modern war and recognized its futility. In the face of rapid change, the future is hard to predict. If the large sums of income from natural resources and foreign aid are applied to development during this time of relative peace, the people of Enga will have more to lose and may continue to turn away from war. However, there is a burgeoning population of discontented youths, and politics are heating up as multinationals invest billions to extract the resources of an otherwise poorly developed PNG. Perks for those in power are many. In some areas, gangs are already serving the interests of politicians (*30*); a new round of warfare could erupt over the politics of tangible resources. If this happens, local institutions founded on principles of kinship, respect, and restorative justice will not suffice, and the Enga may find themselves in another cycle of violence as the scale of their society increases. This was true for many societies in the past (*5*, *44*) and is still the case for societies in similar transitions today.

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Supplementary Materials

www.sciencemag.org/cgi/content/full/337/6102/1651/DC1
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Adaptive Sleep Loss in Polygynous Pectoral Sandpipers

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The functions of sleep remain elusive. Extensive evidence suggests that sleep performs restorative processes that sustain waking brain performance. An alternative view proposes that sleep simply enforces adaptive inactivity to conserve energy when activity is unproductive. Under this hypothesis, animals may evolve the ability to dispense with sleep when ecological demands favor wakefulness. Here, we show that male pectoral sandpipers (*Calidris melanotos*), a polygynous Arctic breeding shorebird, are able to maintain high neurobehavioral performance despite greatly reducing their time spent sleeping during a 3-week period of intense male-male competition for access to fertile females. Males that slept the least sired the most offspring. Our results challenge the view that decreased performance is an inescapable outcome of sleep loss.

Sleep is a prominent yet enigmatic part of animal life (*1*). In humans, and other mammals, sleep restriction and fragmentation diminish waking neurobehavioral performance (such as attention, motivation, sensory-motor processing, and memory), often with adverse consequences for the individual and society (*2*–*5*). Sleep loss even impairs the performance of innate behavioral displays (*6*). These findings suggest that sleep performs essential restorative processes that sustain adaptive brain performance (*1*). An alternative view posits that sleep may be simply a state of adaptive inactivity that conserves energy when activity is not beneficial (*7*). This adaptive inactivity hypothesis proposes that the marked

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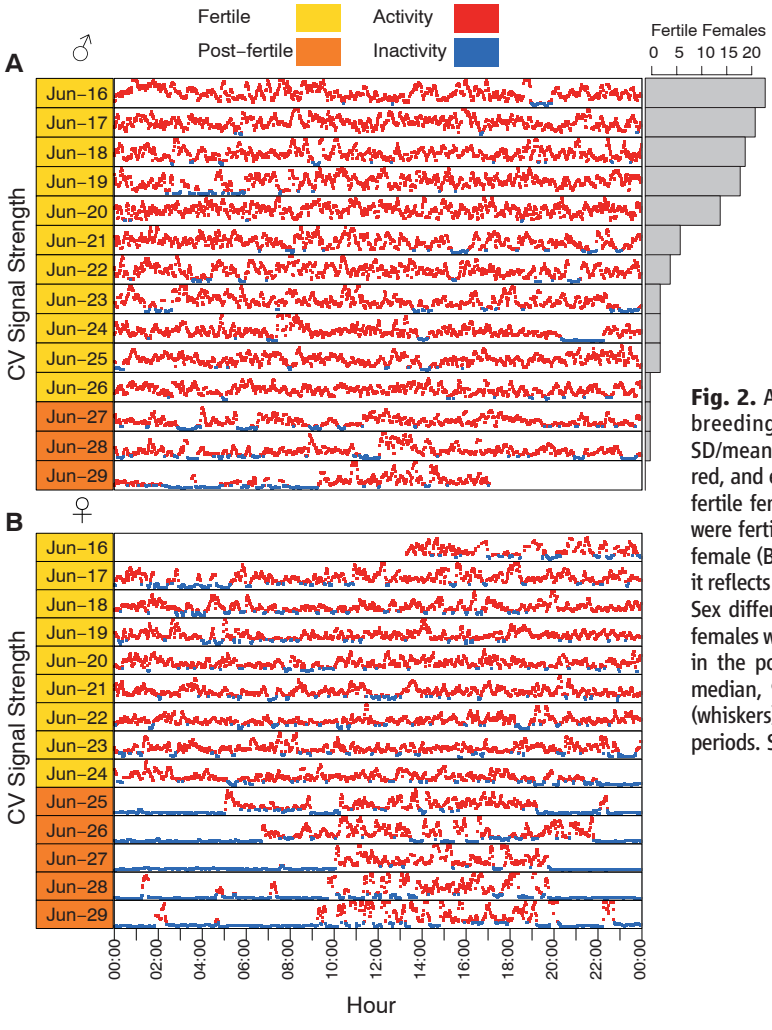
Fig. 1. Behavioral and morphological traits of polygynous male pectoral sandpipers contributing to reproductive success. (**A**) Male flight display characterized by throat inflation and hooting sounds. (**B**) Male (left) engaged in precopulation ground display to a female; illustration of sexual size dimorphism. (**C**) Males engaged in territorial ground display. (**D**) Males engaged in physical fight. (**E**) Male standing vigilant. (**F**) Males engaged in aerial chase. [CREDIT: (A) to (D) and (F) Wolfgang Forstmeier, Max Planck Institute for Ornithology; (E) B.K.]

