Fighting for food: Does food insecurity influence agonistic behavior in the brown anole (*Anolis sagrei*)?

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Introduction

Aggression can be defined as any antagonistic behavior that can involve actual or potential harm to another animal (Huntingford, 2007). Intraspecific aggression between members of the same species are often preceded by elaborate behavioral displays that signal information about the respective competitors (Nijiman and Heuts, 2000). Resource holding potential (RHP) and resource value (motivation) are the two components to intraspecific aggressive behavior that can determine the overall outcome (Nijiman and Heuts, 2000). RHP is defined as an individual's ability to access and defend their resource from other individuals (Enquist and Leimar, 1983). In contrast, resource value, encompasses the motivational component of aggression, which the more valuable or limited a resource is to the individual, the more motivated the individual is to access and defend it (Parker and Rubenstein, 1981). The outcome of an aggressive interaction is determined by the relative effect of both RHP and resource value. Based on this theory, when food is not readily available and energy reserves are being used up, the value of the food resource would increase which motivates an individual to become more aggressive, however this remains understudied with no such research being conducted in reptiles. We aimed to test the hypothesis that low food security (i.e., decreased access to food) would increase aggressive behavior in the brown anole (*Anolis sagrei*) lizard, potentially through the metabolic influence of the stress-steroid corticosterone. We conducted two experiments where male anole lizards exposed to either varying durations of a complete fast or the unpredictable timing of food were made to interact in a dyadic encounter, to determine the effect on behavior, the mobilization of fat reserves (i.e., plasma biomarkers), and circulating and neural corticosterone levels.

Methods

Field sampling and lizard husbandry

Adult male anoles (*N* = 44) were captured by noosing on Rollins College campus in Winter Park, Florida. Anoles were housed in the lizard colony individually in six-gallon plastic tanks separated by a partition. All anoles were provided with a plant, a cloth hammock, a plastic PVC pipe for a perch and a small carpet. Anoles were fed two large house crickets every other day.

Experiment 1. Fasting effects on agonistic behavior

- Randomly-selected control lizards (*N* = 22) were fed the normal cricket diet and treatment lizards were fasted for 24, 48 or 72 hours (*N* = 7-8 / group).
- Control anoles were each matched for weight with a treatment anole and they interacted in a dyadic encounter for 15 minutes and filmed.
- Three separate behaviors were recorded: 1) number of dewlap displays; 2) number of push-ups (done in sets of three); and 3) number of tail raises.
- Data were analyzed with one-way ANOVA and Tukey multiple comparisons

Experiment 2. Food predictability and agonistic behavior

- Anoles were randomly separated into predictable controls and an unpredictable treatment group.
- Controls had access to 2 crickets daily, while treatment anoles though fed an equal amount of crickets over the course of the experiment (1 month), they had access to a variable number during randomly determined times.
- Again anoles were size-matched and pairs interacted in a dyadic encounter with the same three behavioral measures scored from a 15 minute film.
- Following the interactions, anoles were sacrificed and trunk blood was sampled to measure plasma corticosterone (stress steroid), free glycerol (a measure of fat mobilization) and formed triglycerides (a measure of fat deposition).
- Brains were also collected and divided into the telencephalon, midbrain and hindbrain and steroids isolated using solid-phase extraction.
- Brain and plasma corticosterone was measured using enzyme-linked immunoassays (Arbor Assays) and triglycerides and glycerol measured with a sequential endpoint colorimetric assay.
- Data were analyzed with one-way ANOVA and Tukey multiple comparisons

Results

Experiment 1. Fasting does not significantly increase agonistic behaviors in brown anoles.
Various durations of fasting did not effect dewlap displays (F=0.308, p=0.869) nor push-ups (F=2.75, p=0.062; Figure 1). Tail raises were rarely observed which precluded statistical analysis. No differences in body mass were observed between groups (F=1.91, p=0.663).

