

space requirements, and progressively saturates our capacity to learn. This is in agreement with the way Yoo *et al.* [12] interpret their results.

The second part of the hypothesis brings sleep into play. During sleep, slow waves start to emerge and become more frequent and of larger amplitude the deeper we fall asleep. Such slow waves, even though mainly a cortical phenomenon, seem to persist also in the hippocampus [18]. The synaptic homeostasis hypothesis now predicts that the amount of slow waves, quantified as slow wave activity, is reflecting synaptic strength. Thus, the increase of slow wave activity after wakefulness would be a direct reflection of strengthening of synapses. Slow wave activity during sleep is not, however, just an epiphenomenon of increased synaptic strength, but has a role to play. It causes the downscaling of synapses: a generalized decrease in synaptic strength that recalibrates neural circuits [19]. Such synaptic downscaling would be reflected in the well-known progressive decrease of slow wave activity during an ordinary night of sleep, gradually reducing synaptic strength and returning it to an appropriate baseline level. Again, the key functional corollary is that synaptic downscaling has benefits in terms of energy and space requirements and, due to increased signal-to-noise ratios, in terms of learning and memory. Thus, when we wake up, neural circuits do preserve a trace of previous experiences, but are kept efficient at a recalibrated level of synaptic strength, and the cycle can begin again.

The synaptic homeostasis hypothesis is based on a large number of observations at many different levels, from molecular and cellular biology to systems neurophysiology and neuroimaging [15,16]. Thus, according to the hypothesis, to preserve, in the long run, the ability to acquire new information, we need to entertain a healthy balance between wakefulness and sleep. In that respect the new work of Yoo *et al.* [12] provides a very important piece of information, namely that

memory networks, as is the hippocampal complex, seem to be susceptible to even one night of sleep deprivation. Particularly today this could be an important conclusion because many people do not get enough sleep. Accordingly, Walker's team calls their findings "worrying considering society's increasing erosion of sleep time."

References

1. Hendricks, J.C., Finn, S.M., Panckeri, K.A., Chavkin, J., Williams, J.A., Sehgal, A., and Pack, A.I. (2000). Rest in *Drosophila* is a sleep-like state. *Neuron* 25, 129–138.
2. Shaw, P.J., Cirelli, C., Greenspan, R.J., and Tononi, G. (2000). Correlates of sleep and waking in *Drosophila melanogaster*. *Science* 287, 1834–1837.
3. Borbély, A.A., and Achermann, P. (2000). Homeostasis of human sleep and models of sleep regulation. In *Principles and Practice of Sleep Medicine*, M.H. Kryger, T. Roth, and W.C. Dement, eds. (Philadelphia: W.B. Saunders), pp. 377–390.
4. Van Dongen, H.P., Maislin, G., Mullington, J.M., and Dinges, D.F. (2003). The cumulative cost of additional wakefulness: dose-response effects on neurobehavioral functions and sleep physiology from chronic sleep restriction and total sleep deprivation. *Sleep* 26, 117–126.
5. Dinges, D.F. (2006). The state of sleep deprivation: From functional biology to functional consequences. *Sleep Med. Rev.* 10, 303–305.
6. Steriade, M., McCormick, D.A., and Sejnowski, T.J. (1993). Thalamocortical oscillations in the sleeping and aroused brain. *Science* 262, 679–685.
7. Benington, J.H., and Frank, M.G. (2003). Cellular and molecular connections between sleep and synaptic plasticity. *Prog. Neurobiol.* 69, 71–101.
8. Jha, S.K., Jones, B.E., Coleman, T., Steinmetz, N., Law, C.T., Griffin, G., Hawk, J., Dabbish, N., Kalatsky, V.A., and Frank, M.G. (2005). Sleep-dependent plasticity requires cortical activity. *J. Neurosci.* 25, 9266–9274.
9. Steriade, M. (1999). Coherent oscillations and short-term plasticity in corticothalamic networks. *Trends Neurosci.* 22, 337–345.
10. Frank, M.G., Issa, N.P., and Stryker, M.P. (2001). Sleep enhances plasticity in the developing visual cortex. *Neuron* 30, 275–287.
11. Stickgold, R. (2005). Sleep-dependent memory consolidation. *Nature* 437, 1272–1278.
12. Yoo, S.S., Hu, P.T., Gujar, N., Jolesz, F.A., and Walker, M.P. (2007). A deficit in the ability to form new human memories without sleep. *Nat. Neurosci.* 10, 385–392.
13. Basheer, R., Strecker, R.E., Thakkar, M.M., and McCarley, R.W. (2004). Adenosine and sleep-wake regulation. *Prog. Neurobiol.* 73, 379–396.
14. Frankland, P.W., and Bontempi, B. (2005). The organization of recent and remote memories. *Nat. Rev. Neurosci.* 6, 119–130.
15. Tononi, G., and Cirelli, C. (2003). Sleep and synaptic homeostasis: a hypothesis. *Brain Res. Bull.* 62, 143–150.
16. Tononi, G., and Cirelli, C. (2006). Sleep function and synaptic homeostasis. *Sleep Med. Rev.* 10, 49–62.
17. Bliss, T.V., and Collingridge, G.L. (1993). A synaptic model of memory: long-term potentiation in the hippocampus. *Nature* 361, 31–39.
18. Tononi, G., Massimini, M., and Riedner, B.A. (2006). Sleepy dialogues between cortex and hippocampus: who talks to whom? *Neuron* 52, 748–749.
19. Turrigiano, G.G., and Nelson, S.B. (2004). Homeostatic plasticity in the developing nervous system. *Nat. Rev. Neurosci.* 5, 97–107.