variability in sleep duration observed across the animal kingdom reflects varying ecological demands for wakefulness, rather than different restorative requirements. According to this hypothesis, animals can evolve the ability to dispense with sleep when ecological demands favor wakefulness.

Sexual selection has led to the evolution of costly morphological, physiological, and behavioral traits (*8*). In polygynous species, in which postzygotic paternal investment in young is absent, male reproductive fitness is determined exclusively by access to fertile females. For a polygynous male to maximize his fitness, he must successfully engage in competitive displays and physical fights with other males and in courtship displays with females. Although the time available for engaging in visual displays is limited by day length at lower latitudes, it is seemingly unlimited for species that breed in the high Arctic, where the Sun never sets during the mating period. However, under these conditions the need for sleep might limit the time available for pursuing and displaying to fertile females. As such, strong sexual selection may favor an ability in males to forgo sleep without experiencing diminished neurobehavioral performance (*9*, *10*). Such



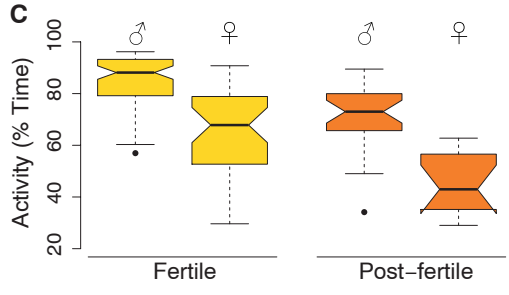


Fig. 2. Activity levels of male and female pectoral sandpipers during the breeding season. (**A** and **B**) Shown is the coefficient of variation (CV; SD/mean) of iTag signal strength (*11*). Episodes of activity are marked in red, and episodes of inactivity are marked in blue. For males, the number of fertile females present is indicated for each day. The period when females were fertile (yellow) and the post-fertile period (orange) are shown. For the female (B), this reflects her individual status whereas elsewhere [(A) and (C)] it reflects the status of all females on the study site (95% upper quantile). (**C**) Sex difference in the proportion of activity during the period when fertile females were present (males) or during a female's fertile period (yellow), and in the post-fertile period (females incubating; orange). Box plots denote median, 95% CI (notches), 1st and 3rd quartile (hinges), 99.3% of data (whiskers), and outliers (dots). Males are significantly more active in both periods. Statistical details are available in table S2.

flexibility in sleep needs could challenge the view that a fixed amount of daily sleep is needed to maintain performance.

We examined the relationship between time spent awake and reproductive output in male pectoral sandpipers (*Calidris melanotos*). The species is characterized by strong sexual size dimorphism (Fig. 1B and table S1) and a polygynous mating system without pair bonds. Males spend large amounts of time defending their territory against intruders and displaying to or chasing females. Male territories vary in size depending on density (fig. S1). Breeding males engage in display flights over females (Fig. 1A and audio S1) and in ground displays, a behavior that precedes copulation (Fig. 1B and movie S1). Females are very reluctant to copulate (*11*). Males often engage in territorial interactions, including parallel walks and physical fights with other males (Fig. 1, C and D). Males remain vigilant for intruders and females (Fig. 1E) and engage in aerial chases of females, often in direct competition (Fig. 1F). Males and females associate only temporarily for courtship and copulation; incubation and chick rearing are done exclusively by the female (*12*).

