

Jet lag-like state affects cognitive performance of great tits

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Abstract

A mismatch between the environment and the internal circadian clock, commonly known as jet lag, can have negative consequences, including cognitive impairment. While many studies have examined jet lag in humans, few have explored its effects on animals, and none have specifically focused on birds. We investigated how a jet lag-like state impacts cognitive abilities in great tits. Birds were kept in constant dim light for two weeks, putting them into a "free running" circadian state. After two weeks, they were exposed to a natural day-night light cycle, causing a misalignment between their internal clock and the external environment. The birds were then tested on two cognitive tasks: problem-solving and motor inhibition, either 1 day (jet lag) or 10 days (recovered) after returning to the natural light/dark cycle. Birds in a jet lag-like state performed worse in the motor inhibition test compared to their recovered counterparts, but their performance in the problem-solving test was unaffected. Furthermore, we explored the relationship between the severity of jet lag, the degree of misalignment between predicted and actual sunrise, and cognitive performance within the jet lagged group. Despite finding no general effect of jet lag on problem-solving task performance, individuals with a higher severity of jet lag performed worse in both motor inhibition and problem-solving tasks. Our results show that disrupted daily timing affects cognitive performance of great tits, particularly in basic abilities like motor inhibition, while having less impact on complex skills like problem-solving. Our research highlights that disruptions in daily timing, particularly those induced by abrupt changes in light regimes, such as exposure to artificial light at night, can adversely affect the cognitive performance of great tits. This study not only contributes to our understanding of the cognitive consequences of circadian misalignment in avian species but also raises important implications for the broader ecological impacts of human-induced changes in light environments on wildlife.

Introduction

In most organisms, behavioural, metabolic, and physiological processes differ systematically between daytime and nighttime (Refinetti and Menaker 1992; Vitaterna et al. 2001; Hardin and Panda 2013; Cassone 2014). These daily rhythms are generated by endogenous circadian clocks and are synchronised to the external environment, primarily by the light–dark cycle (Cassone and Westneat 2012; Hardin and Panda 2013). Proper circadian synchronisation allows animals to align sleep–wake cycles, foraging behaviour, and other vital activities with the 24-hour day, thereby optimising performance and fitness (Rivkees 2007).

Circadian synchronisation can be disrupted when environmental time cues change abruptly or become unreliable. Such disruption leads to circadian misalignment, a state in which internal biological rhythms no longer match the external light–dark cycle (Waterhouse et al. 2005; Atkinson et al. 2014). Circadian misalignment can arise from rapid shifts in environmental timing, irregular light exposure, or loss of reliable synchronising cues, and is associated with wide-ranging physiological and behavioural consequences (Arendt and Marks 1982; Waterhouse et al. 1997, 2005). In general, disruptions of circadian rhythms have been shown to affect a wide range of biological functions in animals, including

physiological processes (Potter et al. 2016; Desmet et al. 2021), immune responses and neurological function (Rea and Figueiro 2014), and behaviour (Acosta et al. 2020; Bauducco et al. 2020), with potential negative consequences for fitness (Kempenaers et al. 2010).

Circadian misalignment refers broadly to any mismatch between the endogenous biological rhythms and the environmental or behavioural time cues (Chellappa et al. 2019). Jet lag is a term normally used when the environmental time shifts more rapidly than the circadian clock can synchronise (Waterhouse et al. 1997). Although jet lag is commonly associated with sleep disruption, its defining feature is a circadian phase mismatch relative to local time cues rather than sleep loss per se. Thus, jet lag is not a distinct phenomenon from circadian misalignment, but a specific and familiar example of it.

Circadian misalignment can be experimentally induced by removing or weakening the environmental synchronising cues. Under constant conditions without light–dark cycles, animals no longer receive reliable temporal information and instead follow the intrinsic period of their circadian clock, which typically deviates slightly from 24 hours. As a result, activity rhythms gradually drift relative to environmental external time, a state known as free-running (Aschoff 1981). When animals in a free-running state are subsequently returned to a natural light–dark cycle, their internal rhythms require several cycles to synchronise, creating a predictable jet lag-like state whose severity depends on the magnitude of phase misalignment between endogenous and environmental external timing.

In animals, experimental studies have similarly demonstrated negative cognitive effects of jet lag-like circadian misalignment. Jet lag paradigms impair memory, learning, and object recognition in rodents (Craig and McDonald 2008; Gibson et al. 2010; Horsey et al. 2020; Clark et al. 2020), and even domesticated species such as dogs show cognitive consequences when their circadian rhythms are disrupted by human schedules (Randler et al. 2018).

Free-living birds are also susceptible to comparable circadian misalignment when their endogenous rhythms drift under weak or inconsistent environmental cues and are then rapidly re-entrained upon sudden exposure to strong time-cues. For example, during migration stopovers, weather-driven movements, or abrupt changes in light conditions. In addition, many bird species are increasingly exposed to artificial light at night (ALAN), which can distort natural light cues, disrupt circadian timing, and fragment sleep (Dominoni et al. 2014; Aulsebrook et al. 2018). Birds experiencing circadian misalignment at inappropriate times of day may therefore show reduced foraging efficiency, impaired predator avoidance, or altered navigation, with consequences for survival and reproduction (Titulaer et al. 2012; Dominoni et al. 2014; Russ et al. 2015; Champenois et al. 2025). Despite this growing body of work, the cognitive effects of jet lag like circadian misalignment have not yet been investigated in birds.

