‘Hangry' Beetles: Reduced aggression in response to food deprivation in a system where males fight for mates

Marquerite Herzog
The University of Texas at Arlington
Olivia Williams
The University of Texas at Arlington
Jeffery Demuth
jpdemuth@uta.edu
The University of Texas at Arlington

Research Article

Keywords: Aggression, Resource holding potential, Gnatocerus cornutus, Hangry, male-male contest, food deprivation

Posted Date: April 11th, 2025

DOI: https://doi.org/10.21203/rs.3.rs-6377782/v1

Additional Declarations: No competing interests reported.

Abstract

Aggression is a key behavior for acquiring resources necessary for survival and reproduction, but it is both energetically costly and risky. Theory predicts that aggression should reflect a balance between an individual's resource-holding potential (RHP) and motivation, yet predicting aggression under conditions of resource scarcity is challenging. Nutritional status is particularly important, as food deprivation reduces RHP but may simultaneously increase motivation to fight. Here, we examined how the duration of food deprivation affects male–male aggression in the broad-horned flour beetle, *Gnatocerus cornutus*, a species where combat is primarily used to secure mating opportunities rather than food. We paired size-matched males that were either fed *ad libitum* or starved for up to 11 days and recorded their aggressive behaviors during 20-minute trials. Our results show that short-term food deprivation reduces aggression, consistent with reduced RHP. However, as the duration of food deprivation lengthened, aggression in starved males gradually increased, resembling the "hangry" response described in other animals. In contrast, aggression levels in fed males remained stable across time. Importantly, these patterns were not explained by differences in general activity levels. These findings highlight a dynamic interaction between RHP and motivation, showing that severe resource limitation can override poor condition to elevate aggression. This work contributes to understanding behavioral plasticity under resource scarcity and demonstrates that aggression responses to food deprivation are complex and context-dependent.

Significance Statement

Aggression is a crucial, yet costly behavior influenced by both physical condition and motivation. While food deprivation typically reduces aggression due to diminished resource-holding potential (RHP), in some systems it can increase aggression by elevating motivation. In *Gnatocerus cornutus*, a species where male-male combat secures mates rather than food, we find that short-term starvation suppresses aggression, but prolonged nutrient deprivation leads to increasing aggression, resembling a "hangry" response. This dynamic reversal occurs independently of general activity, suggesting a context-specific motivational shift. Our results reveal that severe resource limitation can override poor condition to elevate aggression, challenging predictions based on RHP alone. Our findings offer new insight on behavioral plasticity under nutritional stress and have implications for understanding how animals balance risk and reward when faced with resource scarcity.

Introduction

Aggression, particularly between conspecifics, is often beneficial for acquisition of resources such as territory, food, and/or mating opportunities that are necessary to survive and reproduce. In animals, aggression takes the form of various agonistic behaviors, from threat displays to physical combat (Darwin 1888; Lorenz 1966; Archer 1988; Kravitz and Huber 2003; Huntingford 2013). However, aggression is also costly, as engaging in aggressive behavior expends energy and time that could be devoted to other activities such as foraging or mating (Briffa and Sneddon 2007). It also risks physical

harm (Haley 1994). Theory suggests that the intensity of aggressive behavior should be a function of the individuals' motivation to gain a contested resource coupled with their probability of winning, so that they gain maximum net benefit (Brown 1964; Maynard Smith and Price 1973; Clutton-Brock and Albon 1979; Enquist and Leimar 1983; Briffa and Sneddon 2007; Georgiev et al. 2013). In general, motivation is determined by the value of securing the resource; scarce, predictable, defensible resources are expected to have a high valuation and therefore motivate the greatest levels of aggression (Brown 1964). The probability of winning, or resource holding potential/power (RHP), is determined by traits that affect an individual's fighting ability such as size, physiological state, and or prior contest experience (Parker 1974). Although these components of motivation and likelihood of winning are reasonably well defined, predicting the intensity of aggression in natural systems is often challenging, in part because the complex interplay of motivation and RHP is constantly being filtered through mechanisms of self- and opponent- assessment that are often poorly understood (Enquist and Leimar 1983; Taylor and Elwood 2003; Briffa and Sneddon 2007; Arnott and Elwood 2008; Lischinsky and Lin 2020).

