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Food as a supplementary cue triggers seasonal changes in aggression, but not reproduction, in Siberian hamsters

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HIGHLIGHTS

- Hamsters increase aggression when food-restricted in an intermediate photoperiod.
- Hamster reproduction is unaffected by food restriction in permissive photoperiods.
- Male hamsters mount and ejaculate during ongoing gonadal regression.
- Pregnant female hamsters given mild food restriction produce litters normally.

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ABSTRACT

Animals living in temperate regions prepare for harsh winter conditions by responding to environmental cues that signal resource availability (e.g., food, day length). Siberian hamsters (*Phodopus sungorus*) breed in long, summer-like days (LD, >14 h light), i.e., photoperiods, and undergo robust gonadal regression and become more aggressive when exposed to short, winter-like photoperiods that signal impending limited resources (SD, <10 h light). When hamsters are reared within an intermediate photoperiod (ID, 13.5 h light), they are reproductively active, but undergo gonadal regression in response to mild food restriction (FR) over 6–12 weeks. We hypothesized that short-term (1–2 weeks) FR in an ID photoperiod would provide a signal of impending limited resources and initiate the seasonal increase in aggression typical of SD photoperiods, as well as alter reproductive behaviors in advance of gonadal regression. To test this, we housed male and female hamsters in LD or ID photoperiods, with ad libitum (AL) access to food or a 90%-AL ration. We tested aggressive behavior after one week and reproductive behavior after two weeks, and subsequently monitored females for pregnancy and litter production. Both sexes displayed increased aggression in the ID-FR treatment. Untreated male intruders were less likely to ejaculate when paired with ID females during reproductive encounters. ID-FR males were undergoing gonadal regression after two weeks, but were more likely to have ejaculated. Female pregnancy and litter characteristics were unaltered by treatment: females were equally likely to achieve pregnancy and produce comparable litters across treatment groups. Collectively, we demonstrate that a signal of diminishing resources in an ID photoperiod is sufficient to trigger seasonal aggression, but that hamsters are reproductively resilient to inhibitory environmental cues in the short term. Broadly, our findings provide an important context for exploring seasonal changes in behavior and physiology from an ultimate perspective.

1. Introduction

In order to maximize reproductive success, animals living in temperate climates undergo changes in behavior and physiology to coincide with extreme variations in resource availability. Many such species breed seasonally, restricting reproduction to times of year most favorable for survival of self and offspring [1–3]. Rodents such as Siberian hamsters (*Phodopus sungorus*), in addition to adjusting breeding according to time of year, also display changes in aggressive behavior. Siberian hamsters are more aggressive in the non-breeding season, despite low circulating levels of gonadal steroids such as testosterone [4, 5], the primary physiological correlate of aggression in many species (reviewed in: [6–8]).

Photoperiod is the primary environmental cue signaling time of year in Siberian hamsters and many other seasonally breeding animals. Photoperiod is encoded through a physiological signal of melatonin, which is secreted from the pineal gland during the

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night, in the absence of light (reviewed in: [9]). Greater durations of melatonin secretion in longer dark periods of winter (approximately 8–10 h of light) trigger seasonal responses such as robust gonadal regression to curtail reproduction as well as increased aggressive behavior [3–5,10–12]. Hamsters detect the duration of melatonin release in the present as well as the change in the duration of release over time in order to predict future environmental conditions. Thus, shortening photoperiods trigger appropriate changes in reproductive physiology that take place over several weeks in order to prepare for harsh, resource-scarce conditions of winter. It is generally understood that photoperiod functions as a "noise-free" cue that reliably indicates the likelihood of future conditions, but it does not directly affect survival and reproductive success itself. Rather, seasonal species use photoperiod to predict the future status of factors such as precipitation, presence of conspecifics, and perhaps most critical, food availability [13]. Photoperiod can be conceptualized as an "initial predictive" cue, which is used to trigger broad physiological responses over time (gonadal regression), whereas the immediate status of factors such as food availability can act as "supplementary" cues to fine-tune behavior [14]. Adequate food availability is essential to support energy-intensive reproductive processes, and it is reasonable to hypothesize that hamsters similarly increase aggression in response to shortening photoperiod in order to prepare to defend limited food resources, as food availability affects aggressive behavior in a variety of species [15–18]. This specific hypothesis, however, has not been investigated, nor have broader questions related to the relative timelines of behavioral and physiological seasonal shifts in response to changing combinations of initial predictive and supplementary cues.