Children's Hospital of the University of Zurich, Steinwiesstrasse 75, 8032 Zurich, Switzerland.
E-mail: reto.huber@kispi.unizh.ch

DOI: 10.1016/j.cub.2007.03.029

Evolutionary Biology: Variation Isn't Always Sexy

A recent study has found that differences in a male trait, considered a textbook example of sexual selection, are in fact due to naturally selected variation in the aerodynamic optimum for each individual.

Rebecca J. Safran¹
and Mark E. Hauber²

The trouble with Darwinian sexual selection is that it appears to contradict predictions of Darwinian natural selection: sexually

selected traits are considered to be costly, while naturally selected traits are considered to be beneficial in terms of survival-related fitness [1,2]. Both are predicted to increase the lifetime reproductive success of individuals.

Traditional approaches in evolutionary biology have assumed that sexual selection operates on most traits that are sexually dimorphic and that reduce the foraging or survival success of its bearers (reviewed in [3]). Thus, sex differences of an ornamental trait must be under sexual selection and convey information to potential mates and competitors in the population about the individual's quality, status, and fighting ability. Yet, until a study reported in this issue of *Current Biology* [4], the assumption about sexual selection being the primary mechanism underlying variation between individuals in ornamental traits has remained untested.

The reality faced by anyone studying phenotype is that traits that serve an individual in both mating and non-mating contexts may have both naturally and sexually selected components. Although, at times, differences between the mechanisms are hotly debated [3,5], various models of sexual selection predict that it is the sexually selected portion of the trait in question that has evolved to signal individual quality, because it provides useful information to an audience interested in sorting out potential mates (intersexual mate choice) and true competitors in the bunch (intrasexual competition [3]). It is easy to see how peacock trains and loud birdsong all represent classically sexually selected traits, in that these components of the phenotype do little to increase the day-to-day survival or foraging success of individuals, and instead represent a hazard through attracting predators and reducing the chances of escape. So what about those traits that are used to improve the survival of individuals, or their young, but that are also used by potential mates to assess indirect or direct benefits of mate choice? For instance, nest architecture is the basis for mate choice in Baya



Figure 1. A male's outer tail streamers are visible as he approaches the nest to feed his young.

