.) that only received leg bands ($P = 0.93$, linear model controlling for initial mass and the number of days between the two measurements). Recordings were 87 – 226 h in duration (132 ± 16 h, mean ± s.e.m.).

We imported the EEG/EMG signals (sampled at 200 Hz) into Somnologica Science v3.3.1 (Embla®, www.embla.com) for analysis. We visually scored an undisturbed 24-h day, at least 2.5 d after handling (maximum: 7.6 d; 3.5 ± 0.5, mean ± s.e.m., $n = 11$), for wakefulness and sleep using 4 s epochs (for one bird, a day was scored 1.5 d after handling). Wakefulness was typically characterized by low-amplitude, high-frequency (activated) EEG activity, generally with high EMG activity (*15*). As in other birds during periods of particularly high EMG activity (*14*), the EEG signals also showed high amplitude waves. Video recordings confirmed that this pattern was associated with head movements during active wakefulness. Although we cannot rule out artifacts from movement of the cable running down the neck as the source of this signal, previous studies suggest that it reflects field potentials generated by the hyperpallium in conjunction with eye movements (*35*) and motor output (*36*). As with other avian species, sleep onset typically followed within seconds after the cessation of waking activities (e.g., main text, Fig. 3A). Non-rapid eye movement (non-REM) sleep was characterized by high-amplitude, low-frequency EEG waves with low EMG activity. The appearance and amplitude of slow waves during non-REM sleep was largely symmetric between the left and right hyperpallia, although as in other birds we

occasionally observed short interhemispheric asymmetries in the amplitude of non-REM sleep EEG activity (*37*). A minority of epochs contained a mixture of wake-like activation and sleep-like slow waves. We scored these epochs as 'mixed' and added half of the total mixed epochs to the unequivocal sleep and wakefulness totals to provide the most accurate estimate of the amount of each state. Finally, our ability to quantify rapid eye movement (REM) sleep was hindered by the fact that although reductions in EMG activity similar to those observed in mammals during REM sleep can occur during avian REM sleep, in most cases EMG activity does not change from the preceding non-REM sleep level (*38*). In the laboratory, REM sleep is most reliably identified as brief periods of wake-like EEG activation without an increase in EMG activity arising out of non-REM sleep and accompanied by closed eyes and behavioral signs of reduced muscle tone, such as head dropping (*14*). Nonetheless, this was not a significant issue because in contrast to our experience with other bird species, potential episodes of REM sleep were extremely rare in pectoral sandpipers. This most likely reflects the fact that as in mammals (*39*), cold temperatures suppress REM sleep in birds (*40, 41*). Indeed, the mean temperature during the EEG/EMG recording was 0.9 ± 0.6 °C (range: -1.1 to 5.1 °C), 4 °C colder than that which reduces REM sleep to < 1% of total sleep time in magpies (*Pica pica*) (*41*).

To quantify the association between activity and wakefulness, we used 10 – 70 Hz neck EMG activity. We also calculated the number of sleep episodes (i.e., the number of entrances into non-REM sleep) and mean episode duration (period occupied by non-REM sleep only, without intervening wakefulness). We calculated slow wave activity (SWA, 0.8 – 4.7 Hz power density) during non-REM sleep for each artifact-free 4 s epoch. The most stable EEG channel was used for this analysis. Lastly, cumulative SWA (or slow wave energy, SWE) was calculated as mean SWA * number of epochs of non-REM sleep (*17*).

Statistical analyses

Statistical analyses were performed with R Development Core Team (*42*). To assess sex differences in activity levels during the fertile and post-fertile period, we constructed a generalized linear model with activity (% time active) as dependent variable, and sex and year as factors.

Male reproductive output was measured in two ways: (1) mating success, defined as the number of females with whom a male sired at least one offspring, and (2) reproductive success, defined as the total number of offspring a male sired during the entire breeding season. These two measures were highly correlated ($r = 0.98$, $P < 0.001$, $n = 73$ males).

To test whether overall male activity predicted reproductive output, we used generalized linear models with one of the two measures of reproductive success as the dependent variable, and year and proportion of time active during the fertile period as predictors. In model 1 we used mating success with Poisson error distribution and log-link function; in model 2 we used reproductive success, with binomial error distribution and logit-link function.