In the present study, we investigated the cognitive consequences of jet lag-like circadian misalignment in great tits (*Parus major*), a widespread, urban-adapted passerine frequently exposed to anthropogenic light disturbance. We first induced a free-running circadian state by keeping birds under constant dim light. In birds, both daily activity patterns and foraging behaviour free-run under constant conditions (Wenger et al. 1991; Steiger et al. 2013). Subsequently we returned them to a natural light–dark cycle,

generating a jet lag-like misalignment between internal and external timing. Birds were tested either shortly after re-entrainment or after a recovery period once circadian rhythms had resynchronised.

We focused on two cognitive traits with different levels of complexity: motor inhibition, a fundamental inhibitory control mechanism (Urhan et al. 2023), and problem-solving, a higher-order cognitive ability involving learning, executive function, and behavioural flexibility (Griffin and Guez 2014). These traits are ecologically relevant and underpin adaptive responses to rapidly changing environments (Lee and Thornton 2021; Urhan et al. 2026). We tested (i) whether cognitive performance differed between jet-lagged and recovered birds and (ii) whether the severity of circadian misalignment predicted individual variation in cognitive performance within jet-lagged birds. We predicted that circadian misalignment would reduce cognitive performance, with stronger effects on basic inhibitory control than on complex problem-solving, and that increasing misalignment severity would be associated with progressively poorer performance.

Methods

Subjects

The subjects used in this experiment originated from a common garden experiment with eggs collected from forest populations (The Netherlands: Bennekom, Oosterhout, Liesbosch, Hoge Veluwe, Vlieland; Belgium: Boshoeke; Sweden: Gotland) and from city populations (The Netherlands: Amsterdam, Delft, Rotterdam, Utrecht; Belgium: Antwerp). Eggs were hatched in a shared location in The Netherlands by foster parents, and the resulting forest and city chicks ($N_{\text{Forest}}=86$, $N_{\text{City}}=49$) were hand reared from 10 days of age onwards at the Netherlands Institute of Ecology until they fed independently. The aims and results of the common garden experiment are reported elsewhere (Visser et al. 2025; Tomotani et al. 2025).

Free running circadian clock and jet lag

The experimental setup for measuring bird circadian rhythms has been described elsewhere (Tomotani et al. 2023, 2024), but in brief, it consisted of cages that allowed us to visually and acoustically isolate individuals from one another and control their light exposure. Activity was measured via passive infrared loggers mounted on the cages.

Birds were placed individually in the experimental cages and kept under the ambient natural light–dark cycle until sunset on the following day. At that sunset, we changed the light regime to continuous dim light (0.5 lux), which was then maintained both day and night for 14 consecutive days.

Under these conditions, birds were no longer synchronized to external light–dark cues and their circadian clock entered a free-running state. To prevent other time cues, white noise was played continuously, and feeding times were varied so that food availability could not be used as a

synchronizing cue. After 14 days, they were removed from the circadian setup and moved to testing cages under a natural light–dark cycle.

We used two complementary measures of circadian misalignment: i) categorical “jet lag status” that describes whether birds were tested while still in a jet lag-like state versus after recovery. In this categorisation, jet lagged group was tested in cognitive tasks shortly (24 h) after reintroduction to the natural light–dark cycle and recovered group was tested 10 days after reintroduction, when their daily rhythms were expected to be re-synchronized. ii) continuous “jet lag level” that quantifies the *degree* of misalignment between the bird’s internal circadian phase and the external light–dark cycle but was only calculated and analysed for birds in the jet lagged group. For each individual that remained in the dim light, we estimated the “predicted start of the day” (*last onset of activity in dim light + predicted duration of the subjective day based on the bird’s circadian clock period tau*). We then compared this predicted onset with the “actual start of the day” when the aviary lights turned on (08:30, corresponding to real sunrise time). Thus “jet lag level” was defined as: *predicted start of day* − *actual start of day*. The larger absolute values indicate a greater misalignment (larger phase difference between the internal rhythm and the environmental light–dark cycle) (see actograms in the Supplementary material).

Cognitive tests

We divided birds into two groups before testing them in cognitive tasks. The first group was tested 24 hours after it came out of the constant dim light conditions. We called this group the “jet lagged” group ($N_{\text{Forest}} = 46$, $N_{\text{City}} = 17$). For the second group, the testing started 10 days after coming out of the constant dim light conditions. We called this group the “recovered” group ($N_{\text{Forest}} = 40$, $N_{\text{City}} = 32$) as their daily rhythm was re-synchronised to the natural light conditions. None of the individuals in the first group (jet lagged), that were tested after 24 hours of reintroduction to natural cycle, were re-tested in the second group (recovered) that was tested 10 days after reintroduction to natural cycle. For both groups, we first tested the problem-solving performance (jet lagged group day 1; recovered group day 10) and the motor inhibition performance the day after (jet lagged group day 2; recovered group day 11).

Birds were tested in a fixed order to minimize carryover effects, which can affect outcome of the cognitive tests in animals (Cnops et al. 2022).

1) Problem-solving performance

To assess problem-solving performance, we presented birds with a lever-pulling task in their home cage. The device consisted of a vertical transparent tube containing a small platform supported by a horizontal lever. Two waxworms (*Galleria mellonella*) were placed on the platform as a reward. To solve the task, individuals had to remove the lever by pulling it from a specific direction, causing the platform to drop and the worms to fall into a feeding dish. Performance was measured as the latency (seconds) to solve the task within a 2-hour period after the device was placed in the cage.