The effect of nutritional status on aggression has garnered particular attention because many organisms naturally experience periods of food deprivation (reviewed in Wang et al. 2006). During such periods, RHP decreases at the same time that motivation to acquire food increases, making the calculus of optimal aggression even more complex (Houston and McNamara 1988). All else being equal, RHP declines as individuals go without food because fighting ability is compromised by reduction in body size, weapon size, and/or energy reserves (Plaistow and Siva-Jothy 1996; Baker et al. 2003; Briffa and Sneddon 2007; Poças et al. 2022). However, several factors may simultaneously act to increase motivation to acquire food. Most clearly, the duration of food deprivation affects motivation as survival ultimately outweighs the diminished probability of winning a fight (Enquist and Leimar 1983; Elias et al. 2010). Food limitation may additionally affect motivation in less direct ways by providing information about the condition of potential mates (Gibson and Uetz 2012; Zikovitz and Agrawal 2013), competitors (Delisle and Hardy 1997; Engels and Sauer 2007; Fricke et al. 2008), and offspring environments (Trivers and Willard 1973; Taborsky 2006; Cruickshank and Wade 2012b; Cruickshank and Wade 2012a). The specific cue to be aggressive may also be a factor in motivation to fight (Lim et al. 2014). For instance, in systems where males primarily fight over access to females, food limitation may not provoke aggression to the same extent because food does not act as a specific cue for agonistic behavior (reviewed in Kravitz and Huber 2003; Scharf 2016; Lischinsky and Lin 2020). Finally, genetic polymorphisms have also been shown to differentially affect both baseline aggression and the response to food deprivation (Zwarts et al. 2012; Wang and Sokolowski 2017).

While the theoretical and empirical insights above provide substantial foundation for understanding factors that influence aggression in response to food deprivation, the need for additional study is highlighted by inconsistent empirical support within and among species. In humans, feeling hungry is often associated with negative emotions including aggression, a phenomenon commonly known as being "hangry" (Swami et al. 2022). Human studies often, though not exclusively, interpret the elevation of negative emotions in the context of "ego depletion", a lack of energy to impose self-control perhaps mediated by low blood glucose (Baumeister et al. 1998; Kurzban 2010; DeWall et al. 2011; Gailliot 2013;

Bushman et al. 2014; Carter et al. 2015; Anderberg et al. 2016; MacCormack and Lindquist 2019; Dang et al. 2021). Food deprivation has similarly been reported to increase aggression across multiple animal taxa (Stocker and Huber 2001; Nosil 2002; Laidre and Elwood 2008; Hodge et al. 2009). In contrast, other studies demonstrate that in a wide variety of organisms food deprivation may result in decreased aggression, no effect on aggression, and/or a non-linear relationship that depends on factors like severity of food deprivation or social context (reviewed in Scharf 2016). Even within *Drosophila spp.* where food limitation is commonly thought to result in elevated aggression (Lim et al. 2014), outstanding questions remain, and recent studies show elevated (Edmunds et al. 2021), reduced (Wang and Sokolowski 2017), and non-linear associations (Belenioti and Chaniotakis 2020) between aggressive behavior and the availability of food.

Here we test how the duration of food deprivation affects aggression between males of the broad-horned flour beetle, *Gnatocerus cornutus*, a burgeoning model system for studies of sexual selection and behavioral ecology (Okada et al. 2006; Okada and Miyatake 2009; Demuth et al. 2012; Okada et al. 2021). We compare levels of aggression between males that were fed and those that were food deprived for up to 11 days (264 hours). Although the ancestral habitat of *G. cornutus* is not known, they have likely been a human commensal throughout the Anthropocene as a cosmopolitan minor pest of stored grain (Park et al. 1941; Salmond 1956; Tsuda and Yoshida 1985; Throne and Cline 1994). Theory predicts that the inability to monopolize food should result in food not being a strong motivator for adult male aggression. Furthermore, although adult nutritional environment does affect female lifetime reproductive success, only larval nutritional experience affects development of male secondary sex traits (Katsuki et al. 2012). These factors caused us to hypothesize that reduced RHP of food deprived male *G. cornutus* will result in reduced aggression.

Materials and Methods

Study System

G. cornutus adults have pronounced sexual dimorphism wherein males have enlarged mandibular horns, and small horns on the vertex of the head (Fig. 1). Males use the mandibular horns as weapons to fight other males (Okada et al. 2006). Under laboratory conditions, males will fight in the absence of food or females (Demuth et al. 2012). Sporadic but intense bouts of aggression often continue for over 20 minutes before one male “submits”, switching behavior from aggressive to docile, and retreating from conflict for approximately 4 days (Okada and Miyatake 2010; Demuth et al. 2012).

