How do birds deal with sleep in their long nonstop flights?

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With wide use of satellite tracking techniques on birds, more and more bird species have been found to fly continuously for extremely long time (even up to ca. 200 days) (Battley et al., 2012; Liechti et al., 2013; Rattenborg, 2017; Rattenborg et al., 2016, 2017). These extraordinary flights have deeply drawn biologists' interest in that they contradict our deeply-rooted views about sleep (Rattenborg, 2006, 2017). Firstly, if we perceive sleep as a motionless, unconscious and necessary state as shown in most of terrestrial animals, how can birds fly while sleeping (Rattenborg, 2006). Secondly, assuming that sufficient daily sleep is essential to perform well during wakefulness for almost all animals and that birds cannot sleep during flights, how can birds stay awake so long without apparent cognitive decline (Lesku, 2014; Rattenborg, 2006)? This colloquium discussed the main question – how do birds deal with sleep in their long nonstop flights – with emphasis on those two puzzles.

So far only one study has empirically investigated sleep in birds during their long nonstop flights and it is revealed that great frigatebirds (*Fregata minor*) were indeed engaged in sleep in mid-flight, including both slow wave sleep (SWS) and rapid eye movement (REM) sleep (two types of sleep defined in electrophysiology) (Rattenborg et al., 2016). During SWS, birds could sleep unihemispherically, similar to dolphins (Lyamin et al., 2008), and bihemispherically (Rattenborg et al., 2016). Duration of a sleep episode was shorter in flight than on land (Rattenborg et al., 2016). Sleep only occurred during soaring and gliding flight modes when strong wing movement was not required (Rattenborg et al., 2016).

Despite the ability to sleep in mid-flight, birds still lose considerable amount of sleep during their long nonstop flights (Rattenborg et al., 2004, 2016). However, for nocturnally migrating songbirds that experience huge sleep reduction during their migration, they might not suffer from negative cognitive consequences despite little sleep they took per day throughout the migration (Rattenborg et al., 2004). However, their cognitive performance was adversely affected by experiment-induced sleep restriction during the non-migratory season (Rattenborg et al., 2004). This suggests that songbirds might exhibit the capability of foregoing sleep without apparent negative impacts only during migratory season (Fuchs et al., 2006; Rattenborg et al., 2004). Therefore, it is inferred that this capability might evolve with migration or other ecological circumstances (Fuchs et al., 2006; Rattenborg et al., 2004).

Numerous exciting questions still remain to be investigated in the field of avian sleep, especially their sleep during long nonstop active flights (Lesku, 2014; Rattenborg, 2017). For example, we have little knowledge of physiological and neural mechanisms underlying the adaptation of foregoing most sleep over long period as observed in some birds (Lesku, 2014; Rattenborg et al., 2017). About sleep in flight, it remains largely unknown whether continuously flapping birds can sleep on the wing during their long nonstop flights (Rattenborg et al., 2017). All of these exciting questions motivate us to unveil sleep puzzles in the incredible flights many birds

take.

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