2) Motor inhibition ability

Motor inhibition was assessed using the transparent cylinder task. Birds were first trained to retrieve a reward from an opaque cylinder (8 cm length, 3 cm outer diameter) by moving to either of the open ends. Individuals were considered successfully trained if they retrieved the reward in at least 4 of 5 trials. Successfully trained birds then performed the transparent cylinder task the following day. Before starting the main task, we repeated a single opaque-cylinder trial as a reminder. For the main test, the opaque cylinder was replaced by a transparent cylinder of identical dimensions, making the reward visible. A trial was scored as successful if the bird performed a detour response, defined as; approaching one of the open ends and reaching in for the reward, rather than attempting to peck directly through the transparent wall. Motor inhibition performance was quantified as the number of successful responses out of 10 consecutive trials.

Statistical analysis

All analyses were performed using R (R Core Team 2023), to address two complementary questions: (i) whether jet lag status (jet lagged vs. recovered) affected cognitive performance, and (ii) within the jet lagged group only, whether jet lag level (continuous measure of phase misalignment) predicted variation in performance. Population of origin was taken into account in all analyses.

Motor inhibition: To test the effect of jet lag status on motor inhibition, we fitted a generalized mixed model (binomial error structure) with the number of successful and unsuccessful trials in the transparent cylinder task combined using the **cbind** function as the dependent variable. The main fixed effect was jet lag status (binary measure: jet lagged vs. recovered). We also included environment type (forest vs. city origin of the eggs) as a fixed effect to account for potential differences between rural and urban populations. As a random effect, we included origin of the birds, with brood ID nested within area ID (the original location from which the eggs were collected).

To test the effect of jet lag level (continuous measure) on motor inhibition, we fitted a second generalized mixed model on the subset of birds in the jet lagged group only. The dependent variable and random effect structure were identical to the previous model. The main fixed effect was the continuous jet lag level (phase difference between predicted and actual start of day), and environment type (forest vs. city) was again included as a covariate.

Problem solving: We used mixed-effects Cox proportional hazards models to analyse problem-solving performance. Latency to solve the lever-pulling task (in seconds) within the 2-h (7200 s) trial was used as the dependent variable, with unsolved trials right-censored at 7201 s.

First, to test the effect of jet lag status, we fitted a model including jet lag status (jet lagged vs. recovered) as the main fixed effect and environment type (forest vs. city) as an additional fixed effect. As with the motor inhibition models, we included brood ID nested within area ID as a random effect. Second, to test the effect of jet lag level, we fitted an additional mixed-effects Cox model restricted to birds in the jet lagged group. In this model, the main predictor was the continuous jet lag level, with environment type (forest vs. city) again included as a covariate and brood ID nested within area ID as a random effect.

Results

Our generalized linear mixed model showed that motor inhibition ability was negatively affected by the jet lag-like state ($\chi^2_1 = 4.1$, $p = 0.04$; Fig. 1). Birds in the jet-lagged category (binomial classification) succeeded the transparent cylinder task in 6.95 ± 1.99 (mean $\pm$ SD) trials out of 10, whereas recovered individuals succeeded in 7.39 ± 1.77 trials (Fig. 1). When we treated jet lag as a continuous predictor within the jet-lagged group, we also found quantitatively that motor inhibition performance increased as jet lag level decreased ($\chi^2_1 = 6.1$, $p = 0.01$; Fig. 2).

Problem-solving performance (latency in seconds to solve the task) did not differ between the jet-lagged group (3110.09 ± 3093.30 s) and the recovered group (3701.64 ± 3008.33 s; $\chi^2_1 = 0.5$, $p = 0.50$; Fig. 3). However, within the jet-lagged group, problem-solving performance improved as jet lag level decreased ($\chi^2_1 = 6.2$, $p = 0.01$; Figs. 4, 5).

Discussion

We found clear evidence that jet lag impairs avian cognitive performance. Similar effects of circadian disruption on cognition have been demonstrated in humans and rodents (Cho et al. 2000; Cho 2001; Gibson et al. 2010; Fonken et al. 2012), but to our knowledge this is the first clear evidence that bird cognition is also susceptible to abrupt misalignments between the circadian rhythm and the environment. In the wild, comparable circadian misalignments can arise from artificial light at night and other rapid changes in light regimes, which are now widespread in natural and urban habitats (Dominoni 2015; Dominoni et al. 2020; Falcón et al. 2020; Taufique 2022; Helm et al. 2024). Our findings therefore suggest that light induced circadian disruption in free living birds may impair core cognitive abilities that underpin foraging, predator avoidance and parental care (Ouyang et al. 2017; Aulsebrook et al. 2018; Taufique 2022; Meijdam et al. 2023; Champenois et al. 2025).

The negative effect of jet lag was most pronounced in the motor inhibition task. Jet-lagged birds performed worse than recovered birds, indicating that inhibitory control is particularly sensitive to circadian misalignment. One likely contributor to this pattern is sleep loss. For example, sleep deprivation caused by exposure to ALAN reduced motor inhibition performance in great tits (Meijdam et al. 2023) and sleep-deprived Austrian magpies performed worse than rested birds in a reversal learning task (Johnsson et al. 2022). Both tasks assess attention-based abilities that allow animals to suppress more instinctive responses (Urhan et al. 2023). In humans, sleep deprivation similarly impairs attentional processes and reduces performance, especially in fundamental cognitive mechanisms (Weingarten and Collop 2013).