We studied a population of pectoral sandpipers on the Arctic tundra when females were fertile and post-fertile (incubating). We recorded the activity pattern of virtually every resident male pectoral sandpiper and a representative sample of females using a radiotelemetry-based system developed for this study (*11*). The system also recorded interactions between males and females. These data showed that males were more active than were females during both the fertile and post-fertile period ($n = 149$ individuals, $P < 0.001$) (Fig. 2, A to C, and table S2). Male activity declined once fertile females were no longer available ($P < 0.001$) and approached the level of female activity during the fertile period (Fig. 2C and table S2). The overall level of activity varied considerably across males, even when fertile females were available (Fig. 2C). In the most extreme case, a male was active >95% of the time for a period lasting 19 days.

Using a recently developed datalogger (*13*), we obtained combined electroencephalogram (EEG) and neck electromyogram (EMG) recordings from males on their territory (*11*). These recordings allowed us to determine whether inactive males actually spent more time sleeping than did active males or simply spent more time sitting quietly while awake. Sleep typically occurred in brief bouts between periods of activity (Fig. 3A). As in other birds (*14*, *15*), wakefulness and sleep were associated with high and low EMG activity, respectively (Welch t test, $t_{13.9} = 14.4$, $P < 0.001$) (Fig. 3B). Indeed, the sandpipers rapidly transitioned from active wakefulness to sleep without engaging in quiet wakefulness (Fig. 3A). Consequently, inactivity and activity are valid proxies for sleep and wakefulness in this context, respectively. As suggested from the activity recordings, time spent sleeping varied considerably across males (Fig. 3C), with the shortest sleeping 2.4 hours and the longest 7.7 hours (5.2 ± 0.5, mean ± SEM, $n = 11$ males). The total time males spent sleeping was correlated with the number of sleep episodes [correlation coefficient (r) = 0.79, $t_9 = 3.9$, $P = 0.004$], mean duration of individual sleep episodes ($r = 0.59$, $t_9 = 2.2$, $P = 0.057$), and maximum sleep bout duration ($r = 0.66$, $t_9 = 2.6$, $P = 0.027$) (Fig. 3D). We also examined the EEG for signs of deeper (more intense) sleep in short-sleeping males. As in mammals, avian non–rapid eye movement (REM) sleep-related EEG slow wave activity (SWA) increases as a function of the duration and intensity of prior wakefulness (*16*) and therefore may reflect sleep need and intensity. Despite experiencing more fragmented sleep, the males that slept the least showed the greatest SWA ($r = –0.60$, $t_9 = –2.27$, $P = 0.049$) (Fig. 3E), suggesting that they

