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Timothy Coppack, Franz Bairlein

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Circadian control of nocturnal songbird migration

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<u>German abstract:</u>

Circadiane Kontrolle des nächtlichen Singvogelzugs

Der Vogelzug ist unter dem Einfluss von jährlichen und tageszeitlichen Fluktuationen in der Ressourcenverfügbarkeit entstanden. Zahlreiche Singvögel ziehen ausschließlich nachts, wodurch sie die tagsüber zur Nahrungssuche und -aufnahme verfügbare Zeit maximieren. In Gefangenschaft zeigen Nachtzieher in völliger Abwesenheit von Umweltreizen typischerweise Rhythmen nächtlicher Aktivität (Zugunruhe), die mit einer Periodizität von etwa 24 Stunden andauern. Experimentelle Befunde lassen vermuten, dass diese circadianen Zugrhythmen entweder durch eine „Umdefinierung“ der tageszeitlichen Uhr oder durch eine Phasenverschiebung zwischen unabhängigen, endogenen Oszillatoren verursacht werden. Die Rolle des Hormons Melatonin bleibt dabei unklar. In Zugnächten reduzierte Melatoninkonzentrationen könnten der positive Stimulus, ein permissiver Faktor oder eine Folge nächtlicher Wachheit sein. Obwohl bekannt ist, dass der Ernährungszustand eines Zugvogels einen starken Einfluss auf das Auftreten von Zugunruhe hat, ist der physiologische Zusammenhang zwischen der circadianen Zuguhr und den metabolischen/hormonellen Regulationsmechanismen von Zugereignissen unbekannt. Ein funktionell-genetischer Ansatz verspricht die Lücke zwischen verhaltensbiologischem und physiologischem Wissen zu schließen. Die Aufklärung der Mechanismen, die bei der täglichen Zeitplanung des Zugs beteiligt sind, ist entscheidend für das

übergeordnete Verständnis der Steuerung des Vogelzugs, da die Summe der Zugnächte bestimmt, wie lange und wie weit ein Individuum zu ziehen vermag.

Title:

Circadian control of nocturnal songbird migration

Authors:

Timothy Coppack[1] & Franz Bairlein[2]

[1]Institute of Applied Ecology (IfAÖ), Dept. of Ornithology, Alte Dorfstraße 11, 18184 Neu Broderstorf, Germany

[2]Institute of Avian Research "Vogelwarte Helgoland", An der Vogelwarte 21, 26386 Wilhelmshaven, Germany

Correspondence: coppack@ifaoe.de

Abstract Bird migration has evolved under the influence of annual and daily fluctuations in resource availability. Numerous passerine migrants migrate exclusively by night, maximizing the time available for foraging and feeding during the day. When held in captivity, and in total absence of environmental cues, nocturnal migrants typically show rhythms of night-time restlessness (Zugunruhe), which persist with a periodicity of about 24 hours. Experimental evidence suggests that these circadian rhythms of Zugunruhe may either result from a "redefinition" of the diurnal clock or from changes in the phase relationship between independent endogenous oscillators. The role of melatonin in this control system remains ambiguous. Lowered levels of circulating melatonin found during migratory nights could either be the positive stimulus, a permissive factor or a side effect of nocturnal wakefulness. Although the nutritional state of a migrant is known to strongly influence the incidence of migratory activity, the physiological link between the circadian clock controlling Zugunruhe and the metabolic/hormonal path-ways that regulate the incidence of migration is uncertain. A functional genetic approach promises to bring behavioural and physiological knowledge together. Determining the mechanisms that are involved in the day-to-day scheduling of migration is crucial for understanding the overall control of migration, as the sum of migratory nights determines for how long, and how far, a migrant potentially travels.

Key words: circadian clock, melatonin, migratory restlessness, photoperiod, Zugunruhe

"*That strange and mysterious phenomenon in the life of birds, their migratory journeys, repeated at fixed intervals and with unerring exactness, has for thousands of years called forth the astonishment and admiration of mankind.*"

H. Gätke (1895)

Introduction

Prehistoric humans must have been well aware of the recurring appearance of migratory birds, as much of their own seasonal and daily organisation depended on anticipatory reactions to cues from the environment. Even today, mankind uses migratory birds (and their prey) as environmental indicators to reveal shifts in the timing of the seasons due to climate change (Lehikoinen and Sparks 2010) and to draw attention to the ecological risk of trophic desynchronisation (Both et al. 2006). Hence, it is not surprising that much of the interest in avian migration has – and still is – focussed on the factors that determine its timing (Gwinner 1996, Berthold 1996, Coppack and Both 2002, Newton 2008).