However, several studies indicate a more direct role of the circadian clock in cognitive performance, independent of total sleep duration. Humans with desynchronised circadian clocks show reduced cognitive performance even when sleep duration is optimal (Wright et al. 2006), and some work suggests that the circadian clock actively inhibits cognitive processes during the biological night (Chellappa et al. 2018). In our experiment, we did not actively prevent birds from sleeping during the

day, but the combination of dim light and husbandry disturbances (e.g. feeding) may have reduced opportunities for sleep in some individuals. Thus, both sleep disruption and direct circadian effects are plausible mechanisms underlying the reduced motor inhibition we observed.

In contrast, performance in the lever-pulling task did not differ between jet-lagged and recovered birds. Problem-solving is a complex trait involving multiple cognitive and behavioural components (Funke 2010; Griffin and Guez 2014; Prasher et al. 2019; Wat et al. 2020), including learning, understanding of physical task properties, executive functions and a broad behavioural repertoire (Funke 2010; Griffin and Guez 2014). Motivational factors can also strongly modulate problem-solving outcomes. If jet lag selectively affects some of these components but not others, unaffected mechanisms may partially compensate, resulting in relatively stable performance at the task level. For example, increased motivation can compensate for cognitive decline up to a certain point. Our results (Fig. 4) suggest, however, that such compensation may fail at higher levels of circadian misalignment.

Motivation may also help explain why motor inhibition was impaired while problem solving performance appeared less affected at the group level. Motivational mechanisms can influence performance in opposite directions depending on the task. If jet lag elevates motivation (e.g. via altered energetic state or hunger) in some individuals, this could buffer problem solving performance while simultaneously exacerbating impulsive responses in the inhibition task (Van Horik and Madden 2016). This highlights that circadian disruption can interact with motivational state in task specific ways, affecting different cognitive domains differently.

Across jet lagged individuals, greater jet lag severity (jet lag level) was associated with poorer performance in both cognitive tasks. Thus, the magnitude of misalignment between the circadian rhythm and the external light–dark cycle was negatively correlated with both motor inhibition and problem solving performance. This pattern parallels human studies showing that larger misalignments between the environmental light–dark schedule and the sleep–wake rhythm reduce cognitive performance (Leahy et al. 2024). Similarly, shift workers not only perform worse than individuals working stable morning shifts, but also show further declines in cognition as sleep efficiency decreases with increasing circadian misalignment. Our results therefore support a dose dependent effect of circadian disruption on cognition, consistent across taxa and types of circadian challenges (Chellappa et al. 2019).

Several physiological processes regulated by the circadian system may contribute to these cognitive deficits. For example, key neurotransmitters promoting alertness and vigilance, are crucial for cognitive performance and in many organisms, their levels follow a daily rhythm governed by the endogenous circadian clock, typically peaking during the active phase and declining during the rest phase (Nieoullon 2002; Korshunov et al. 2017; Acosta et al. 2020). Although we did not measure any of those neurotransmitters and hormones in our study such as dopamine, melatonin, serotonin, etc., circadian misalignment could lead to a mismatch between neurotransmitter and hormonal rhythms and behavioural demands. Individuals with greater jet lag severity may experience lower dopamine levels during the subjective day, reducing alertness and impairing performance in attention demanding tasks.

Thermoregulation provides an additional potential mechanism. The internal circadian clock tightly regulates core body temperature, which is usually lowest during the early morning and highest in the late afternoon or early evening. Misalignment between circadian phase and environmental time can disrupt this temperature rhythm and has been linked to reduced cognitive performance in humans (Molzof et al. 2019). Cognitive abilities tend to be lowest when core body temperature is minimal and highest near its daily peak (Schmidt et al. 2007). In jet lagged birds, misalignment could cause core body temperature to be suboptimal during the daytime testing period, thereby contributing to poorer task performance.

Artificial light at night is rapidly transforming nocturnal environments and is known to alter avian activity patterns, endocrine pathways and fitness in the wild (Dominoni 2015; Ouyang et al. 2017; Alaasam et al. 2021; Taufique 2022; Helm et al. 2024; Champenois et al. 2025). Experimental and field studies in songbirds, including great tits, show that ALAN shifts circadian timing, disrupts sleep and physiology, and can have detrimental effects on birds' reproductive success and health (Alaasam et al. 2021; Taufique 2022; Helm et al. 2024; Champenois et al. 2025; but see: Tomotani et al. 2023). By demonstrating that circadian misalignment also impairs cognition, our results identify an additional mechanism through which light pollution and other anthropogenic disturbances may affect survival and reproduction in natural bird populations.

In conclusion, we show that circadian disruption impairs core cognitive abilities in birds, and that the degree of impairment is positively related to the level of misalignment between the internal clock and the environmental light–dark cycle. These results are consistent with findings from humans and other mammals, suggesting that the influence of circadian rhythms on cognition is broadly conserved across taxa. Our findings underscore the importance of considering circadian health when assessing the cognitive and fitness consequences of anthropogenic change, especially light pollution.