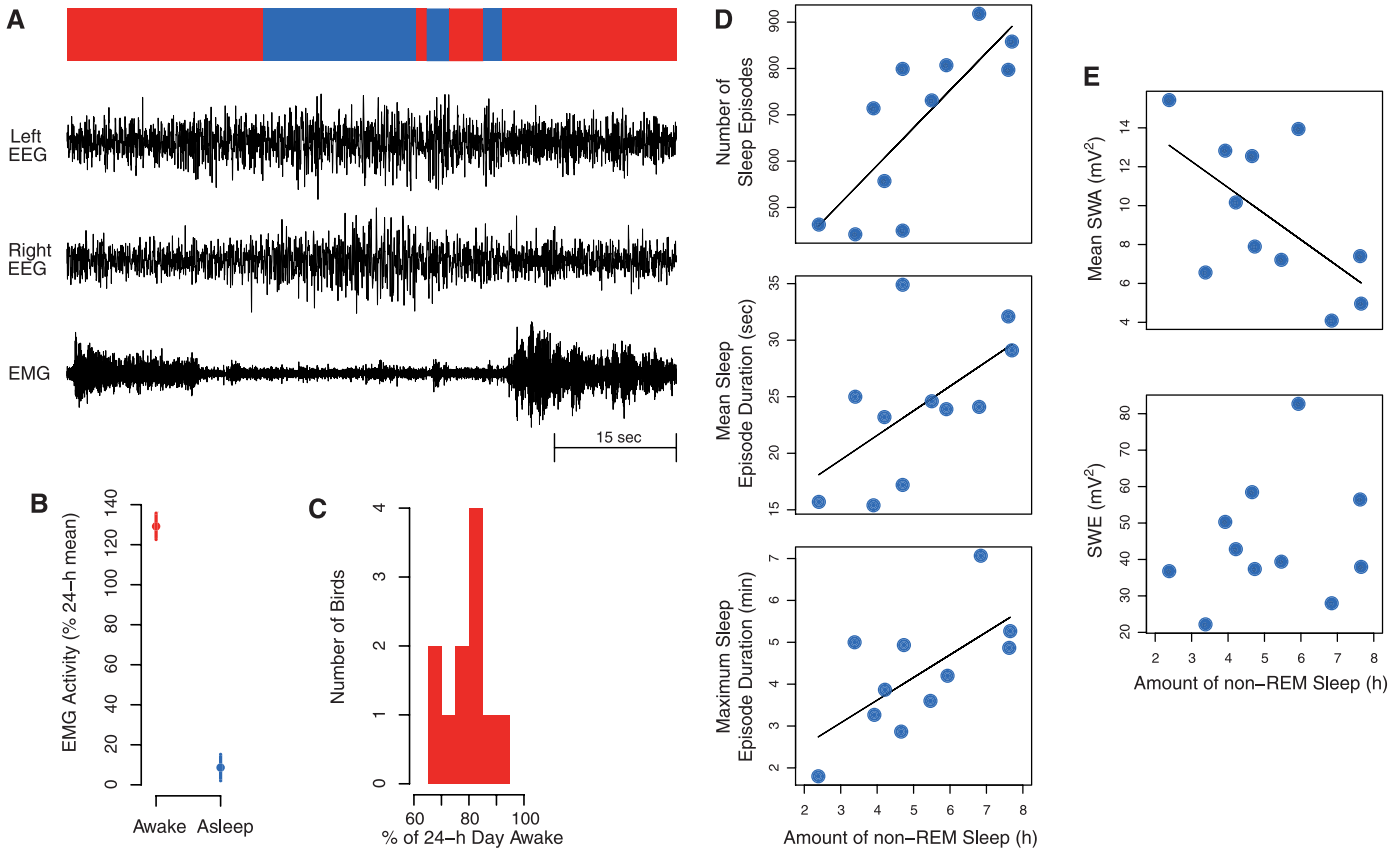


Fig. 3. Short, fragmented, but deeper sleep in extremely active males. (**A**) EEG and EMG signs of wakefulness (red) and non–REM sleep (blue) in a pectoral sandpiper. (**B**) EMG activity (mean ± 95% CI) was highest during wakefulness, reflecting virtually continuous movement. (**C**) Large variation in the amount of EEG/EMG–defined wakefulness across birds. (**D**) Short-sleeping males had fewer and shorter sleep episodes relative to long-sleepers. (**E**) SWA during non–REM sleep was greater in short-sleeping males, but SWE was not, suggesting that short-sleeping males experienced a deficit in sleep despite sleeping more deeply.

compensated, at least partially, for sleep loss by sleeping deeper. To determine whether the increase in sleep intensity compensated fully for the lost sleep, we next calculated slow wave energy (SWE; mean SWA × number of non–REM sleep epochs), a measure of cumulative non–REM sleep that accurately tracks sleep need during chronic sleep restriction (*17*). Short-sleeping males should show greater SWE than that of long-sleeping males if they compensated completely for sleep loss by sleeping deeper; however, we did not find an inverse correlation between sleep duration and SWE ($r = 0.22$, $t_9 = 0.70$, $P = 0.50$). Consequently, short-sleeping males still experienced a deficit in sleep.

We examined the relationship between male activity during the fertile period and the number of male-female interactions (telemetry-based) and resulting paternity (using microsatellite markers) (*11*). The number of different females with which a male interacted (Fig. 4A) and the total number of interactions with females (Fig. 4B) were predicted by the amount of time males were active ($n = 73$ males, $P < 0.01$ and $P = 0.017$, respectively) (table S3). Moreover, time spent active was significantly correlated with the number of females with which a male sired young ($n = 73$ males, $P = 0.004$) (Fig. 4C) and with the total number of young he sired ($P = 0.004$) (Fig. 4D). Indeed, the males that sired the most young were among the most active.

To determine whether there are long-term costs associated with sleep restriction and fragmentation during the breeding season, we examined the return rate and reproductive success of males across years. Males rarely returned to the study site ($n = 13$ out of 640 males across 6 years). Nonetheless, the probability of return was 10% higher [confidence interval (CI) 95%: 0 to 20%] for successful males than for males that did not sire offspring (generalized linear model with binomial error, two-tailed test, $P = 0.08$), a trend opposite to that expected if short-sleeping males experienced reduced survivorship. Moreover, 58% of the returning males were successful in siring at least one offspring in the second year, compared with only 20% of other males in the population (Fisher's exact test, $P = 0.005$). This suggests that reproductively successful males either survive better across years than do unsuccessful males or show greater fidelity to areas where they have successfully reproduced.