Virtually all current knowledge of the mechanisms underlying the timing of songbird migration is based on measurements in captive specimens held under controlled environmental conditions. Results from common-garden experiments suggest that endogenous circannual rhythms (in conjunction with photoperiodic cues) control the seasonality of passerine migration (Gwinner 1967; for reviews, see Gwinner 1975, 1990, 1996, Gwinner and Helm 2003, Berthold 1996, Coppack 2007). Species- and population-specific differences in annual rhythmicity, however, depend strongly on differences in photoperiodic reaction norms and on latitudinal photoperiodic variation (Gwinner et al. 1989, Helm et al. 2005, Noorwijk et al 2006, Coppack 2007, Maggini and Bairlein 2010).

While annual rhythms of migration have been extensively studied at the phenological, behavioural, physiological and quantitative genetic level (Berthold 2001), day-to-day migratory routines have

received less attention, despite the fact that the sum of migratory bouts determines the overall extent of migration. In this review, we attempt to briefly summarize current knowledge of the physiology and functional significance of circadian rhythms (*sensu* Halberg 1959) in avian migration, focussing on evidence from nocturnal passerine migrants. Principles found in this group of obligate migrants cannot be generalized to other groups of migrants, such as long-lived social or facultative migrants, which regularly migrate during the day and appear to be less dependent on endogenous timing factors (Newton 2008).

Nocturnal passerine migration: a circadian rhythm

Most migratory birds accomplish their journeys by intermittent flight and stopover phases (Berthold 2001, Newton 2008). Long-distance terrestrial migrants crossing vast bodies of water naturally deviate from this pattern, but for the majority of Afro-Palaearctic and Neotropical-Nearctic species, landing opportunities *en route* enable migrants to stopover on a more or less regular basis. Many insectivorous passerines restrict their migratory activity to the night (Berthold 2001, Newton 2008). In captivity, this is reflected in the occurrence of nocturnal migratory restlessness (German: Zugunruhe), which was first described in detail by aviculturists in the 18th century (cf. Birkhead 2008). Although the analysis Zugunruhe has played a pivotal role in the establishment of theories to explain the physiology and evolution of bird migration (e.g., Schildmacher 1933, Wagner 1930, Merkel 1938, Palmgren 1944, Farner 1950, Helms 1963, King and Farner 1963, Merkel et al. 1964, Gwinner 1967, Wiltschko and Wiltschko 1972, Berthold 1973, Czeschlik 1977, Berthold & Querner 1980, Gwinner 1996, Berthold 1996, 2001, Pulido and Berthold 2003, Mueller et al. 2011), questions regarding its circadian control have been addressed only occasionally and infrequently (McMillan et al. 1970, MacMillan 1972, Gwinner 1975, 1996, Berthold 1996, Gwinner and Helm 2003).

Just a hand full of studies have explicitly tested whether the generation of Zugunruhe obeys to circadian principles, for which two criteria must be met: (1) Rhythms persist in the absence of

external cues. (2) Rhythms can be reset to match local time by exposure to external cues (Zeitgeber). Criterion (1) can be tested by keeping individuals over extended periods under constant (dim) light. Through this approach, circadian rhythms of Zugunruhe have been experimentally demonstrated in the white-throated sparrow *Zonotrichia albicollis* (McMillan et al. 1970), the European robin *Erithacus rubecula* (Gwinner 1975), the blackcap *Sylvia atricapilla* (Gwinner 1996), the garden warbler *Sylvia borin* (Bartell and Gwinner 2005), and the blackheaded bunting *Emberiza melanocephala* (Rani et al. 2006). In these species, Zugunruhe persisted with free-running circadian periodicities for several days under constant lighting conditions. In contrast, Gambel's white-crowned sparrows *Zonotrichia leucophrys gambelii* exposed to constant dim light continued to show migratory activity during subjective days, and individuals held under constant bright light became arrhythmic after three days, suggesting that migratory restlessness in this species may not be driven by endogenous oscillators but rather by ambient light cycles (Coverdill et al. 2008).