We also tested whether male activity is related to the total number of interactions with females. This was tested with a generalized linear model with the number of interactions as dependent variable and with year, proportion of total time active and the

number of days recorded as predictors. For this model, we used a Poisson error distribution with log-link function.

Supplementary Text

Why might females choose to mate with males that sleep the least? Activity levels may provide females with valuable information on the genetic quality of males, if only high quality males are able to reduce sleep without experiencing decrements in performance (*9*). Females might assess males by monitoring how often they are encountered sleeping or by simply monitoring how often they display. Indeed, we observed that females are highly reluctant to copulate (only 5 copulations were observed during a total of 195 h of round-the-clock focal female observations), usually terminating a courtship display by running or flying away, and only the most persistent males will obtain copulations.

How are pectoral sandpipers able to stay awake and perform adaptively on little sleep? Because the time spent sleeping varied considerably across males under the same lighting conditions and sleep increased around the summer solstice when light levels were maximal, but fertile females were no longer available, it is unlikely that light *per se* suppressed sleep. Furthermore, although short-sleeping males slept deeper than long-sleeping males, this did not compensate fully for lost sleep. While pectoral sandpipers may have delayed full recovery until the post-breeding season (a time when we could no longer catch males), their ability to postpone this potential recovery for up to three weeks while maintaining high neurobehavioral performance is unprecedented.