Reduced sleep has been described in caged white-crowned sparrows (*Zonotrichia leucophrys gambelii*) and Swainson's thrush (*Catharus ustulatus*) exhibiting nocturnal migratory restlessness (*14*, *18*). However, in contrast to pectoral sandpipers, which only compensated partially for sleep loss by sleeping more deeply, songbirds compensated for sleep loss at night by increasing the time spent drowsy and sleeping during each day. Furthermore, sleep loss was associated with decreased performance on certain cognitive tasks (*19*), and the relationship between sleep duration and reproductive output was not addressed. Similarly, in dolphins the relationship between extended periods of constant swimming with environmental awareness and reproductive success has not been determined (*20*, *21*).

Three pieces of evidence suggest that the amount of wakefulness is under strong sexual selection. First, males were more active than were females when females were fertile. Second, the total time a male was active during the fertile period was a strong predictor of his reproductive output. Third, the relationship between activity and reproductive output is probably directly related to competition for access to fertile females because a male's reproductive success was strongly related to the proportion of time he was observed showing territorial or courtship behavior (table S4). Moreover, male activity was also a good predictor of the total number of interactions with females, and of the total number of different females with which a male interacted.

The recent discovery of sleep-like neuronal activity occurring locally in the cortex during wakefulness in sleep-deprived rats (*5*) raises the possibility that the "missing" sleep occurred in a similar manner in short-sleeping male pectoral sandpipers. This is unlikely, however, because local sleep only occurred while the rats were immobile, and performance on a foraging task was impaired if local sleep occurred in the motor cortex shortly before the task. The high reproductive success of our short-sleeping males suggests that they were not similarly impaired.

Male pectoral sandpipers forgo sleep to ensure paternity, exactly as the adaptive inactivity hypothesis predicts. However, if sleep is expendable, why do some males sleep more than others when fertile females are available? Although defeated males may give up and resort to sleeping to save energy, the energy saved by sleeping instead of sitting quietly awake (*22*) would need to offset the potential cost of increased predation risk during sleep (*23*). Moreover, the increase in sleep intensity in short-sleeping males suggests that sleep serves a restorative function. In this case, long-sleeping males may lack genetic traits that enable short-sleeping males to maintain high performance on little sleep. Indeed, interindividual variation in neurobehavioral vulnerability to sleep loss was recently linked to genetic polymorphisms in humans (*24*). If there is a genetic basis to male-male variability in sleep duration and resulting neurobehavioral performance in pectoral sandpipers, then the persistence of the long-sleeping phenotype suggests that it may be equally suc-