Circadian rhythms of Zugunruhe are robustly entrainable by artificial photoperiodic stimuli (Bartell and Gwinner 2005, Rani et al. 2006) and by food cycles (Rani 2010). Under natural conditions, daily rhythms of Zugunruhe closely track sunset cues *en route*, as suggested by a study on wild-caught common redstarts *Phoenicurus phoenicurus* (Coppack et al. 2008; Fig. 1). Redstarts captured during stopover at Heligoland Island and subjected to constant dim light conditions with *ad libitum* food showed clear-cut activity bouts that coincided with projected local sunset. During subjective days, migratory restlessness ceased and birds concentrated their activity to the vicinity of the feeding dish. Infrared-videography revealed distinct behavioural transitions between night- and daytime activities. The timing of these activity transitions was repeatable within individuals (Coppack et al. 2008). Individual consistency in the daily timing of migratory restlessness has also been found in a non-passerine migrant, the European quail *Coturnix coturnix coturnix* (Bertin et al. 2007).

Findings from telemetric studies on departure times in various nocturnal passerine migrants at stopover sites (reviewed by Bolshakov et al. 2007) have questioned whether birds actually initiate migration within a fixed time window around sunset. But in one of the most detailed studies on day-

to-day migration schedules in free-ranging migrants, Cochran et al. (2008) showed that departures (N=64) and landings (N=31) of individual Swainson's thrushes *Catharus ustulatus* rarely occurred after dusk or before dawn. It has been hypothesized that songbirds use the setting sun as a reference to recalibrate their magnetic compass *en route* (Cochran et al 2004). This may additionally explain why departure decisions often take place around sunset (Coppack et al. 2008). Further telemetric studies are needed to determine the relative contributions of acquired and developmentally fixed physiological attributes that shape daily activity budgets in free-ranging migrants. Comparing successive measurements on the same individuals in the lab and the field could clarify to what extent the internal clock determines the onset of nocturnal migration under natural conditions (Coppack et al. 2008).

The physiological machinery

Which intrinsic factors cause songbirds to migrate like clockwork? And which mechanism enables individuals to adjust their timing system to capricious environmental conditions?

In the dissection of the physiological control mechanisms underlying the circadian rhythms of Zugunruhe, it is essential to distinguish between the timing and incidence of nocturnal activity. While the timing of Zugunruhe is predominantly affected by endogenous oscillators and external Zeitgeber (Berthold 1996, Gwinner 1996), the incidence of nocturnal activity is modified by the nutritional state of the bird (Bairlein and Gwinner 1994). The interaction between these levels of control is still poorly understood.

Evidence suggest that the timing of Zugunruhe is controlled by an endogenous pacemaker system, located predominantly in the pineal gland, which rhythmically synthesizes and secretes melatonin (Gwinner and Brandstätter 2001, Underwood 2001, Kumar et al. 2010). Pinealectomy has been shown to abolish circadian rhythms of Zugunruhe in white-throated sparrows (McMillan 1972). Other components of the avian circadian system could potentially contribute to the scheduling of

Zugunruhe: the hypothalamic oscillator (comparable to the mammalian superchiasmatic nucleus), the retina of the eye, as well as encephalic photoreceptors (EP). Both the pineal and the retina rhythmically synthesise melatonin and act as photoreceptors. The relative contribution of these different components and their apparent redundancy could reflect the complexity and diversity of the lifestyles birds have evolved in adaptation to the diverse environmental conditions they live in (Gwinner and Brandstätter 2001). The expression of Zugunruhe may either result from a "redefinition" of the endogenous circadian clock regulating day-time activity (Rani et al. 2006) or from a change in the phase relationship between separate circadian oscillators (Gwinner 1975, Gwinner 1996, Bartell and Gwinner 2005). Both models have found experimental support (cf. Bartell and Gwinner 2005, Rani et al. 2006).

