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DO MIGRATORY BIRDS NEED A NAP AFTER A LONG NON-STOP FLIGHT?

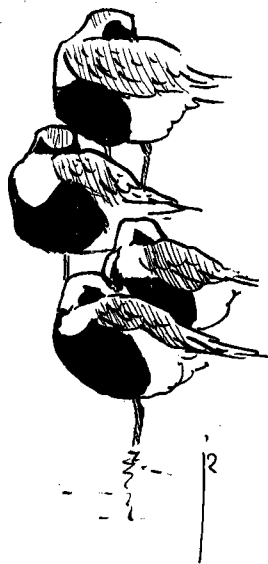
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After a prolonged period of sleep deprivation, the urge to sleep overrules all other activities. Despite this well-known fact, the occurrence of sleep after naturally occurring sleep deprivation during long non-stop migratory flight in birds has hardly been investigated. The aim of this communication is to stimulate quantitative studies on the requirement for sleep in migrating birds. We present some observations on birds just after landing from a long non-stop flight which indicate that the urge to sleep may take preference over other activities. We ask the question whether sleep deficits should be considered as an important factor shaping the behaviour after long flights and whether the need for sleep compensation during the day might shape the preferred duration of non-stop flights in night migrants.

Key words: migrant birds - sleep

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INTRODUCTION

The significance and function of sleep in animals and humans is largely unknown. It is, therefore, unfortunate that deprivation of sleep caused by prolonged migratory flight in birds has hardly attracted any attention (Amlaner & Ball 1983; Skutch 1989); this naturally occurring sleep deprivation might be particularly instructive. There are two main lines of theories on the function of sleep: (i) to bodily recover from wakefulness, (ii) to restore/reset brain functions (see Horne 1988; Moorcroft 1995; Benington & Heller 1995 for an overview). Sleep is regulated partly by the circadian system and partly homeostatically, i.e. sleep deprivation is followed by sleepiness, although the deprivation is not compensated to full extent (Horne 1988). The urge to sleep following sleep deprivation may overrule all other activities

(Rechtschaffen 1998). Despite this fact and despite our own human experience of the effects a wakeful night has on our longing for sleep, there are to our knowledge no studies on sleep in migrating birds after a long flight and hardly any published observations. The reasons are probably that sleep is hard to identify during field conditions and that sleep deprivation has no known measurable physiological correlate (Rechtschaffen 1998).

Birds have been shown to be able to sleep unihemispherically with one eye closed on the ground (Rattenborg *et al.* 1999, 2000). Although birds may sleep unihemispherically during flight (Rattenborg *et al.* 2000), unihemispheric sleep may hamper the motor system and directed migratory flight. Orientation depends on visual and magnetic cues that are currently thought to be light-dependent and perceived with the eye (e.g.

Wiltshko *et al.* 1993). In any case, the amount of sleep obtained during flight is likely to be less than on the ground. Birds during long-distance flights may incur deficits in various respects, e.g. in fat, protein, water (Jenni & Jenni-Eiermann 1998; Battley *et al.* 2000) and possibly in many more respects. Therefore, birds landing after a long flight bout may have special needs and may at the same time be confronted with various difficulties in the new habitat. Such special needs may be rehydration, the uptake of quickly available energy in the form of carbohydrates, the uptake of essential amino acids to restore catabolised protein, and the uptake of vitamins, minerals and trace elements. Apart from these needs for substrates, it seems reasonable to assume that a bird might have an urge to rest and sleep, since sleep deprivation is usually followed by sleepiness and since endurance exercise in humans (a 92 km marathon) entails longer and deeper sleep during the following three nights (Shapiro *et al.* 1981). Sleep after long migratory flights entails a time cost for birds that try to maximise speed of migration (cf Alerstam & Lindström 1990). On the other hand, there is probably a cost associated with not sleeping after sleep deprivation. The nature of this cost depends on the function of sleep, e.g. flight muscle power may be reduced or the ability to find the correct flight route may be hampered.

The aim of this communication is to present some observations on birds indicating that the urge to sleep after a long flight may take preference over other activities. We discuss the implications of sleep deprivation for migrants, and hope to stimulate quantitative studies on the need to sleep after long migration flights.

OBSERVATIONS

In order to demonstrate whether birds after migration are prone to sleep, birds should be observed just after landing from an extended migratory flight and during a period of the diurnal cycle during which sleep normally does not occur, and be compared with birds that did not fly during the

previous night. Such situations are not commonly encountered and observations have generally been made by chance in the context of other studies.

As has been adopted by several field researchers (e.g. Amlaner & McFarland 1981; Rattenborg *et al.* 2000), sleep in the field is usually identified by eye closure while in a sleep posture.