Fig. S1

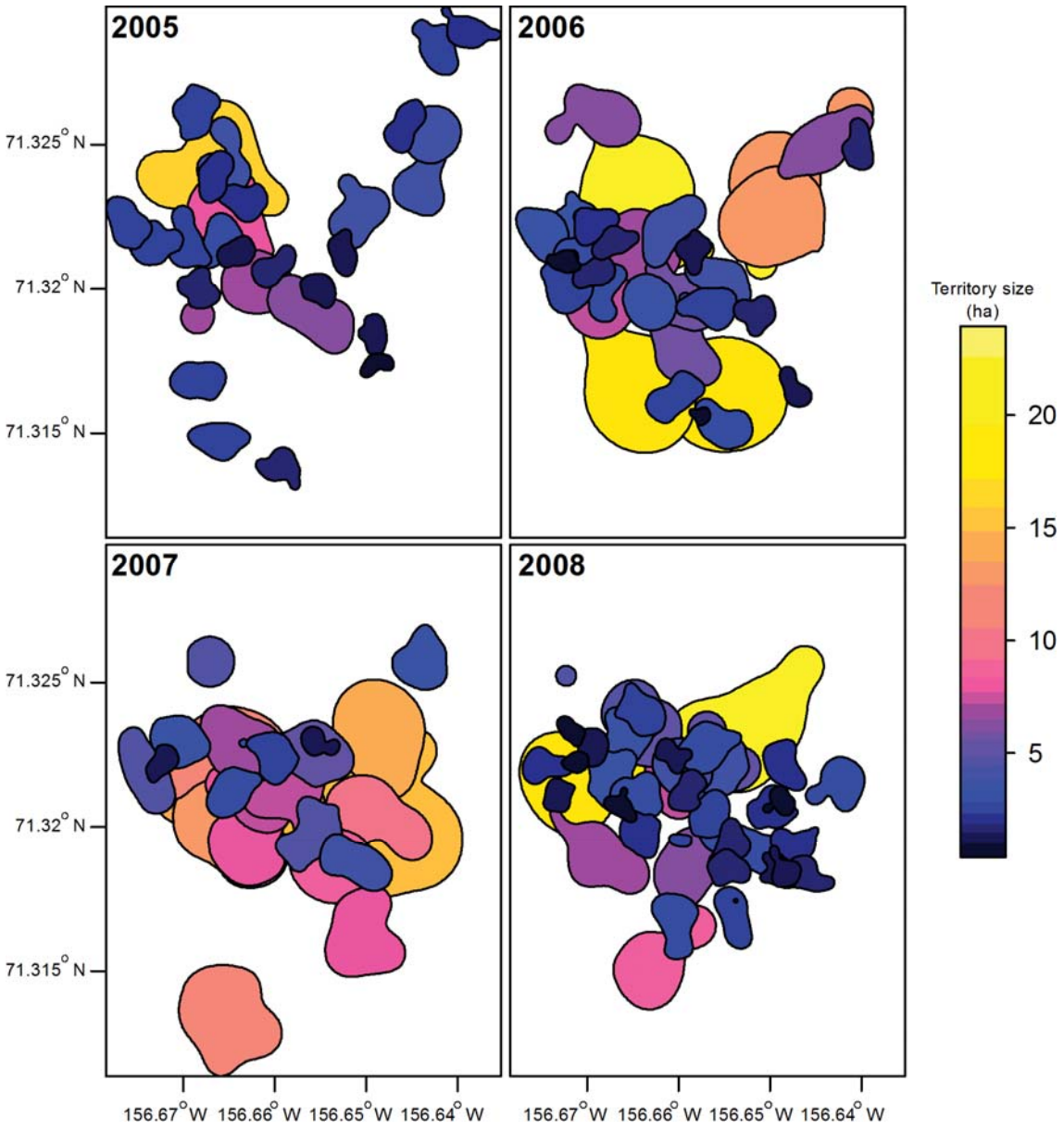

Fig. S1. Maps depicting density of male territories. Territories of male pectoral sandpipers during four breeding seasons (2005 – 2008) in Barrow, Alaska. A fixed kernel density estimator was used to construct 80% utilization distribution probabilities based on sets of GPS locations for each male. Only males with more than 5 relocations and at least 48 h tenure were included in the analyses. Data were collected in June during the period when more than 50% of the females in the population were still fertile.

Fig. S2

Fig. S2. Photo of a male pectoral sandpiper performing a territorial flight with an iTag on his back.