Food availability and fat load are known to profoundly affect the incidence of nocturnal migratory activity and, consequently, determines stopover duration (King and Farner 1963, Berthold 1976, Bairlein 1985, Biebach 1985, Biebach et al. 1986, Gwinner et al. 1985, Yong and Moore 1993, Fusani et al. 2009, Goymann et al. 2010, but see Salewski and Schaub 2007). In garden warblers held on nutrient-poor food, the resulting drop in body mass was associated with a temporary decrease in migratory activity (Berthold 1976). In other food-deprivation experiments with captive migrants, nocturnal activity ceased as soon as birds were refed (Biebach 1985, Gwinner et al. 1985, Gwinner et al. 1988, Schwabl et al. 1991, Fusani and Gwinner 2004). This suppression of Zugunruhe by refuelling after fasting is associated with increasing melatonin levels (Fusani and Gwinner 2004).

The role of melatonin in the temporal control of nocturnal migration is unclear. Exogenous application of melatonin suppressed the amount of Zugunruhe in bramblings *Frigilla montifringilla* (Pohl 2000). In Sylvia warblers (Gwinner et al. 1993, Gwinner 1996, Fusani and Gwinner 2001) and stonechats *Saxicola torquata* (cf. Gwinner and Brandstätter 2001) expressing Zugunruhe, the amplitude of night-time melatonin levels significantly decreases. Lowered levels of circulating melatonin found during migratory nights could either be the positive stimulus, a permissive factor or simply a consequence of nocturnal wakefulness (Gwinner 1996, Fusani and Gwinner 2004). It has

been suggested that low levels of melatonin may render the circadian clock more responsive to photic stimuli, facilitating its readjustment to latitudinal and longitudinal photoperiodic shifts during migration (Gwinner 1996, Pohl 2000). This “jet-lag compensation” hypothesis awaits rigorous experimental corroboration.

Hormones regulating metabolic processes and stress responses (notably corticosterone, which promotes the mobilization of stored lipids) have regularly featured in migration physiology and ecology (Wingfield et al. 1990), but an involvement in the control of nocturnal migration is uncertain (Schwabl et al. 1991, Ramenofsky et al. 1999, Landys et al. 2004). For example, garden warblers expressing Zugunruhe showed elevated levels of corticosterone at the end of the dark phase and low levels during daytime (Schwabl et al. 1991). When Zugunruhe was experimentally disrupted by food deprivation and subsequent refeeding, or after spontaneous termination of migratory activity, this rhythm was absent, suggesting that diel changes in adrenocortical hormonal activity could be involved in the regulation of nocturnal migration (Schwabl et al. 1991). In line with this, Gambel’s white-crowned sparrows tended to increase plasma corticosterone levels during the transitional quiescent period that precedes the onset of Zugunruhe (Landys et al. 2004). Ramenofsky et al. 2008 showed that extending the dark phase prolonged the period of Zugunruhe with sustained elevated levels of baseline corticosterone in captive white-crowned sparrows. Such results may suggest that the energetic demands of flight are related to glucorticoid levels. However, migrating passerines caught out of active flight or just after landing showed low levels of corticosterone (Gwinner et al. 1992, Jenni et al. 2000), questioning its functional involvement in the control of migration.

Other hormones signalling the energetic state (fat load) of the bird and regulating food intake have been suggested to play a role in the control flight and stopover decisions: leptin (Kochan et al. 2006, Fusani et al. 2009, Singletary 2009) and neuropedtide Y (Singletary 2009). Leptin, secreted by fat cells, is generally associated with the regulation of adiposity, feeding behaviour, reproduction and immune function. Although leptin cDNA has been cloned in chicken, its existence could not been

confirmed by a number of researchers, nor has corresponding genomic DNA been identified (Ohkubo and Adachi 2008, Sharp et al. 2008).

The expression of Zugunruhe could also relate to the physiological mechanism controlling sleep-wake behaviour. Despite being adversely affected by sleep loss during the non-migratory season, nocturnal migrants can obviously reduce sleep for longer periods without associated deficits in cognitive abilities (Rattenborg et al. 2004). Sleep-loss during nocturnal migration could be compensated through “micro-napping” during the day (Fuchs et al. 2006, Fuchs et al. 2009, Németh 2009, Jones et al. 2010). However, whether the expression of Zugunruhe represents a disruption of the neural system controlling diurnal sleep-wake cycles is currently uncertain. Recently, Singletary (2009) excluded a direct involvement of orexin – a key neuropeptide stabilizing sleep-wake cycles in mammals (Saper et al. 2005) – in the initiation and maintenance of Zugunruhe in white-crowned sparrows, though, an indirect role of the orexin system could not be ruled out.