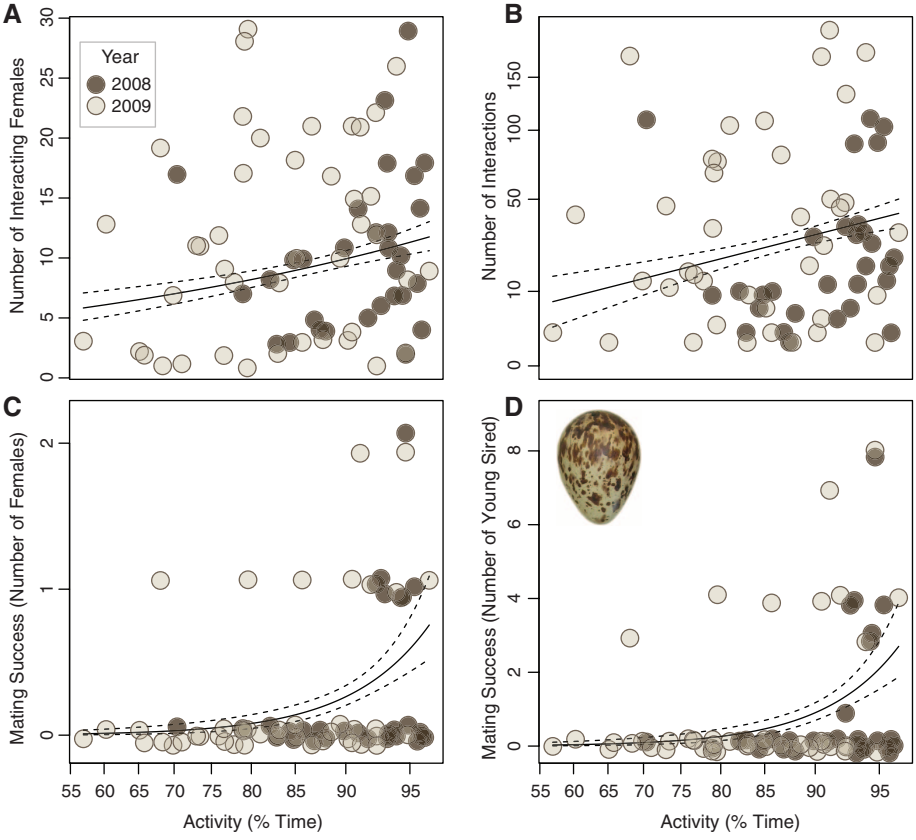


Fig. 4. High activity contributes to male reproductive success. The proportion of time a male was active during the period when fertile females were present is a significant predictor of (**A**) the total number of different females with whom he interacted, (**B**) the total number of interaction bouts with females, (**C**) the number of females with whom he sired offspring, and (**D**) the total number of offspring he sired in a given year. Shown are the raw data and the fitted lines together with 95% CIs. Statistical details are available in table S3.

cessful over the long term. However, our limited across-season data suggests that short-sleeping males may actually perform better than do long-sleeping males over the long term, suggesting ongoing sexual selection instead. Ultimately, a greater understanding of potential short- and long-term costs of reproductive sleep loss in pectoral sandpipers may provide insight into the evolution of this extreme behavior, as well as the ongoing debate over the functions of sleep (*25*) and its relationship to health and longevity in humans (*26*, *27*).

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Supplementary Materials

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Database S1

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Mutations in the *neverland* Gene Turned *Drosophila pachea* into an Obligate Specialist Species

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Most living species exploit a limited range of resources. However, little is known about how tight associations build up during evolution between such specialist species and the hosts they use. We examined the dependence of *Drosophila pachea* on its single host, the senita cactus. Several amino acid changes in the Neverland oxygenase rendered *D. pachea* unable to transform cholesterol into 7-dehydrocholesterol (the first reaction in the steroid hormone biosynthetic pathway in insects) and thus made *D. pachea* dependent on the uncommon sterols of its host plant. The *neverland* mutations increase survival on the cactus's unusual sterols and are in a genomic region that faced recent positive selection. This study illustrates how relatively few genetic changes in a single gene may restrict the ecological niche of a species.

Losses of enzymatic activities are frequent during evolution (*1*). For example, humans lost the ability to produce nine amino acids and six vitamins, for which we rely on our diet (*2*). The reasons for such losses are unknown, but it is generally believed that "superfluous" metabolic activities were lost by chance during evolution (*3*). We examined the dependence of the fly *Drosophila pachea* on the senita cactus (*Lophocereus schottii*), a plant species endemic to the Sonoran desert (northwestern Mexico and southwestern United States). In insects, developmental transitions and egg production are regulated by the steroid hormone ecdysone (*4*). However, *D. pachea* has lost the first metabolic reaction in the ecdysone biosynthetic pathway, i.e., the ability to convert cholesterol into 7-dehydrocholesterol (7DHC) (Fig. 1A) (*4*–*7*). The senita cactus, which *D. pachea* requires as a host (*5*), does not contain common sterols and is the only plant in the Sonoran desert (*7*) known to produce Δ7-sterols such as lathosterol (*6*). *D. pachea* flies do not reach the adult stage if not raised on senita cactus, but supplementing standard food with senita cactus or with 7DHC fully restores *D. pachea* viability and fertility (*5*), indicating that Δ7-sterols are essential compounds required for *D. pachea* development and survival. Interestingly, *D. pachea* appears to depend on the senita cactus solely for its sterols, as we raised *D. pachea* on an artificial diet supplemented with 7DHC for more than 4 years (~60 generations) with no apparent defect (*8*).

Conversion of cholesterol into 7DHC is catalyzed by the evolutionarily conserved Rieske-domain oxygenase Neverland (NVD) in insects and nematodes (*9*, *10*). To investigate whether mutation(s) in *nvd* are responsible for *D. pachea* dependence on its host cactus, we sequenced the *nvd* coding region (*8*) from *D. pachea* and the three most closely related species—*D. nannoptera*, *D. acanthoptera*, and *D. wassermani*—which feed on other cacti (*11*) (tables S1 and S2 and fig. S1). No stop codon or insertions/deletions were found in the *D. pachea* sequence, but the ratio of rates of nonsynonymous substitution (d_N) over synonymous substitution (d_S) is significantly higher in the branch leading to *D. pachea* (table S3 and fig. S2). We noticed that several amino acids showing high conservation across insects and vertebrates are different in *D. pachea* NVD (Fig. 1, B and C).