Observations of passerines

During a study on food choice after long-distance flights in 1997 and 1998 in collaboration with the Istituto Nazionale per la Fauna Selvatica, Bologna, we investigated passerine migrants caught on Ventotene, a small island in the Tyrrhenian Sea, 50 km off the Italian coast. In spring, using the island as a stepping stone before they fly on to the mainland, many migrants land there. Direction and time of arrival at Ventotene indicate that these birds completed a 14–16 h non-stop flight and crossed the Mediterranean Sea on a distance of at least 500 km (Pilastro *et al.* 1995). The ringing station is situated at the southern tip of the island, where most birds first landed. Freshly caught Subalpine Warblers *Sylvia cantillans*, Garden Warblers *Sylvia borin*, Common Whitethroats *Sylvia communis* and Willow Warblers *Phylloscopus trochilus* were put singly in experimental cages with two perches. For food choice experiments they were offered mealworms and artificial nectar (for details see Schwilch *et al.* 2001). In preliminary experiments during 1997 other food types were also offered. The cages were in a quiet room under outdoor temperature and daylight regime, but reduced luminosity. In 1997 the birds were kept for one hour and were continuously observed from a hide. In 1998 they were kept for 30 min and only observed occasionally until release.

Most birds showed escape behaviour for almost the whole period they were in the experimental cages. Only a minority started to eat (Table 1). In 1997, when birds were observed continuously, two Subalpine Warblers fell asleep in the cage, two Garden Warblers and two Common Whitethroats started dozing. In 1998 when birds were only observed occasionally, four Garden

Table 1. Number of birds held in experimental cages that were eating within the first half hour of captivity and that were observed to sleep or doze.

Species	1997			1998		
	<i>n</i> total	<i>n</i> eating	sleeping/dozing	<i>n</i> total	<i>n</i> eating	sleeping/dozing
Garden Warbler						
<i>Sylvia borin</i>	43	13	2 doze	153	20	4 sleep
Common Whitethroat						
<i>Sylvia communis</i>	21	6	2 doze	89	24	
Subalpine Warbler						
<i>Sylvia cantillans</i>	46	21	2 sleep			
Willow Warbler						
<i>Phylloscopus trochilus</i>	9	1				

Warblers were seen sleeping (Table 1). One of them even did not wake up when RS approached the cages in order to release the birds. Sleeping behaviour ranged from dozing in upright position to sleeping in complete sleeping position with the head resting on the back, the beak under the wing and the eyes closed. Except for one Garden Warbler and one Common Whitethroat, all birds that were sleeping or dozing had consumed some of the offered nectar before.

Other chance observations concerned free-living passerines after long-distance flights. LJ observed migrants arriving at the Mediterranean coast of Egypt after having crossed the Mediterranean Sea during southward migration (site 'coast' in Biebach *et al.* 1991). The majority of migrants probably landed during the night and, hence, probably departed the evening before from Crete or southern Turkey, at least 500 km across the sea. During the morning until midday, some birds were observed arriving from the sea, among them two Thrush Nightingales *Luscinia luscinia* which landed just nearby our observation point on 31 August at 11:30 h and 2 September 1985 at 10:10 h. They probably started also after sunset the evening before, but from areas further north, thus landed after a flight of 16 - 17 h. The first bird was seen landing on the ground, rested visibly breathing (not panting) for about 2 min, then moved under a tamarisk bush and rested for sever-

al hours. The second bird was not seen landing, but must have arrived some seconds before first seen. It rested motionless in the shade of a bush until the evening without any signs of foraging. These birds did not assume a typical sleeping posture. Many other birds observed in this area were foraging.

Observations of geese and waders

A clear record of sleep of free-living birds after long distance flights has been found during a study on Pink-footed Geese *Anser brachydactyla* wintering in Scotland (Newton & Campbell 1970). Arriving from Iceland, these geese landed mostly by day, but also by night, and assembled on a mud bank on an island at Loch Leven. The authors report: "On first alighting they drank a good deal, but then spent many hours sleeping, standing on one leg in the shallow water. At times they also waded into deeper water, splashed and preened for long periods." The birds did only begin to feed at dawn of the next day in the large fields nearby. On the first day after arrival most birds took probably no food at all (Newton & Campbell 1970).

During the first days in May of several years, TP observed Red Knots *Calidris canutus*, Bartailed Godwits *Limosa lapponica* and Grey Plovers *Pluvialis squatarola* arriving at the southern tip of the island of Texel, The Netherlands, most

probably from their direct journey from West Africa. They landed in groups and very often went to sleep on the mudflats within minutes. After maybe a sleep of a few hours, they usually went on further into the Wadden Sea, a distance of several km to feed. Similarly, TP observed Red Knots which tucked their bills under the back feathers, closed their eyes and slept as soon as they arrived at northern Ellesmere Island in early June 1990 on at least two days. These birds, however, might have had little to eat on the snow-covered tundra hills.

The first Dunlins *Calidris alpina* seen by NH on autumn migration after a period without birds at Ottenby bird observatory, were all standing resting in a 'sleeping posture' for approximately half a day or one day and were not seen feeding. The birds had their eyes closed during that time.

Beth Brown reported the following observation from Access Bay Spit, South Auckland, New Zealand (reported in OSNZ News no 37, December 1985, in the section Regional Roundup): "On 21 September newly arrived godwits [Bar-tailed Godwits] and Knots [Red Knots] kept separate from those which had overwintered. While the latter fed on the falling tide, two flocks of recent arrivals slept on. Next day, many more had arrived and the pattern was repeated."