The current view of the physiological elements controlling flight and stopover schedules in night-migrating songbirds is summarized in Figure 2.

The functional significance of circadian clocks in avian migration

While circannual/photoperiodic timers provide a physiological mechanism by which migrants can anticipate seasonal environmental changes, circadian clocks adapt migratory birds to daily fluctuations in environmental conditions. There is no doubt that endogenous circadian rhythms of Zugunruhe are of functional significance and do not simply represent laboratory artefacts caused by overshooting physical urge. Even day-to-day changes in the intensity of Zugunruhe can be brought into accordance with the observed temporal course of migration in the wild (Berthold 1978). Thus, daily bouts of Zugunruhe can be viewed as the subunits of annual migration routines, and endogenous circadian clocks controlling this activity would provide the functional basis for the overall control of migration (vector-navigation hypothesis, cf. Berthold 1978, 2001). Strong

correlations between the number of nights with Zugunruhe measured in captive individuals and the duration and length of migration found in wild conspecifics support this classic theory of bird migration, both inter- and intraspecifically (Berthold 1973, Berthold 2001). However, it is hitherto unproven whether circannual rhythms of migration are controlled by a “counting” of circadian periods or whether circannual and circadian rhythms of Zugunruhe are controlled (and have evolved) independently. While frequency demultiplication has so far found no experimental support (Wikelski et al. 2008), the problem of whether circannual rhythms are organised by endogenous oscillators via molecular feed-back loops (as seen in the circadian system) or represent sequences of interdependent physiological states remains to be resolved (Dawson et al. 2001).

Besides playing a role in the timing and extent of migration, circadian clocks may be involved in time-compensated celestial orientation (Emlen 1975, Able 1980, Cochran et al. 2004) and could play a role in the navigational processing of geographic latitude and longitude (cf. Chernetsov et al. 2008).

A more general aspect is that circadian pacemakers may provide the functional basis (“Grundlage”; sensu Bünning 1936) for seasonal photoperiodic time measurement. Though, as Bradshaw and Holzapfel (2010) have recently pointed out, photoperiodic mechanisms controlling annual seasonality do not necessarily require a circadian system. While circadian clocks cycle via molecular feedback loops and can be reset by photic cues on a daily basis, seasonal photoperiodism is more likely to involve physiological switches which are stimulated directly by photoperiod and which kick-off physiological processes that run to completion and are irreversible (Bradshaw and Holzapfel 2010). In agreement with this notion, the molecular mechanism controlling the seasonal photoperiodic stimulation of the hypothalamic-pituitary-gonadal axis in the Japanese quail *Coturnix japonica* (Yoshimura et al. 2003) has been shown to be independent from circadian clock-gene expression in the putative suprachiasmatic nucleus (SCN) and pineal, indicating that differential expression of clock genes in these circadian pacemakers is not an absolute requirement for encoding and decoding seasonal photoperiodic information (Yasuo et al. 2003). Hence, when variation in clock genes is found within and among populations, its adaptive significance is more likely to be explained

by circadian function than by seasonality/photoperiodism *per se* (Bradshaw and Holzapfel 2010). However, the lack of evidence for pineal and SCN in mediating a circadian regulation of photoperiodic responses is not definitive. A circadian based photoperiodic timer appears to be located in the mediobasal hypothalamus (MBH) of birds (Yasuo et al. 2003). Furthermore, experiments using skeleton photoperiods suggest that circadian clocks are involved in photoperiodic time measurement, and this may be the case for the seasonal control of Zugunruhe (Gwinner and Bartell 2005).

Mueller et al. (2011) have recently reported the first candidate gene to be associated with variation of migratoriness among blackcap populations: ADCYAP1, which encodes the pituitary adenylate cyclase-activating polypeptide (PACAP). How this gene and its product are functionally linked to the expression of nocturnal migratory restlessness is currently unknown, though PACAP could potentially influence clock gene expression and the regulation of the avian circadian system (cf. Mueller et al. 2011). The genes and physiological pathways that are directly involved in the control of nocturnal migration and its seasonal/photoperiodic programming have yet to be established. Further functional genetic analysis of the migratory syndrome promises to bring new insight into the proximate control of bird migration and its evolutionary potential.

