



## Adaptive Sleep Loss in Polygynous Pectoral Sandpipers

John A. Lesku *et al.*  
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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](http://www.sciencemag.org/cgi/content/full/337/6102/1651/DC1)

Materials and Methods

Supplementary Text

Table S1

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Database S1

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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.

**S**leep 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 con-

sequences 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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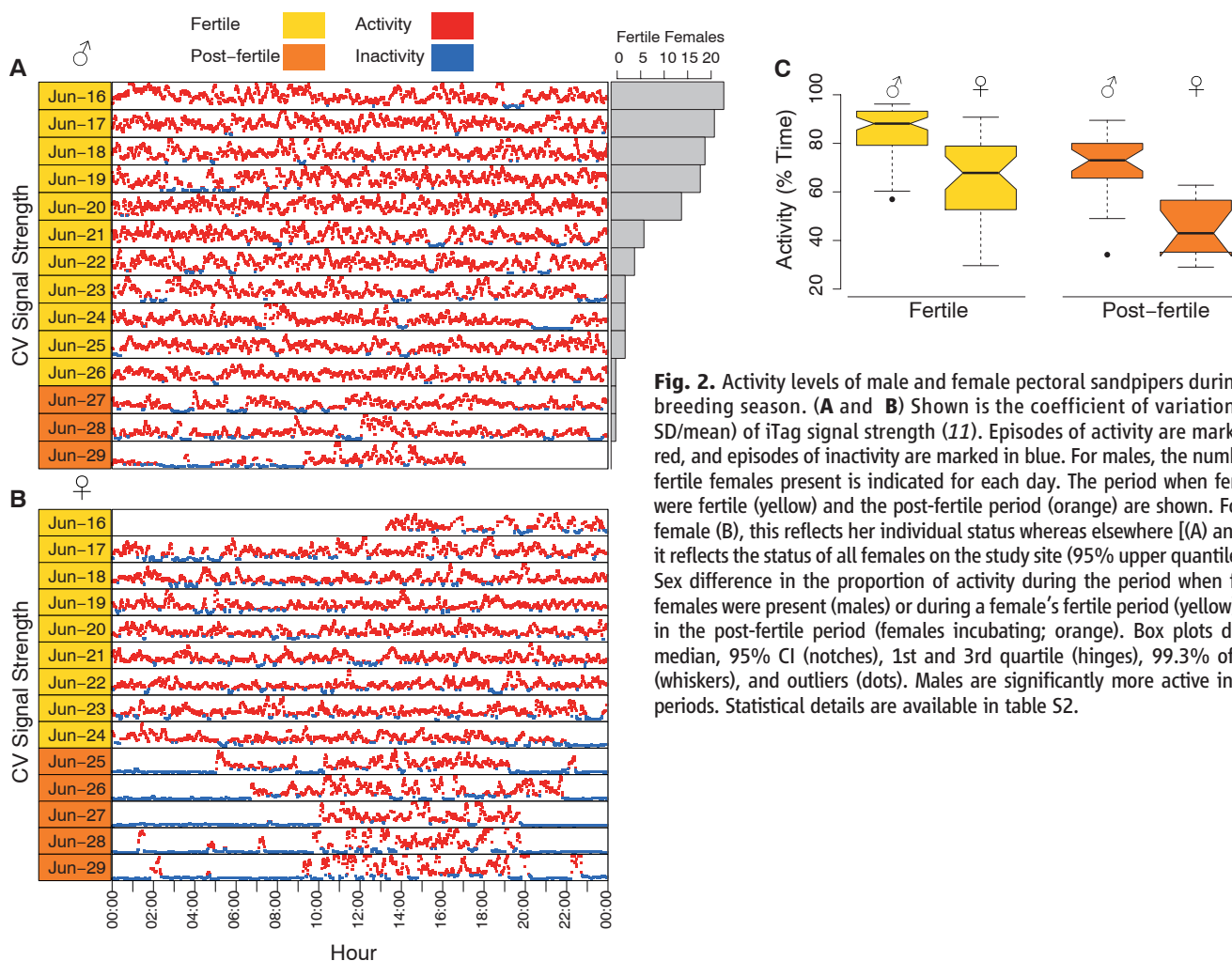
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**Fig. 1.** Behavioral and morphological traits of polygynous male pectoral sandpipers contributing to reproductive success. (A) Male flight display characterized by throat inflation and hooting sounds. (B) Male (left) engaged in precopulation ground 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.