Fig. S3

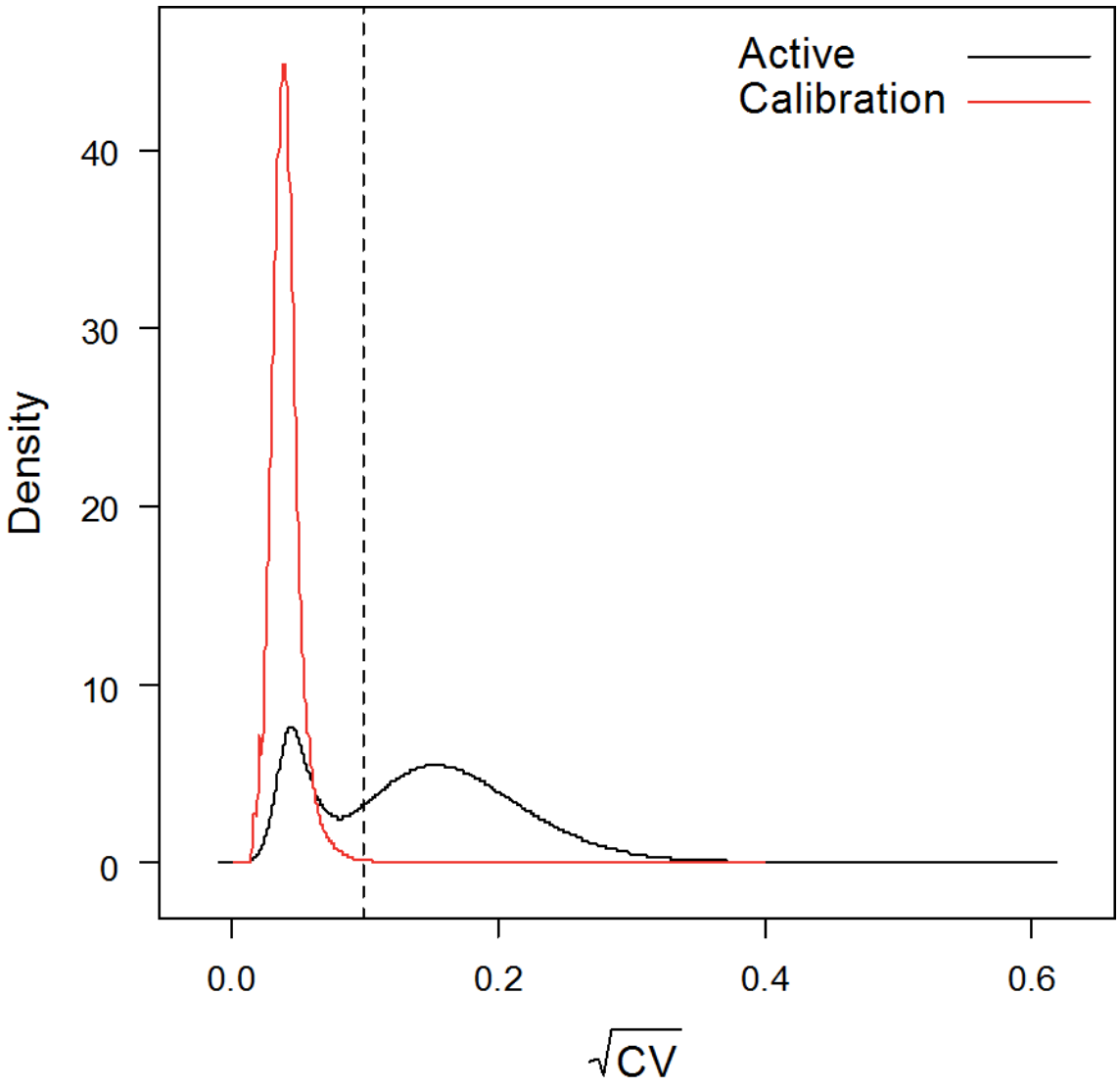

Fig. S3. Calibration of activity tags. Density plot of signal strength coefficient of variance (CV, square-root transformed) of the calibration tags (red) and the tags attached to a bird (black). Note the bimodal distribution of the tags on birds. The vertical dotted line is the 99% upper confidence interval of the signal strength CV of the calibration tags and indicates the threshold value for the separation of activity from non-activity.

Table S1

	Males (n = 714)	Females (n = 452)
Tarsus (mean ± s.d.)	29.2 ± 1.1 mm	27.6 ± 1.0 mm
Wing	144.5 ± 3.1 mm	131.5 ± 3.0 mm
Body mass	99.6 ± 7.6 g	68.4 ± 8.7 g

Table S1. Sexual size dimorphisms in pectoral sandpipers captured in Barrow (Alaska) during June and July (2004 – 2009 and 2011).

Table S2

Predictor	Estimate	s.e.	z-value	P-value§
Intercept	0.799	0.030		
Year*	-0.092	0.023	-3.980	<0.001
Breeding stage†	0.189	0.026	7.296	<0.001
Sex‡	0.265	0.024	10.897	<0.001
Simultaneous Tests for General Linear Hypotheses (Tukey Contrasts):				
Female fertile period vs. female post-fertile period	0.22	0.047	4.658	<0.001
Male post-fertile period vs. female post-fertile period	0.28	0.050	5.662	<0.001
Male fertile period vs. female post-fertile period	0.46	0.044	10.48	<0.001
Male post-fertile period vs. female fertile period	0.06	0.037	1.647	0.346
Male fertile period vs. female fertile period	0.24	0.030	8.19	<0.001
Male fertile period vs. male post-fertile period	0.18	0.033	5.392	<0.001

*Relative to 2008; †Relative to the post-fertile period; ‡Relative to females
§For Tukey Contrasts adjusted P-values (single-step method) are reported.
Interaction Breeding stage * Sex, $F_{(1,144)} = 0.67$, $P = 0.41$
Adjusted R-squared: 0.54

Table S2. Relationship between activity and breeding phase. The table shows the statistical results pertaining to Fig. 2. The proportion of time males (n = 99, of which 52 recorded during both breeding stages) and females (n = 50, of which 26 recorded during both breeding stages) are active depended on the year (higher in 2008, when density of breeding males and females was higher), on breeding stage (higher during the period when females are fertile) and on sex (higher in males). Proportion of activity was arcsine square-root transformed.