Weavers *Ploceus philippinus* (mating investment, sexual selection), but it also indicates sturdier nest structures that protect eggs and young better (parental investment, natural selection [6]).

Elongated tail streamers of Barn Swallows, *Hirundo rustica* (Figure 1), are a textbook example of a trait that is involved in mate acquisition and also affects an individual's survival [7]: individuals with longer streamers suffer from impaired aerodynamic performance which may result in lower foraging efficiency [8,9]. But swallows with too short a set of streamers also suffer from reduced flight skills, implying that natural selection already shaped the morphology of this species to accommodate elongation and sexual dimorphism of tail streamers [10]. In a novel set of experiments, Bro-Jørgensen *et al.* [4] have taken an individual-based approach to elucidate the extent to which variation in the length between male swallows' streamers either reflects differential ability to withstand the costs of 'too long' streamers, as predicted by handicap-models of sexual selection [11], or represents the individual-specific match between body size and tail streamer length to optimize

flight and foraging performance, as predicted by survival-based natural selection.

Ever since the notable experimental studies of Anders Møller in the late 1980s [12], the elongated tail streamers of barn swallows have been considered a classic example of sexual selection: in several populations of barn swallows, males with longer tail streamers have been shown to enjoy greater reproductive success than their short-streamered neighbours. Although there is mounting evidence of fascinating geographic differences in the extent of sexual selection on this trait across populations [13–16], using tail length manipulations researchers have shown that males from the European sub-species with streamers that had been experimentally elongated garnered greater reproductive success, both in terms of social pairbonds and genetic measures of reproductive output, compared to males whose streamers were experimentally shortened (for example [17]).

But tail streamers are also critical for barn swallow flight performance, as they need to function efficiently for this aerial insectivore. One needs to look no further than female and juvenile barn swallows — they too exhibit extensively forked

tails used in flight control. Evans and colleagues, in a series of publications [10,18,19] culminating in the most recent work published in this issue [4], have addressed this primary question: what is the underlying evolutionary cause of tail streamer length variation in barn swallow males? The authors have devised an experimental protocol that allows them to identify the length of the streamers that maximize flight-performance (the naturally selected optimum), and to calculate the extent of exaggeration represented by sexual selection (mate choice for longer tail streamers), by taking the difference of the actual streamer length and the estimated flight-optimising length. Using sophisticated equations, in the new paper [4] they then answer the question: does variation in streamer length represent differences in the naturally selected optimum associated with each individuals' phenotype? Or does it represent differences in the sexually selected exaggeration of tail streamers?

Through their serial manipulations of the same individuals' tail lengths, Bro-Jørgensen *et al.* [4] worked out the relative importance of natural and sexual selection contributing to the variation in the length of the tail streamer. Specifically, these elegant series of streamer manipulations of the same males were employed to determine each individual's aerodynamic performance tested in a flight maze and in terms of the size of prey captured, to estimate foraging efficiency. The authors' conclusions are surprising, as no evidence was found to support the basic assumption that the sexually selected component of this trait reflects individual variation in some aspects of male quality as an advertisement to choosy females or competitive males. Instead, the authors conclude that the optimal

streamer length varies significantly among males, but that the additional component of the streamer — assumed to be caused by sexual selection — does not. This result counters the patterns predicted for variable sex-dimorphic traits under sexual selection. The conclusion is that it is the naturally selected, and not the sexually selected, component of the streamer that conveys information about a male's flight and foraging performance, leaving open the question of why streamers are elongated past this optimal value. In other words, swallow tail streamers are in fact not a true ornament, and variation beyond the naturally selected optima may simply serve to signal the age and sex of the individual (adult male versus female or juvenile).