The beetles used in our study were obtained from the laboratory of Dr. Michael Wade (Indiana University) and reared in the Demuth laboratory for over 10 years. Stocks are reared on media made up of a 95:5 ratio of whole wheat organic flour: brewer's yeast by weight in 45cm L x 30cm W x 8cm D covered plastic trays filled ~ 3 centimeters deep with media. These stocks are housed in a ~ 100sq ft environmental chamber maintained at 26–30ºC and ~ 70% relative humidity (RH) with a 24D:0L photoperiod when not in use for experiments. Prior to experimental trials, to facilitate pupation, single final-instar larvae from

the stock cultures were extracted and transferred to individual glass vials (25 mm Diam x 95 mm H) containing 2g of media. Upon eclosion, male beetles were identified by the presence of mandibular horns and remained in the vials for two weeks. To prepare for competition experiments, each male's weight was measured (+/-0.001mg) using an AT261 Delta Range precision balance (Mettler-Toledo Inc., Columbus, OH). After weight measurement, pairs of beetles were matched with the male most similar in weight and given identification numbers. One male from each pair was arbitrarily chosen to receive a white spot on the elytra to facilitate identification while scoring behavior during contests (Fig. 2) and then one beetle from each pair was arbitrarily assigned to either the fed or starved treatment (fed = food available *ad libitum;* starved = deprived of all food). Previous studies show that this marking method does not affect contest outcome (Demuth et al 2012). All contest participants were maintained in isolation until use in the behavior trials described below.

Behavior Trials

Trials were conducted on size-matched fed/starved pairs at 24-hour intervals from 0 to 256 hours. Males in each pair were naïve (reared in isolation) and used for only one trial. Before each contest, new filter paper (Whatman® qualitative filter paper) was added to the bottom of the fighting arena (diameter: 2.5cm) to provide traction. Trials were conducted under red light in a Percival I-66VL incubator maintained at 30ºC and 70% RH. Competitors were placed in the fighting arena (Fig. 2) and separated with a plastic divider until recording began. We used a Sony HandyCam HDR-SR5 under red lighting to record behavior for 20 minutes per trial, after which competitors were removed from the arena.

We quantified behavior by reviewing the video recordings. Behaviors were categorized according to an ethogram consisting of seven aggressive and three non-aggressive behaviors (Table 1). Every five seconds, the observer recorded a 1 in the category of behavior being displayed by each male. All other behavioral categories were given a 0 for that time point. Observers scoring the competitions were blind to the treatment status (starved or fed) of the beetles. To account for the sparsity of the resulting data matrix (i.e. many zeros), statistical analyses were computed on the aggregate of aggressive behavior types.

Statistical Analyses

To assess whether starvation impacted aggression levels, we computed general linear and polynomial regressions using feeding status and hours of food deprivation (time) as categorical and continuous predictors respectively, and included their interaction. To mitigate violation of regression assumptions (homoscedasticity) in our count data, we square root transformed the dependent variables, aggression or travel. To test whether aggression levels differed on average between fed and starved groups we computed Welch's t-statistic (unequal variances). We used Python (v3.9.12) statmodels (v 0.13.2) in Jupyter Labs (v3.3.2) to conduct the analyses. Results were considered significant at $\alpha = 0.05$. To test for

non-linear relationships, polynomial models were compared using the Akaike Information Criterion (AIC) to determine the best model (Akaike 1998).

Results

We conducted 33 contests between pairs of food deprived and fed males. Contestants performed typical fighting maneuvers for this species, such as interlocking mandibles, shoving or pushing the opponent, and lifting an opponent from the fighting arena (Okada et al. 2006, Okada and Miyatake 2010). Frequently one male initiated contact with the side of the other male, often resulting in flipping the opponent onto its back. After righting themselves, the opponent would occasionally reciprocate the aggression by approaching the initiating male and engaging in head-to-head contact. Head-to-head encounters were often prolonged, lasting minutes with interlocked horns while both males seemed to attempt to push their opponent backward. After prolonged interactions one beetle would regularly climb on top of the other beetle. Since the individual aggressive behaviors in Table 1 were rare for any given male across a 20-minute bout, the resulting data matrix was sparse, containing many zeros. Therefore, we pooled behavioral observations into two categories, aggressive and non-aggressive, for our analyses. Among non-aggressive behaviors, we use Travel as the best proxy for beetles' general activity level not related to aggression (Supplementary Table S1).