Table S3

Predictor	Estimate	s.e.	Statistic†	P-value
*(a) Total number of interaction bouts**				
Intercept	-4.875	3.778		
Recording time	0.260	0.063	4.110	<0.001
Date	0.011	0.002	5.375	<0.001
Year‡	0.626	0.770	0.813	0.419
Proportion of activity	7.212	2.950	2.445	0.017
(b) Total number of interacting females				
Intercept	0.102	0.664		
Recording time	0.071	0.012	5.738	<0.001
Date	0.004	0.000	8.149	<0.001
Year‡	0.011	0.135	0.080	0.936
Proportion of activity	1.350	0.508	2.656	0.0098
(c) Number of females				
Intercept	-12.770	3.960		
Recording time	0.001	0.002	0.802	0.423
Date	-0.016	0.051	-0.310	0.756
Year‡	0.775	0.521	1.488	0.137
Proportion of activity	8.401	2.956	2.842	0.004
(d) Number of young sired				
Intercept	-12.218	3.966		
Recording time	0.001	0.002	0.702	0.485
Date	-0.042	0.052	-0.806	0.423
Year‡	0.980	0.524	1.870	0.066
Proportion of activity	8.738	2.946	2.966	0.004

*Square root transformed; †t-value for (a), z-value for (b), (c), (d); ‡Relative to 2008
R-squared values (deviance/ null deviance): 0.44 (a), 0.55 (b), 0.21(c), 0.24 (d).
Dispersion parameter for quasipoisson family: 2.39(b), 3.51(d).

Table S3. Relationship between male activity, interactions with females, and young sired. The table shows the statistical results pertaining to Fig. 4. The proportion of time a male was active during the period when fertile females were present predicts the total number of different females with which he interacted, the total number of interaction bouts with females, the number of females with whom he sired offspring, and the total number of offspring sired in a given year (Fig. 4A-D). Proportion of activity was arcsine square-root transformed. Results are from generalized linear models with Poisson error distribution and log-link function (Fig. 4A-C) or normal error distribution (Fig. 4D) with measure of male 'success' as the dependent variable and the total number of recording time (in hours), recording date, year and proportion of time active as explanatory variables.

Table S4

Predictor	Estimate	s.e.	z-value	P-value
Intercept	-3.68	0.623	-5.902	
Arrival date*	0.06	0.019	2.951	0.003
log(tenure)†	0.37	0.162	2.267	0.023
Male behavior (%)‡	4.78	0.929	5.142	<0.001

*Day one is 1st of June

†Tenure (number of days resident on the study area)

‡Proportion of observations (square-root transformed) of courtship and territorial behavior (vs. feeding, preening, resting).

Table S4. Relationship between male behavior and the number of females with whom he sired offspring, accounting for arrival date and tenure on the study area. The analysis is based on 38,007 independent observation sessions of a total of 289 males during June 2006 – 2009 (mean number of observation sessions per male was 128). Results are from a generalized linear mixed effect model with Poisson error distribution and log-link function and year and male identity as random factors. All predictors are independent (variance inflation factors computed for the equivalent generalized linear model smaller than 1.2). Interactions with year (2006 as reference year) were non-significant (Simultaneous Tests for General Linear Hypothesis, Tukey Contrasts, $P > 0.52$). During each independent observation bout, male behavior was scored as territorial (fight, including ritualized conflict, territorial advertisement flight, vigilant watch), courtship (flight display, ground display, female guarding), feeding, preening or resting.

Caption for Movie S1

Movie S1. Male with EEG/EMG logger courting a female. In this movie a male that underwent surgery for attaching the EEG/EMG logger (white spot on back) 1.5 d earlier can be seen courting a female. Following a period of running after the female with his tail raised (see also Fig. 1B in main text), the male attempts (perhaps successfully) to copulate with the female (i.e., brief wing fluttering over the female) and then flies away. Movie recorded by Martina Oltrogge, Max Planck Institute for Ornithology – Seewiesen, Germany.

Caption for Audio S1

Audio S1. Male hooting during display flight (Fig. 1A).

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