Teasing apart the extent to which variation in a phenotypic trait is the result of natural selection, sexual selection, or both is not a trivial endeavor but the resulting information is critical for determining the evolutionary forces at hand. The compelling results reported by Bro-Jørgensen *et al.* [4] bring to light new questions not only about the information content that individuals may glean from a male's streamer length in a classic study system for sexual selection theory. These results also open doors for investigators to carefully consider experiments that test for relative contributions of natural and sexual selection as explanations for variation in traits used in the context of female mate choice and male-male competition. Previously, all models of sexual selection made the assumption that variation in ornamental traits are the result of mate-acquisition behaviours, but this new study forces us to adopt a broader perspective.

References

1. Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (London: John Murray).

2. Darwin, C. (1871). *The Descent of Man, and Selection in Relation to Sex* (London: John Murray).
3. Andersson, M. (1994). *Sexual Selection* (Princeton: Princeton University Press).
4. Bro-Jørgensen, J., Johnstone, R.A., and Evans, M.R. (2007). Uninformative exaggeration of male sexual ornaments in barn swallows. *Curr. Biol.* *17*, 850–855.
5. Andersson, M., and Simmons, L.W. (2006). Sexual selection and mate choice. *Trends in Ecol. Evol.* *21*, 296–302.
6. Quader, S. (2006). What makes a good nest? Benefits of nest choice to female Baya Weavers (*Ploceus philippinus*). *Auk*. *123*, 475–486.
7. Dugatkin, L.A. (2004). *Principles of Animal Behavior* (New York: W.W. Norton).
8. Møller, A.P., and de Lope, F. (1994). Differential costs of a secondary sexual character: an experimental test of the handicap principle. *Evol.* *48*, 1676–1683.
9. Møller, A.P., Barbosa, A., Cuervo, J.J., de Lope, F., Merino, S., and Saino, N. (1998). Sexual selection and tail streamers in the barn swallow. *Proc. R. Soc. Lond. B* *265*, 409–414.
10. Evans, M.R. (1998). Selection on swallow tail streamers. *Nature* *394*, 233–234.
11. Zahavi, A. (1975). Mate selection — a selection for a handicap. *J. Theor. Biol.* *53*, 205–214.
12. Møller, A.P. (1988). Female choice selects for male sexual tail ornaments in the monogamous swallow. *Nature* *332*, 640–642.
13. Smith, H.G., Montgomerie, R., Pöldmaa, T., White, B.N., and Boag, P.T. (1991). DNA fingerprinting reveals relation between tail ornaments and cuckoldry in barn swallows, *Hirundo rustica*. *Behav. Ecol.* *2*, 90–98.
14. Safran, R.J., and McGraw, K.J. (2004). Plumage coloration, not length or symmetry of tail-streamers, is a sexually selected trait in North American barn swallows. *Behav. Ecol.* *15*, 455–461.
15. Safran, R.J., Neuman, C.R., McGraw, K.J., and Lovette, I.J. (2005). Dynamic paternity allocation as a function of male color in barn swallows. *Science* *309*, 2210–2212.
16. Neuman, C.R., Safran, R.J., and Lovette, I.J. (2007). Tail streamer length does not predict apparent or genetic reproductive success in North American barn swallows. *J. Avian Biol.* *38*, 28–36.
17. Saino, N., Primmer, C.R., Ellegren, H., and Møller, A.P. (1997). An experimental study of paternity and tail ornamentation in the barn swallow (*Hirundo rustica*). *Evolution* *51*, 562–570.
18. Buchanan, K.L., and Evans, M.R. (2000). The effect of tail streamer length on aerodynamic performance in the barn swallow. *Behav. Ecol.* *11*, 228–238.
19. Rowe, L.V., Evans, M.R., and Buchanan, K.L. (2001). The function and evolution of the tail streamer in hirundines. *Behav. Ecol.* *12*, 157–163.

¹Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08540, US. ²School of Biological Sciences, University of Auckland, PB 92019, Auckland, New Zealand.
E-mail: rsafran@princeton.edu,
m.hauber@auckland.ac.nz