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Supplementary Material for

Adaptive Sleep Loss in Polygynous Pectoral Sandpipers

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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

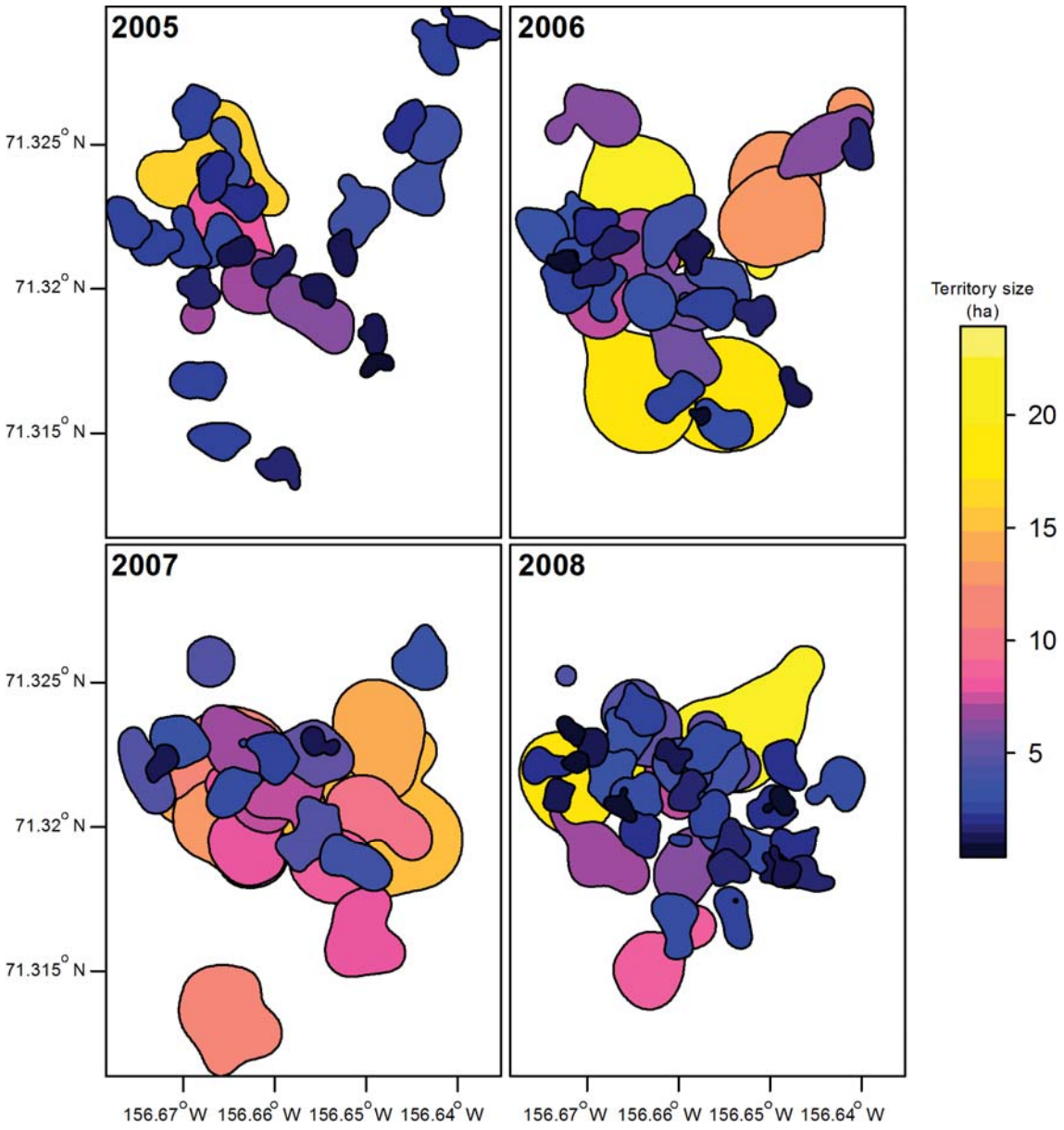

Fig. S1. Maps depicting density of male territories. Territories of male pectoral sandpipers during four breeding seasons (2005 – 2008) in Barrow, Alaska. A fixed kernel density estimator was used to construct 80% utilization distribution probabilities based on sets of GPS locations for each male. Only 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