Declarations

Ethics

All experimental procedures in the laboratory and in the field were carried out under licences of the Central Authority for Scientific Procedures on Animals (Project AVD 801002019 9005) and the Animal Welfare Body (IvD) of the Royal Netherlands Academy of Sciences (KNAW; protocol NIO021.04).

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Author Contribution

Conceptualization: UU (lead), BMT, KvO; Methodology: UU (lead), BMT; Investigation: UU (lead), BMT, KvO; Data curation: UU; Formal analysis: UU; Resources: UU, BMT, KvO, SMD; Writing the original draft: UU; Reviewing, editing and the approval of the final draft: UU, BMT, KvO, SMD

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Data Availability

All data used in this study are available in the Supplementary material

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Table

Table 1 is available in the supplementary files section.

Figures

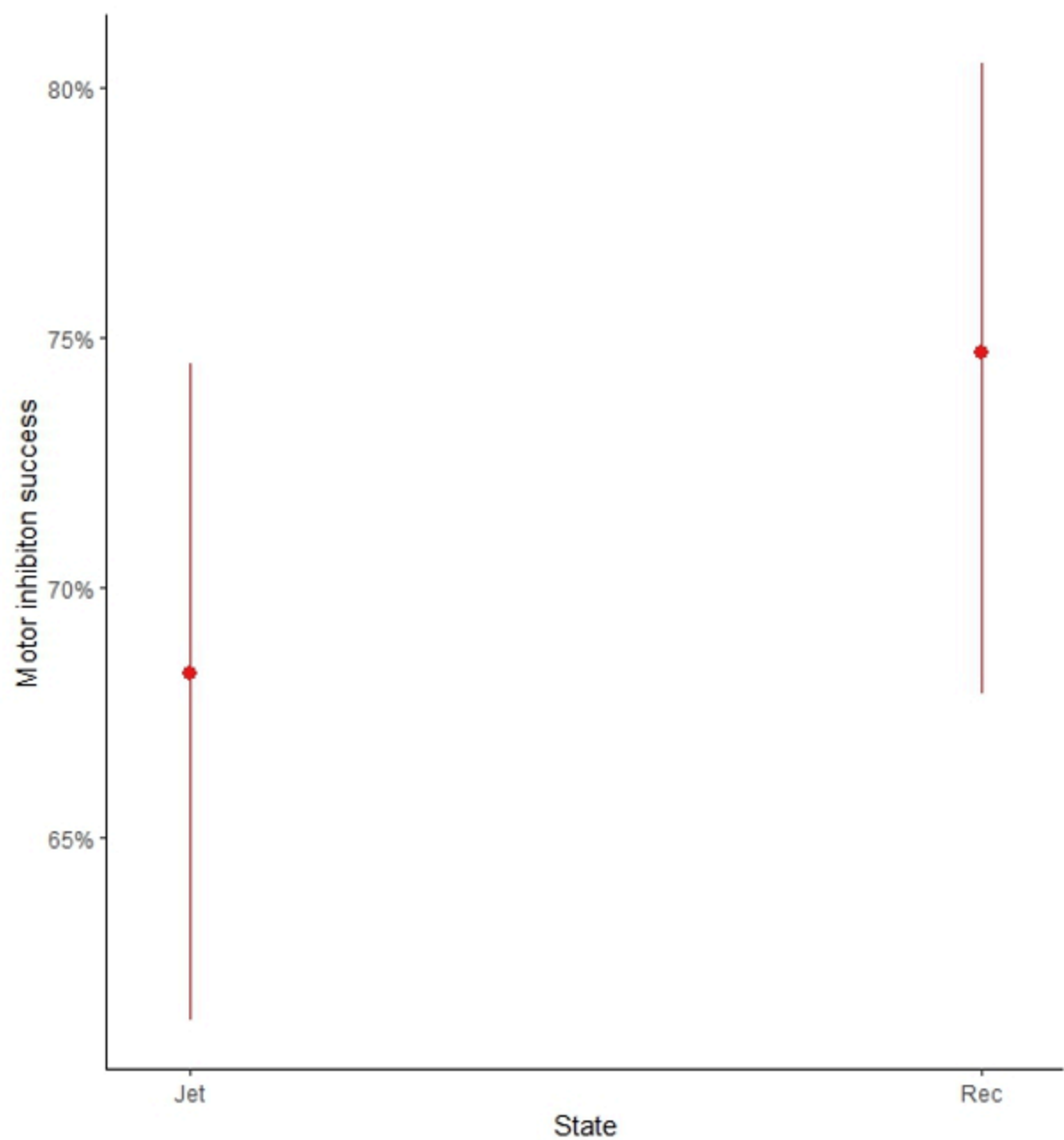


Figure 1

Percentage of motor inhibition success in jet lagged (Jet) and jet lag recovered (Rec) individuals. The error bars are 95% confidence intervals.