DISCUSSION

The few observations listed above all concerned birds just landed after a non-stop long-distance flight over at least 500 km. Some of the birds in the experimental cages were reliably identified as sleeping. Some of the free-living birds were probably also sleeping with the eyes closed in sleeping postures. However, also birds dozing or resting with the one eye towards the observer open may have slept unihemispherically, as shown in Mallards *Anas platyrhynchos* and European Blackbird *Turdus merula* (Szymczak *et al.* 1993; Rattenborg *et al.* 1999).

Although only few individuals were observed sleeping in the cages, we considered this observa-

tion as remarkable since the behaviour of the majority of the other birds indicated that they found themselves in a stressful situation and that they usually do not sleep during daytime. It seems that the need to sleep only over-rode the stress of being caged in a minority of the birds. This could be due to differences between individuals in either sleepiness or in how stressful they perceived the situation.

It is noteworthy that 8 out of the 10 sleeping birds were consuming nectar before dozing or falling asleep. This coincidence might simply be an intercorrelation of feeding and sleeping both being enabled by a suppressed stress-reaction. It might on the other hand reflect an order of priority in which birds after long distance flights may meet their needs. Indeed, one of the reasons for sleep may be to replenish the glycogen content in the brain which has been depleted as a function of prior wakefulness (Benington & Heller 1995).

In the case of the Pink-footed Geese in Scotland, the Thrush Nightingales at the coast of Egypt and the waders on Texel, at Ottenby and in New Zealand, sleep and rest may have had a higher priority than feeding after a long distance flight. Although the delay in the onset of feeding in the geese and waders could have other reasons (e.g. metabolic and physiological recovery after flight, i.e. glycogen restoring), it may well be that it is the urge to sleep that postpones the onset of refuelling after long-distance flights.

Together, the observations suggest that migrants landing after long-distance flights may first replenish water and possibly carbohydrates (nectar consumption or possibly endogenous glycogen restoring), secondly sleep, and thirdly replenish protein and fat. The observations presented above indicate that the urge to sleep after a long flight may take preference over other activities and, hence, that there is compensation for sleep deprivation during flight after landing. In nocturnal migrants, which otherwise are strictly diurnally active, this apparently may alter the diurnal rhythm of sleep and activity with unknown consequences. Therefore, sleep should be taken into account as one of the resources that

might incur deficits after long-distance flights and influence the behaviour after landing.

It has been found that many night migrants probably fly for only a few hours over continental Europe, as evidenced by strongly decreasing numbers of night migrants observed aloft by radar from midnight onwards (Bruderer & Liechti 1998), and may thus not incur a sleep deficit. However, if birds cross an ecological barrier in a long non-stop flight of an entire night duration or more (up to an estimated transit time of more than a week in the case of the Bar-tailed Godwits overflying the Pacific from Alaska to New Zealand; Piersma & Gill 1998), a deficit in sleep may accumulate which, when (partly) compensated for after landing, adds to the time which cannot be used for fuel deposition (called search-settling time). Hence, in this case post-migratory sleep time as a function of non-stop flight time may be an additional factor to be considered in optimal migration models (Alerstam & Lindström 1990; Alerstam & Hedenström 1998). It can only be speculated whether nocturnal migrants may prefer short migratory flights during only part of the night over long flights, in order to avoid the adverse effects of the need to sleep during the day, such as lost feeding time and higher exposure to predators.

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SAMENVATTING

Naarmate organismen langere tijd niet hebben geslapen neemt de slaapbehoefte toe. Op zo'n moment kan een slaapbehoefte alle andere behoeften overwinnen. Het is opmerkelijk dat bij vogels het voorkomen van slaap na lange trekvluchten zo weinig bestudeerd is. Door een aantal waarnemingen over het voorkomen van slaap bij vogels onmiddellijk na afloop van langeafstandsvluchten bij elkaar te brengen en in perspectief te zetten, hopen we meer kwantitatief onderzoek naar slaapbehoefte tijdens vogeltrek te stimuleren. Zo is het bijvoorbeeld mogelijk dat de, tijdens lange trekvluchten opgebouwde, slaapte korten mede bepalend zijn voor de

lengte van de 'optimale' trekafstand. De behoefte aan slaap zou dus, samen met factoren als voedselbeschikbaarheid, onderhoudskostenniveau en predatierisico, de trekstrategieën van vogels sterk kunnen beïnvloeden.

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Footnote

Recently, Kanavau (2001; *Anim. Behav.* 62: 1219-1224) hypothesised that birds flying at night, or in flocks by day, do not need to sleep because they do not, or only unihemispherically, process complex visual information, and the brain can consolidate memory (which cannot occur simultaneously with processing complex incoming information) during flight. However, evidence that birds during migratory flight do not analyse complex visual information is equivocal. There is strong evidence that birds process continuously visual information during flight by day and night when keeping distance to the neighbours in flocks or V-formations to avoid collisions, when assessing speed and direction of flight relative to ground for the selection of flight altitude relative to wind, and for compensating wind drift when keeping flight direction relative to landmarks or celestial cues, when reacting to topography, when selecting habitat for landing, etc.