signatures of sleep in the paper wasp *Polistes flavus*

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INTRODUCTION

Sleep may significantly define the behavior, ecology and evolution of animals, both vertebrate and invertebrate. To understand sleep's potential roles within a community, both an individual and its entire society must be examined.

Paper wasps (Hymenoptera: Vespidae: Polistinae) are cosmopolitan foragers, visual predators, and architects, forming societies atop their paper cities.

We experimentally tested colonies of paper wasps, primarily *Polistes flavus* (Cresson, 1868), for signs of sleep. Observational studies of caged wasps preceded experiments testing circadian metabolic rates, arousal thresholds, behavior-dependent thoracic temperatures, and the existence of a homeostat regulating sleep.

METHODS

Collection and maintenance

Four colonies of *P. flavus* (mean = five adult wasps) were collected from the Sonoran Desert (Pima County, Arizona, USA) during the summer of 2001. Wasps were individually marked with oil-based, fast-drying pens, and reunited with their nests in transparent cages.

All wasps were maintained under ambient light and temperature conditions, excepting red light for nocturnal viewing and moderate heating during the late fall. Wasps were transferred to a temperature and light controlled laboratory prior to experiments measuring metabolic rates and arousal thresholds.

Statistical analyses

All summary statistics of continuous variables are reported as ± standard error means. Proportional data are presented in their raw, untransformed states, but were arcsine square root transformed for all statistical analyses.

EXTENDED, RECURRING PERIODS OF IMMOBILITY were distinguished from periods of heightened activity by behavioral censusing of wasps every ten minutes.

Circadian immobility was analyzed in darkness, between periods of ambient lighting in four colonies for four evenly-distributed three hour periods each day for four days.

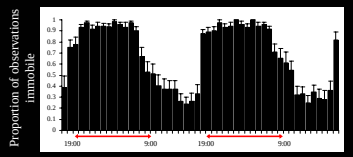
INCREASED AROUSAL THRESHOLDS were elicited by a vibrating device used to stimulate individually housed inactive wasps in a dark environmental control room.

HOMEOSTATIC REGULATION of sleep was tested via sleep deprivation on three colonies across three 50 hour weekends. Wasps were disturbed every five minutes (night, day, or not at all) and were censused every 15 minutes when not being disturbed. In addition, one colony was monitored every 30 minutes throughout a night of disturbance.

DECREASED BODY TEMPERATURES of wasps were measured using an infrared camera with accompanying software. Temperature differences were calculated by subtracting the average temperature surrounding each wasp from its average thoracic temperature.

EXTENDED, RECURRING PERIODS OF IMMOBILITY

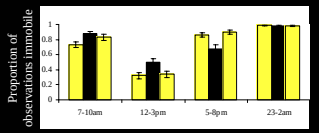
Circadian immobility



50 consecutive hours

Wasps (n = 17 from three colonies) spent extended periods, beginning soon after dusk and lasting until several hours after sunrise (= "inactive period," denoted by horizontal arrow bars) in a relatively motionless state, irrespective of sex and not controlled by ambient temperature.

Circadian immobility does not change in darkness

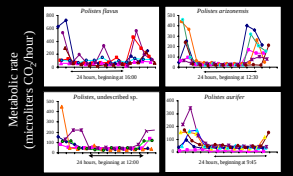


Periods of day

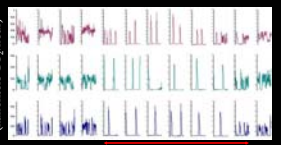
Ambient lighting (day 1 & 4 of study, respectively)
Darkness (day 3 of study, 24 hours into dark period)

Wasps in darkness were immobile as often as they were during control periods.

Metabolic rates were measured using flow-through respirometry.



Metabolic rates followed a circadian rhythm across all wasp species examined.



24 hours: 15 minute snapshots every two hours

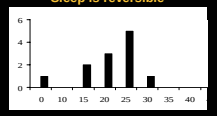
Exhalation during the inactive period = discrete, single bursts of CO_2; active period = erratic bursts of CO_2.

POSTURE

Wasps exhibited a specific, prone posture, with antennae and body lowered in the direction of gravity.

⬆ AROUSAL THRESHOLD

Sleep is reversible

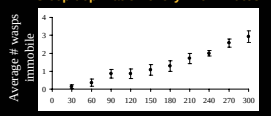


Vibratory stimulus level

Immobile wasps were aroused at a consistent stimulus level. Intense perturbations were frequently required to arouse a profoundly immobile wasp, and less was typically required to instigate flight or sting responses by immobile, vigilant wasps. Reaction to arousal by long-immobile wasps was more pronounced than the reactions to arousal by recently moving wasps.

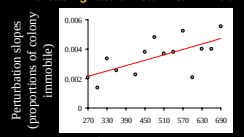
HOMEOSTATIC REGULATION

Sleep deprivation every five minutes



Seconds after disturbance

Increasing rate of return to immobility

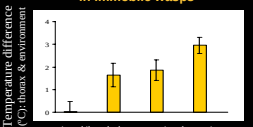


Minutes after sunset (r^2 = 0.44, P < 0.01)

Wasps reverted to an immobile state following each five minute disturbance, and exhibited a faster reversion to immobility as the night of sleep deprivation progressed. (Sleep deprivation did not result in an increase in immobility over the 12 or 24 hours following deprivation. Sleep onset was not earlier, nor was arousal time later for sleep deprived colonies.)

⬇ BODY (thoracic) TEMPERATURE

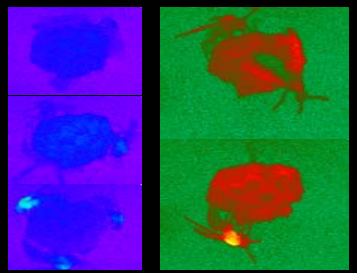
Thoracic temperature is lower in immobile wasps



Behavioral state

(P < 0.05, 1-way ANOVA: Student's t; n = 25 pooled wasps)

Immobile wasps were cooler than wasps exhibiting other behaviors.



Thoracic temperature changed rapidly with respect to behavioral state change following disturbance.

CONCLUSIONS

Wasps

1) exhibited a specific, prone posture primarily during extended, recurring and rapidly reversible periods of relative immobility.
2) did not show an expected sleep rebound following sleep deprivation. Instead, wasps responded through increased rates of return to the immobile state as the night of disturbance progressed. Also, wasps maintained their circadian immobility in spite of a two day absence of light.
3) experienced decreased body temperatures during their immobile states.

Results from the suite of sleep signs support the hypothesis that *Polistes flavus* wasps exhibit a sleep-state, opening up prospects for studying social aspects of sleep in paper wasps.

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