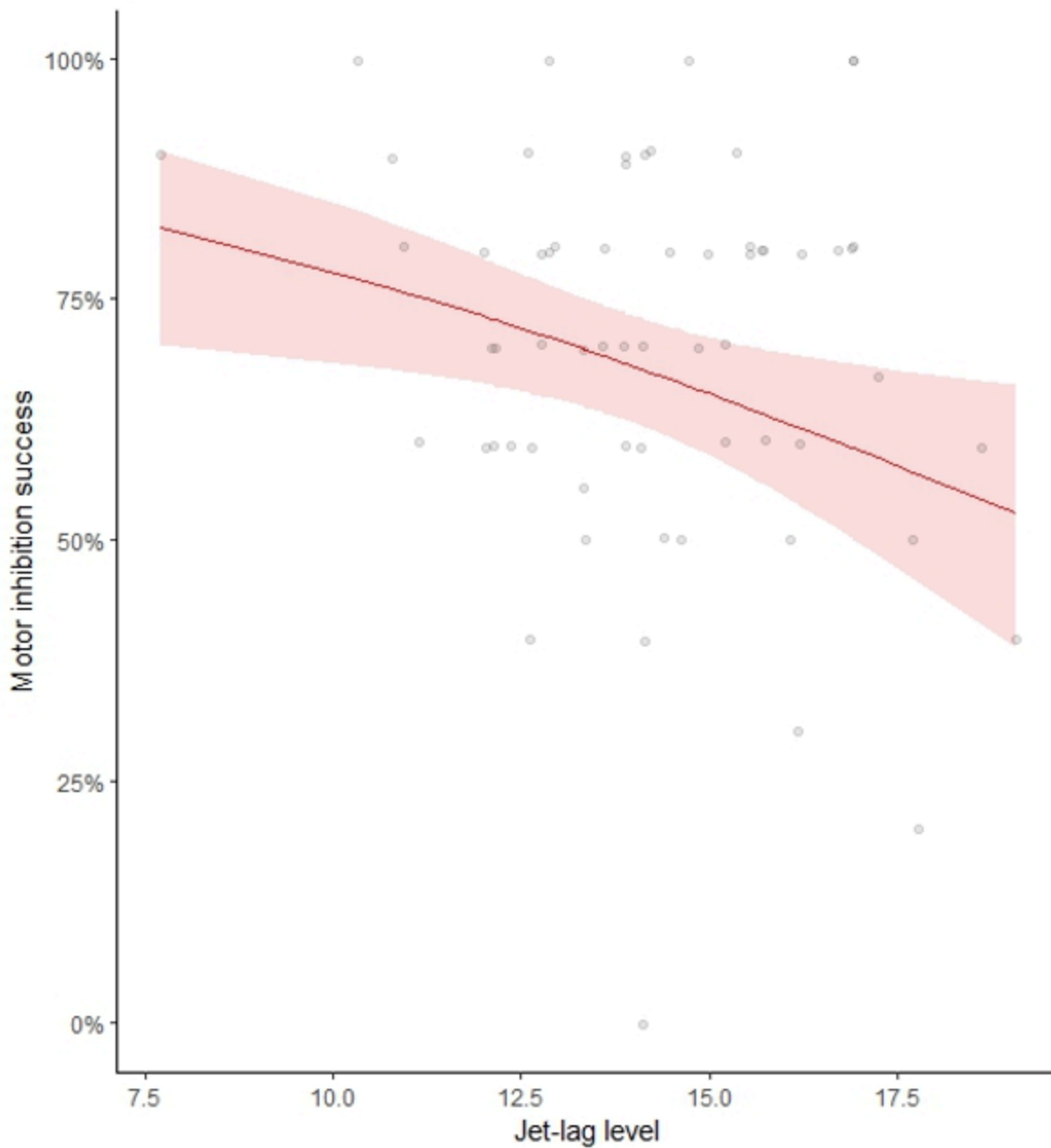


Figure 2

Relationship between motor inhibition success and circadian clock's level of divergence from natural light conditions. The light red band is the 95 % confidence interval. The level of jet lag calculated as follows: Jet lag level = *predicted start of the day (according to the individual circadian rhythm) – the actual start of the day.*