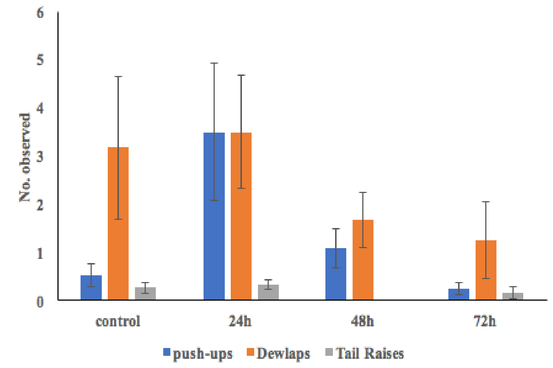
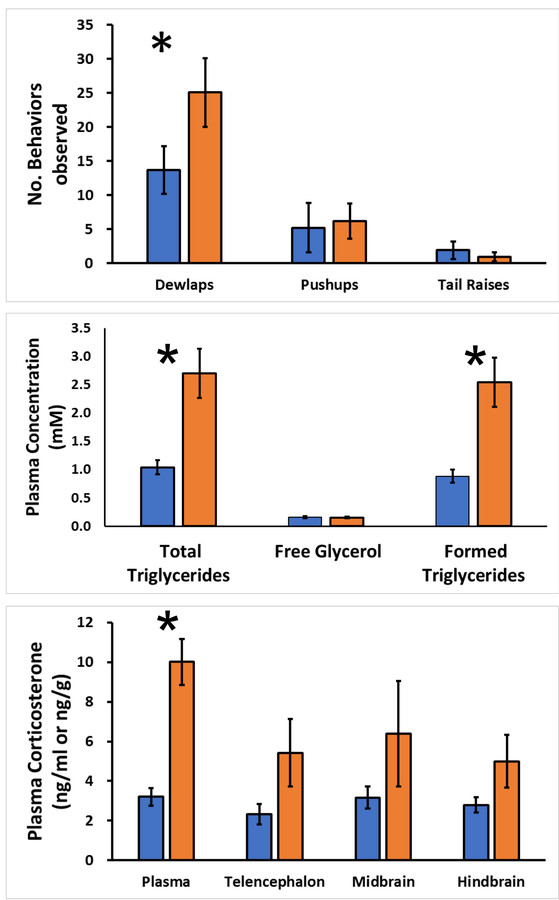


Figure 1. Antagonistic behaviors (per min) displayed between unfasted anoles and those fasted for varying periods during dyadic encounter. No significant differences were observed at p<0.05.



Experiment 2. Food unpredictability increases dewlap displaying, fat deposition and plasma corticosterone in brown anoles.
Anoles in the unpredictable group exhibited more dewlap displays (F=8.838, p=0.009), particularly in the largest anoles (interaction with mass: F=8.572, p=0.010). No other behavioral effects were observed (all p>0.612; Figure 2, *top*). Unpredictable feeding conditions also increased circulating triglyceride levels (F=8.838, p=0.009), but not glycerol (F=0.516, p=0.484; Figure 2, *middle*). Plasma corticosterone was also higher in the unpredictable group (F=27.627, p<0.001), but no significant difference in corticosterone between brain regions was observed. (all p>0.373; Figure 2, *bottom*).

Figure 2:. Differences in agonistic behaviors over a 15 min period (top), circulating energy metabolites (middle) and corticosterone concentrations in plasma and brain regions (bottom) in brown anoles exposed to either unpredictable (*orange*) or predictable (blue) food availability. Asterisk indicates significant differences at p<0.05.

Discussion

During energy challenges, food resource value increases, but as energy reserves are used up, individual's may be conservative about expending energy, thus limiting costly behaviors, like aggression, thus generating a trade-off (Fokidis et al., 2013). Our data supports this, since anoles displayed fewer behaviors as they were fasted longer. Interestingly, at 72 hours, anoles continued to do dewlap extensions, though limiting other behaviors, possibly because this behavior is energy-efficient (Paterson and McMann, 2004), but this would have to be tested. When a feeding schedule is predictable, metabolic processes may adapt, but unpredictable food availability can promote strategies for conserving energy, including increasing fat deposition, as seen in our study where anoles in the unpredictable group had higher concentrations of triglycerides that those on predictable feeding schedules. As expected, unpredictable access to food initiated increased corticosterone concentrations in circulation, however this did not translate into differences in the brain. Thus unpredictable timing in food access, regardless of actual caloric content (which was controlled) induces significant physiological and behavioral changes and thus warrants further study.

Acknowledgments

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