Siberian hamsters housed in constant photoperiods of either >14 h (summer) or <10 h (winter) of light per day in laboratory conditions show definitive physiological and behavioral states such that supplementary cues (e.g., food) do not trigger reproductive responses ([19, 20]; Bailey et al. in review). In these conditions, although hamsters cannot track changes in photoperiod over time, photoperiod provides an accurate prediction of conditions in the near future. However, if hamsters develop within a constant, intermediate (13.5 h light) photoperiod occurring closer to the vernal and autumnal equinoxes in nature, photoperiod cannot act as an accurate predictor of future conditions without providing the additional information of change in duration of melatonin release. In these conditions, supplementary cues like food availability can trigger the initiation of gonadal regression ([19,20,50]). This laboratory paradigm can be used to address questions of how animals respond to dynamic changes in environmental conditions.

The goal of this study was to investigate how hamsters coordinate changes in behavior and physiology in response to fluctuating supplementary environmental cues. We compared changes in aggressive and reproductive behavior in response to short-term mild food restriction (FR) in male and female hamsters housed in either a long-day (LD), summer-like photoperiod or an intermediate (ID), fall-like photoperiod. We also investigated effects on reproductive success by monitoring females' pregnancies. We hypothesized that hamsters become more aggressive in winter-like photoperiods because short photoperiod is a signal that food will be limited in the future. We therefore predicted that only hamsters in the ID-FR treatment would show an increase in aggressive behavior. We further hypothesized that changes in reproductive behavior would occur in advance of gonadal regression, with the prediction that ID-FR hamsters would exhibit impaired reproductive behaviors; we predicted females to be especially responsive, as reproduction is primarily energy-limiting for females, and sex differences in reproductive responses to seasonal shifts have been shown in related species [21]. Further, we predicted that the occurrence of pregnancy would be limited in ID-FR hamsters, and pregnancies that did occur would be characterized by smaller litter mass or fewer pups, through possible mechanisms of embryo resorption or infanticidal behavior.

2. Materials and methods

2.1. Animals and housing

Adult (>60 days of age; specific ages ranged from 4 to 10 months) male and female Siberian hamsters were obtained from 31 litters produced by 10 breeding pairs in our long-day (LD) photoperiod (16:8 h light:dark cycle, lights on at 0300 h Eastern Standard Time, EST) breeding colony and from 23 litters produced by 14 breeding pairs in our intermediate-day (ID) photoperiod (13.5:10.5 h light:dark cycle, lights on at 0130 h Eastern Standard Time, EST) breeding colony at Indiana University. Animals were weaned at 18 days of age and subsequently housed either individually or with 1–4 same-sex littermates before entering the experiment in adulthood. Hamsters subject to experimental treatments (females: $n = 60$, 30 from each photoperiod; males: $n = 60$, 30 from each photoperiod) were individually housed in polypropylene cages (27.5 × 17.5 × 13.0 cm) with Sani-Chip® bedding material for one week prior to the start of experimental treatments. These animals received ad-libitum access to food (Lab Diet 5001, PMI Nutrition) throughout development prior to the experiment and ad-libitum access to water at all times. Hamsters assigned as behavioral intruders (females: $n = 25$ from LD photoperiod, $n = 36$ from ID photoperiod; males: $n = 35$ from LD photoperiod, $n = 26$ from ID photoperiod) were housed in same-sex sibling pairs when possible, and in triplicate when needed, in polypropylene cages with the same dimensions and bedding material for one week prior to the first behavioral trial. Intruder hamsters received ad-libitum access to food and water at all times. Temperature and humidity were maintained at 20 ± 2 °C and 50 ± 10%, respectively. All animal procedures were performed in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and were reviewed and approved by the Indiana University Bloomington Institutional Animal Care and Use Committee.

2.2. Experimental design

Hamsters within each sex were randomized by breeding pair source and litter into 4 experimental groups, in a full factorial design by photoperiod (LD or ID) and food availability (ad-libitum, AL or food restriction, FR). All animals were weighed weekly. FR animals began receiving daily food rations after 1 week of individual housing and monitoring of baseline food intake, and continued receiving daily rations until time of euthanasia. AL animals' food intake was assessed weekly. After 1 week of FR, all animals participated in an aggressive behavior trial with a same-sex intruder. After 2 weeks of FR, all animals participated in reproductive behavior trials with an opposite-sex intruder nightly for up to 5 nights, to allow for females to display reproductive receptivity during their estrous cycle (see Section 2.5). Male hamsters were euthanized for tissue collection immediately following a trial with a receptive female, or on the fifth night if the female did not display receptivity. Female intruder hamsters were vaginally lavaged to collect any sperm present in the vaginal canal immediately following the trial, and were subsequently euthanized. Female experimental hamsters were monitored for pregnancy following reproductive behavior trials for up to 20 days (gestation for first litters is 18–19 days [22]). Pregnant female hamsters that produced a litter were further monitored for infanticidal behavior for 5 days after birth, at which time the females and litters were euthanized. Non-pregnant females were euthanized for tissue collection after confirming the absence of a litter after 20 days. All females' uterine horns were stained to detect embryo implantation sites indicating pregnancy (see Section 2.6).