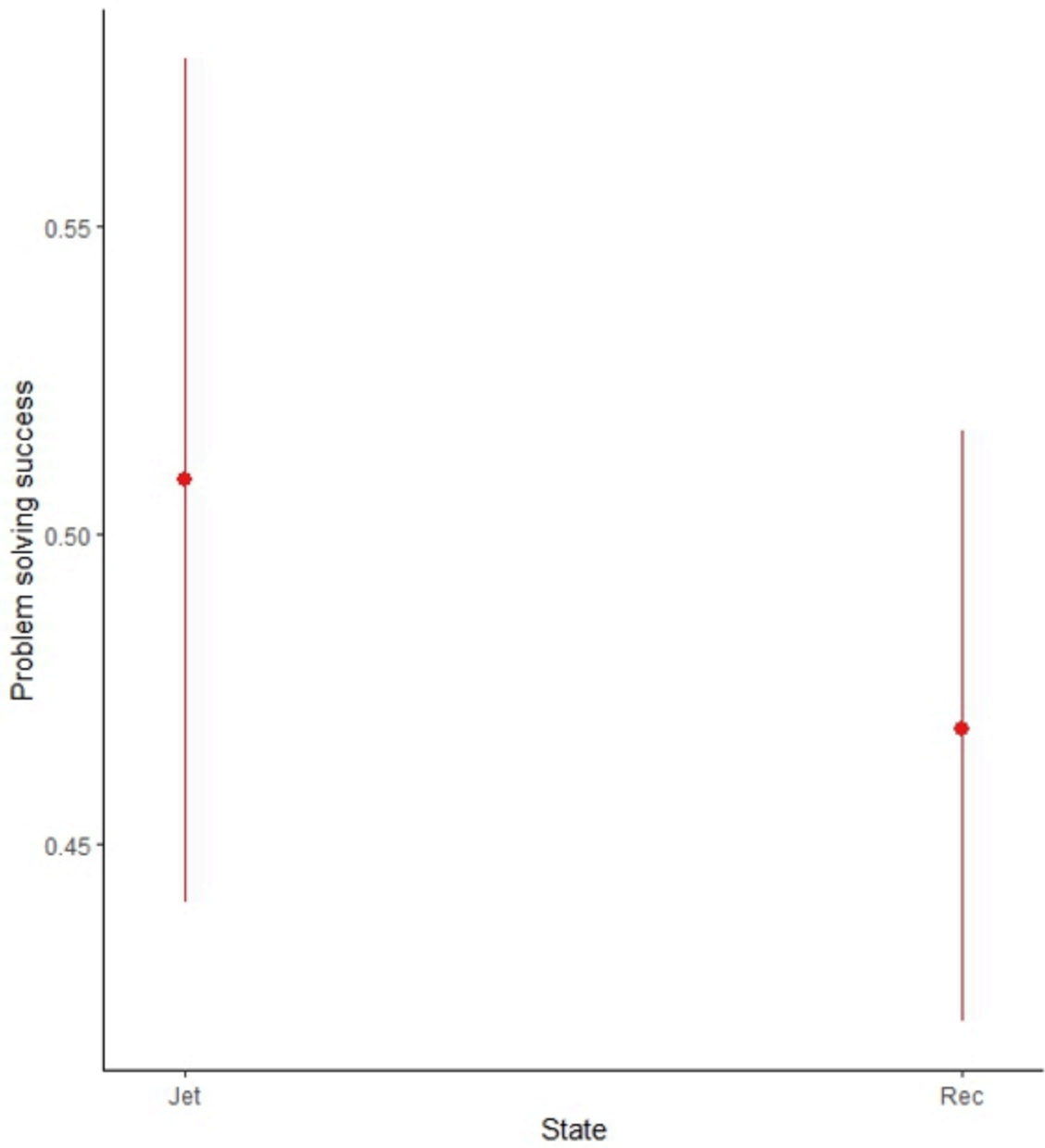


Figure 3

The problem-solving success of jet lagged and recovered birds. The values are derived from mixed mixed-effects Cox Hazard model. The error bars are 95% confidence intervals.