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Figures

Fig. 1 Circadian flight and stopover schedule of a male redstart *Phoenicurus phoenicurus* caught during spring migration on Heligoland Island and kept in a cylindrical feeding cage for three days under constant dim light conditions. The above graph shows the position of the bird relative to the feeding dish in the cage centre as detected by motion-controlled infrared videography. The spline curve in the below graph represents the average amount of locomotor activity (locally weighted). Adapted from Coppack et al. (2008).

Fig. 2 Schematic representation of the physiological processes and components involved in the day-to-day scheduling of nocturnal songbird migration (after Gwinner and Brandstätter 2001 and Singletary 2009). The link between the circadian clock system that schedules nocturnal migration and the metabolic/hormonal path-ways that regulate its expression is presently uncertain.

Figure 1
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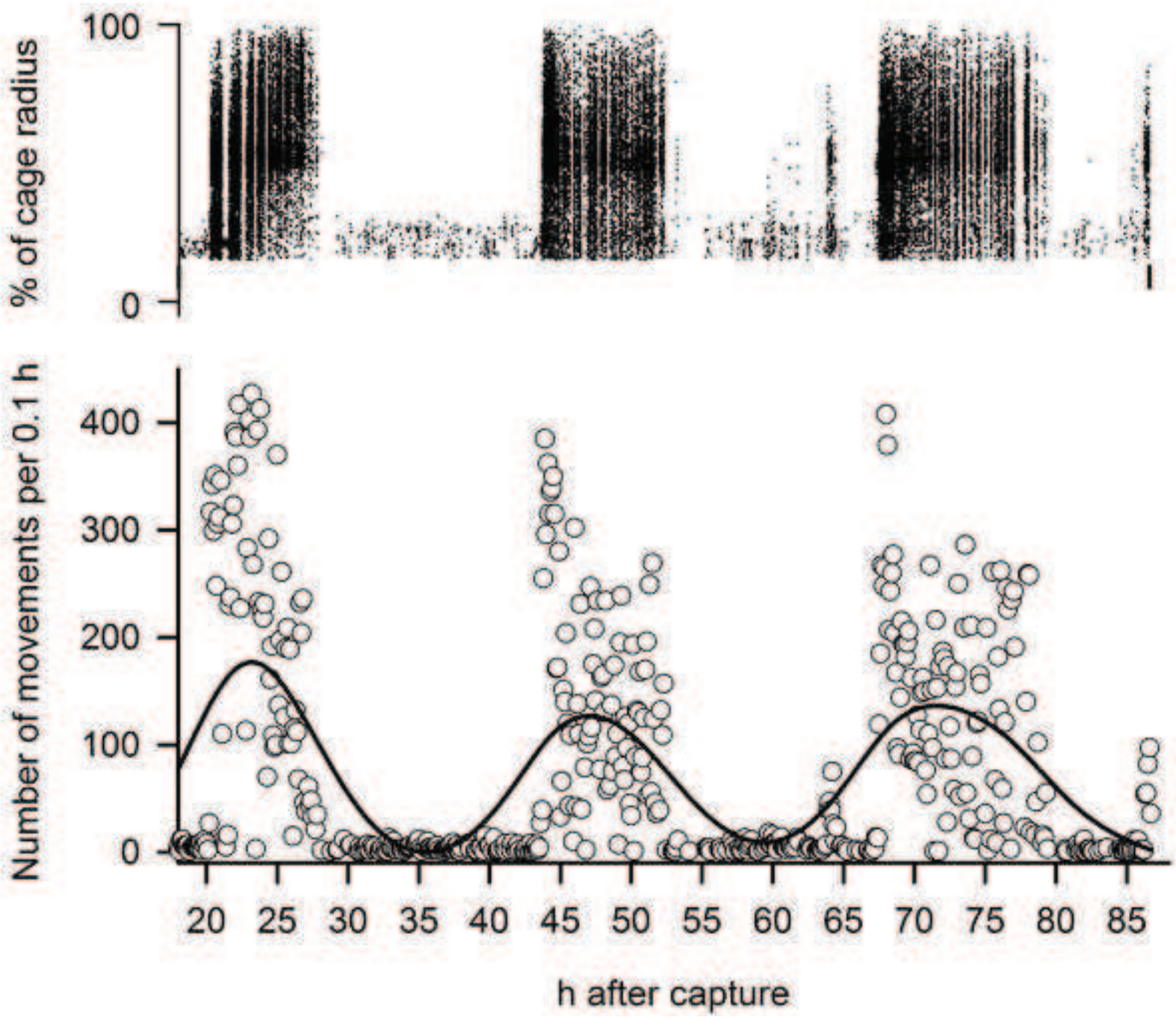
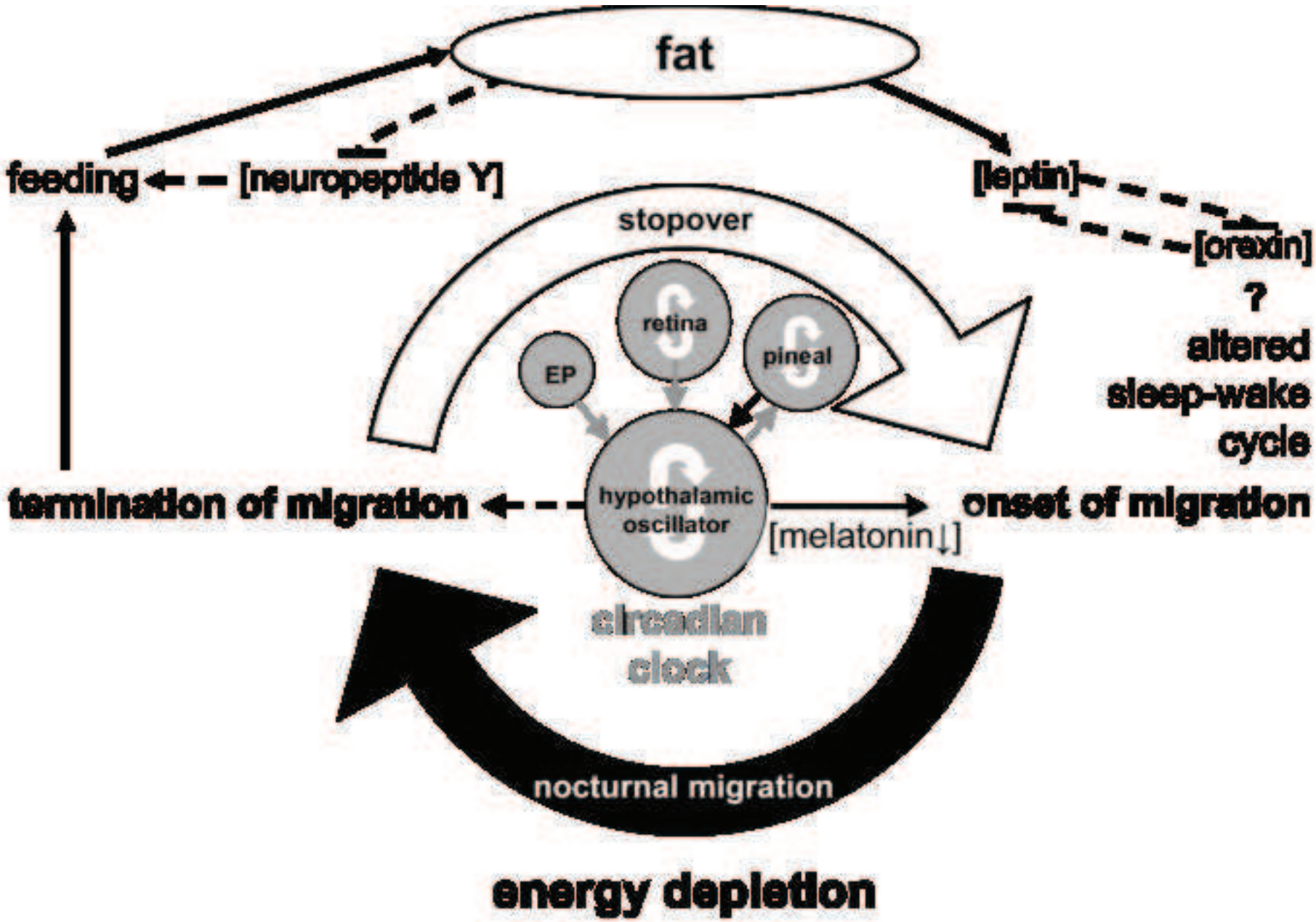
Figure 2
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