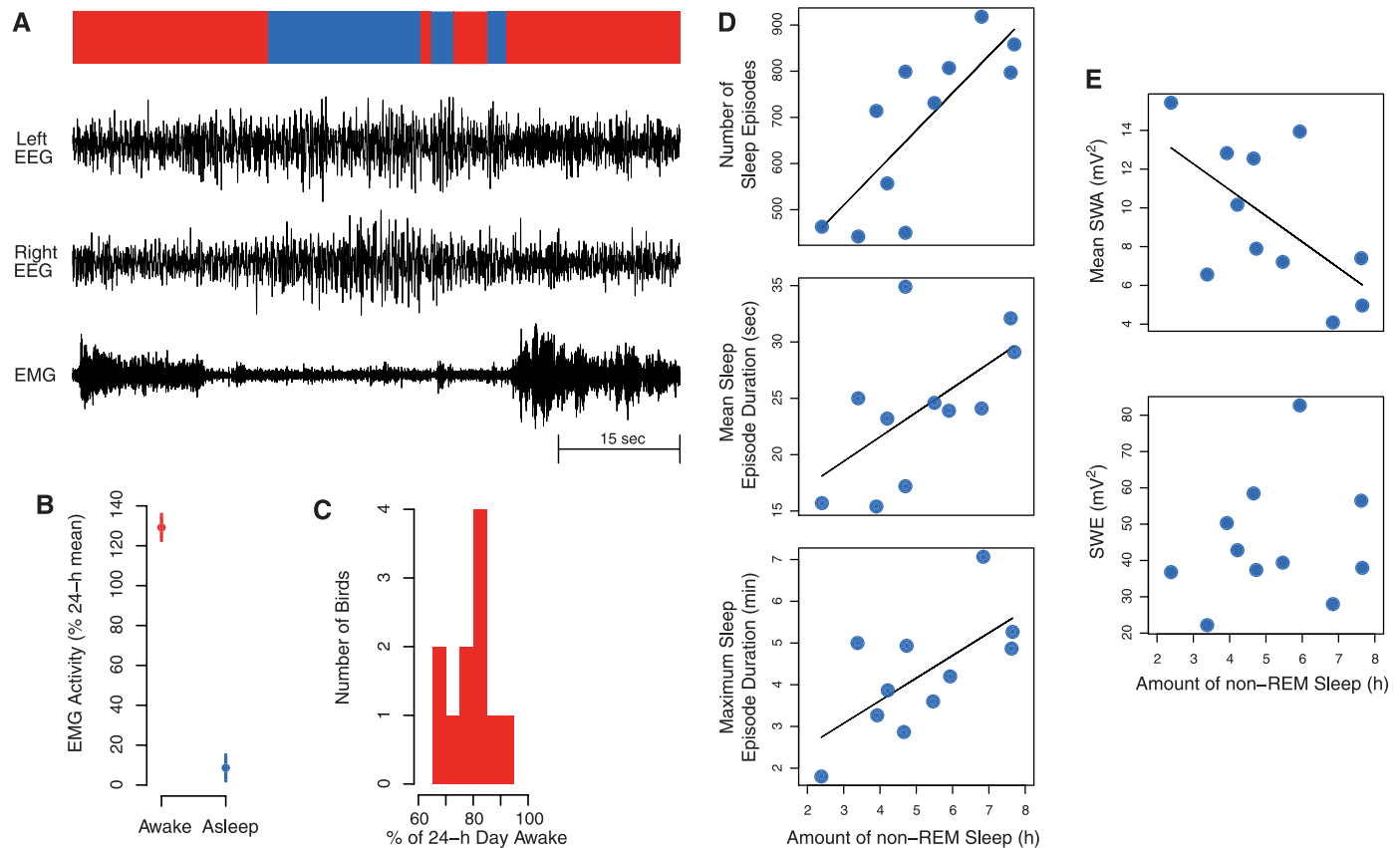
We examined the relationship between time spent awake and reproductive output in male pectoral sandpipers (*Calidris melanotos*). The species is characterized by strong sexual size dimorphism (Fig. 1B and table S1) and a polygynous mating system without pair bonds. Males spend large amounts of time defending 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 ( $5.2 \pm 0.5$ , mean  $\pm$  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  $\pm$  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  $\times$  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.

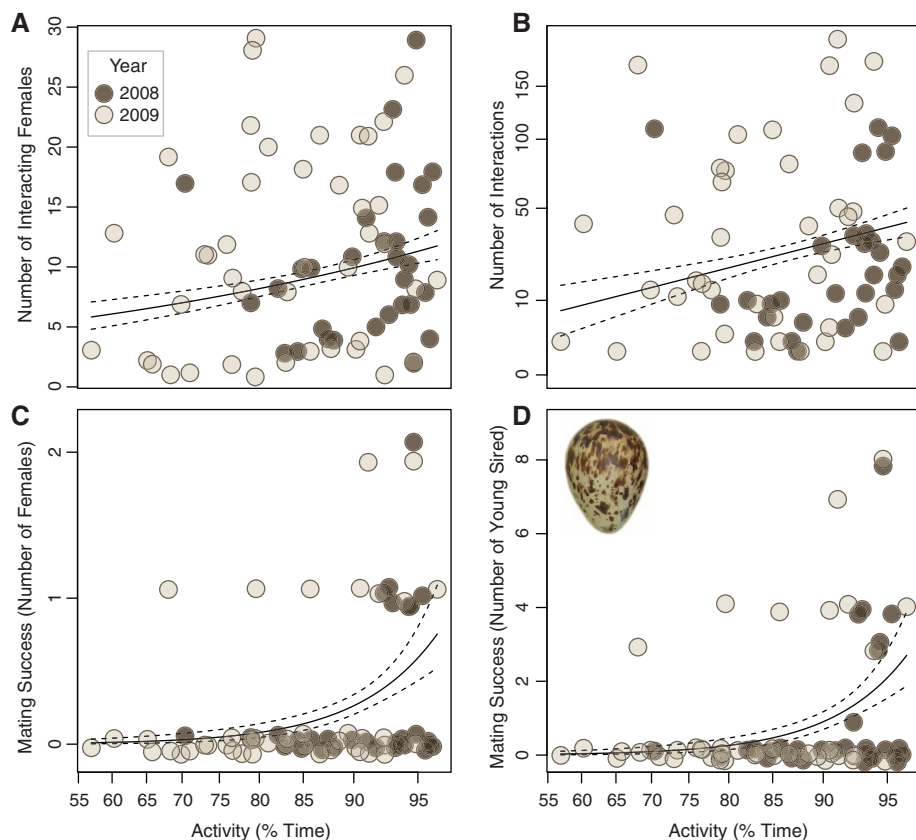
Reduced sleep has been described in caged white-crowned sparrows (*Zonotrichia leucophrys*

*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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Tables S1 to S4  
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Movie S1  
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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  $\Delta 7$ -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  $\Delta 7$ -sterols are essential compounds required for *D. pachea* development and surviv-

al. 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. nanoptera*, *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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