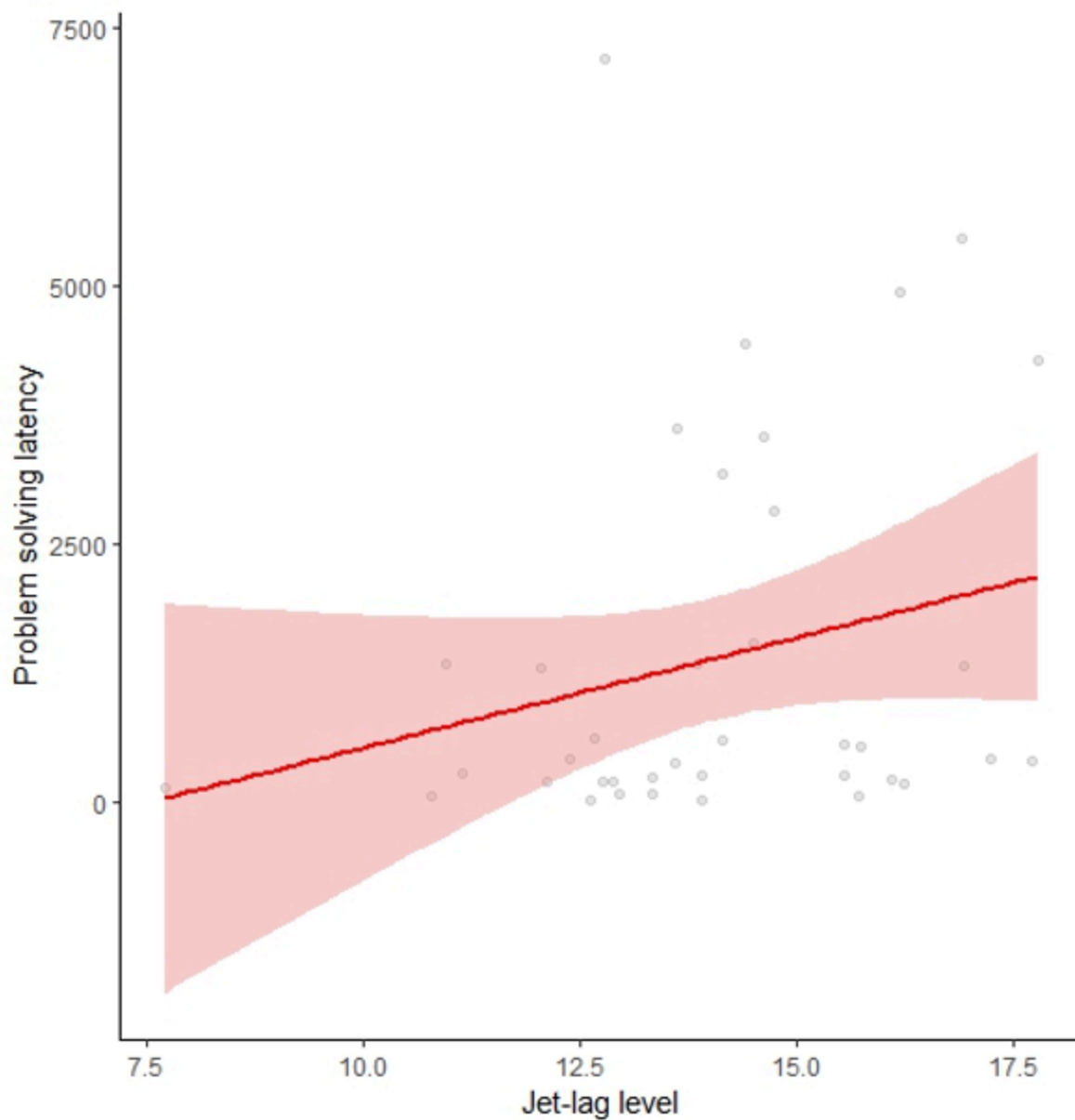


Figure 4

The relationship between problem-solving speed and the jet lag level. The light red band is the 95 % confidence interval. The level of jet lag calculated as: Jet lag level = *predicted start of the day (according to the individual circadian rhythm) – the actual start of the day*.

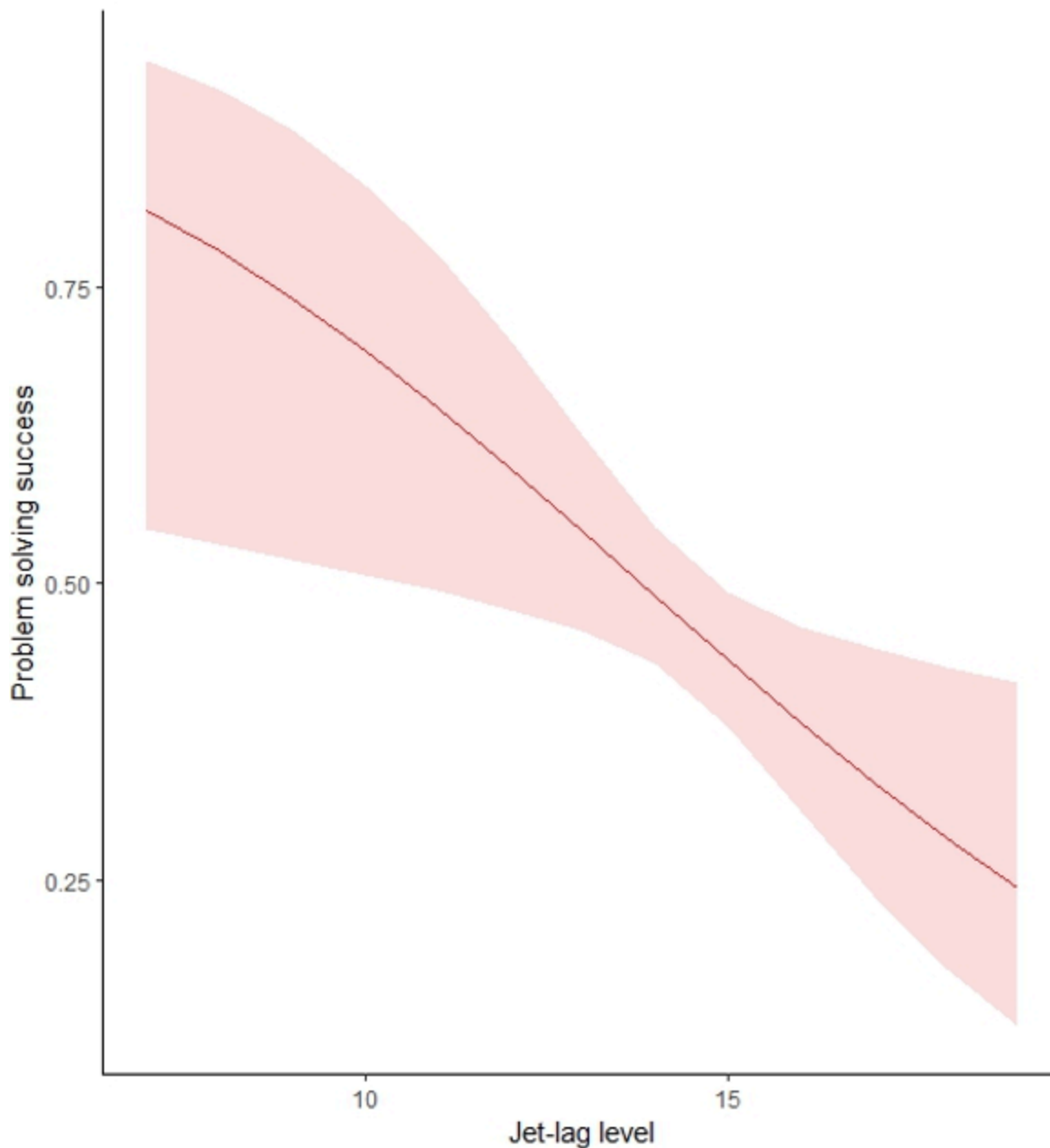


Figure 5

The relationship between problem-solving success and the jet lag level. The line is derived from a mixed mixed-effects Cox Hazard model. The light red band is the 95 % confidence interval. The level of jet lag calculated as: Jet lag level = *predicted start of the day (according to the individual circadian rhythm) – the actual start of the day.*

Supplementary Files

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