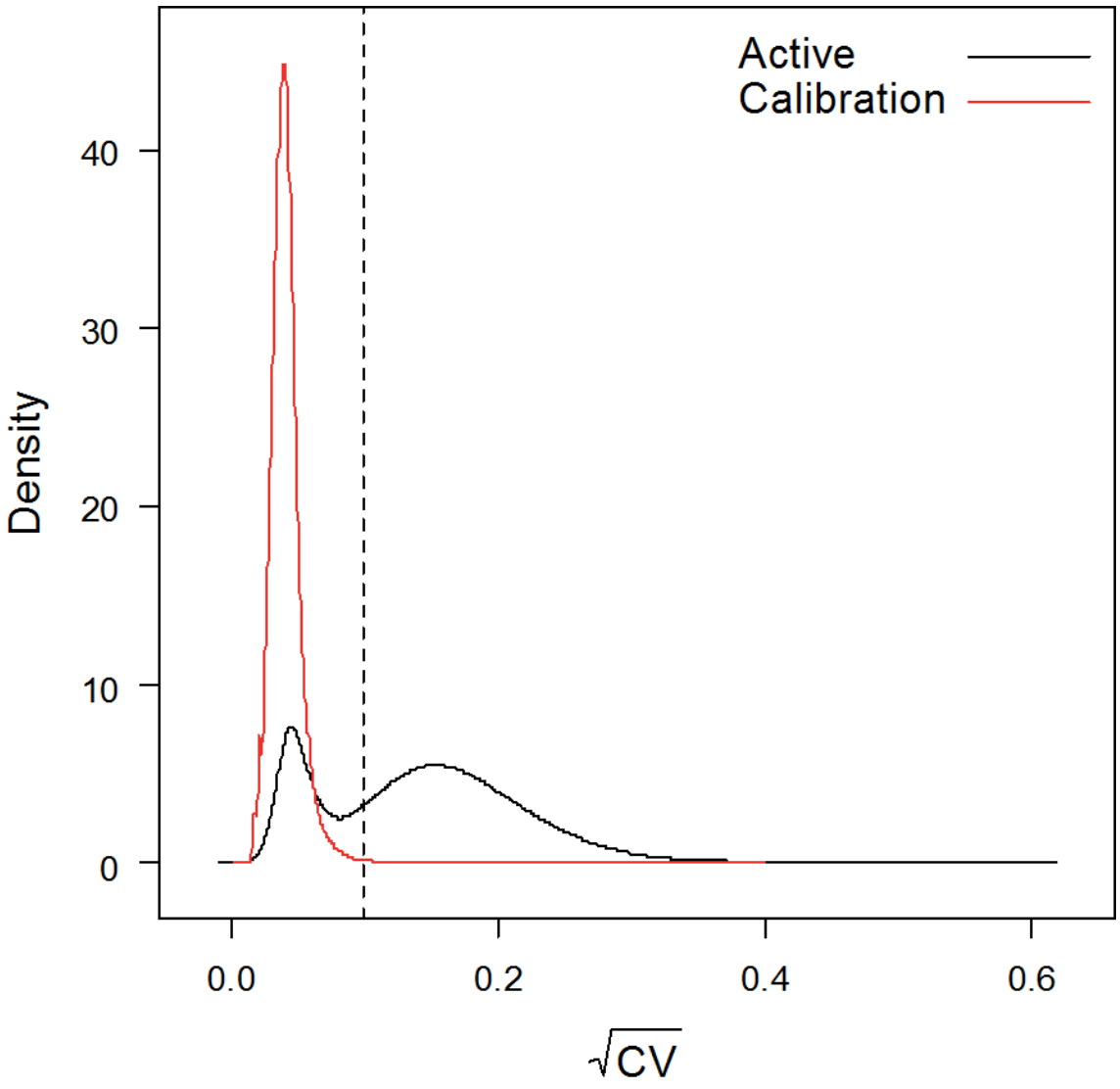

Fig. S3. Calibration of activity tags. Density plot of signal strength coefficient of variance (CV, square-root transformed) of the calibration tags (red) and the tags attached to a bird (black). Note the bimodal distribution of the tags on birds. The vertical dotted line is the 99% upper confidence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