Both feeding status (fed or starved) and time (hours of food deprivation) were significant predictors of aggression ($F_{3,62}$ = 11.32, p < .001, R^2 = .354; Table 2). Figure 3A illustrates that fed males maintained consistent levels of aggression throughout the study. Starved beetles demonstrated dramatically lower aggression than fed beetles in the earliest time points after food was withheld, but gradually increased their frequency of aggressive behaviors as food deprivation was prolonged. Despite this trend for starved males to increase aggression over time, fed males were significantly more aggressive across the entire experiment (Fig 4; *Welch's t* = 5.186, p <0.001).

To test whether the observed trends in the frequency of aggressive behavior could be explained by differences in general activity level, we analyzed the frequency of Travel behavior in the same way as aggressive behavior (Figure 3B). We find no significant effect of feeding status or time on Travel ($F_{3,62}$ = 1.676, p = .181, R^2 = .075; Table 2).

To assess whether any of the relationships between aggression and feeding status were non-linear over time, we compared the linear model above, to quadratic and cubic polynomial regression models. We found no evidence that the higher order models provide a better fit than the linear model based on their AIC scores (Table 3).

Discussion

Our findings provide new insight into the complex interplay between resource-holding potential (RHP) and motivation in shaping aggression, particularly in the context of food deprivation. In male Gnatocerus

cornutus, we observed that short-term food deprivation reduces aggression, consistent with theoretical predictions that diminished RHP due to declining energy reserves or physical condition suppresses costly aggressive behaviors (Baker et al. 2003; Briffa and Sneddon 2007).This aligns with the idea that animals should avoid unnecessary conflict when the likelihood of winning is low and the costs of aggression are high (Maynard Smith and Price 1973; Parker 1974).

However, our results also reveal that as the duration of food deprivation is prolonged, aggression in starved beetles gradually increases, a pattern analogous to the “hangry” phenomenon documented in both human and non-human systems (Laidre and Elwood 2008; Swami et al. 2022). This increase in aggression after extended food deprivation suggests that motivational factors eventually outweigh reduced RHP, compelling individuals to engage in aggressive encounters despite compromised condition. The shift from reduced aggression under moderate deprivation to heightened aggression under severe deprivation reflects a dynamic behavioral adjustment to changing ecological circumstances. When starvation becomes severe, the perceived value of contested resources (in this case, access to mates) and the urgency to secure reproductive opportunities may override the diminished probability of success in combat (Enquist and Leimar 1983; Elias et al. 2010).

Interestingly, aggression levels were not correlated with general locomotor activity, as travel distances remained stable across treatments. This finding suggests that the observed increase in aggression among long-term starved beetles is not a byproduct of increased general activity or restlessness, but rather a specific behavioral adaptation to prolonged deprivation. This distinction is important because it indicates that aggression is modulated by context-dependent motivational states rather than simply changes in energy levels or movement patterns.

In the ecological and evolutionary context of *G. cornutus*, where male combat is primarily linked to securing mating opportunities rather than food monopolization, our findings support and refine existing theoretical models. Initially, reduced aggression following food deprivation is consistent with decreased RHP in a system where adult nutritional status does not influence secondary sexual traits (Katsuki et al. 2012). However, the subsequent rise in aggression with extended deprivation suggests that motivational factors tied to reproductive urgency can override the suppression of aggression caused by poor condition. This dual-phase response highlights the need to consider both RHP and motivation as dynamic, interacting factors rather than static traits.

Our study also contributes to the broader understanding of aggression under resource limitation by demonstrating that responses are not always linear or predictable. Although food deprivation often reduces fighting ability and can suppress aggression, severe or prolonged deprivation may trigger compensatory increases in aggression as organisms attempt to maximize their remaining reproductive opportunities. Such behavioral flexibility could have adaptive significance in environments where resource availability and social context fluctuate unpredictably.

Future work should explore whether similar patterns of aggression in response to prolonged food deprivation occur in other species and contexts, particularly where the stakes of resource acquisition

vary. Additionally, it would be valuable to investigate the physiological and neuroendocrine mechanisms underlying this shift in aggression, as well as whether individual differences or genetic polymorphisms influence the thresholds at which motivational factors override reduced RHP (Zwarts et al. 2012; Wang and Sokolowski 2017).

In conclusion, our results demonstrate that in *G. cornutus*, aggression is initially suppressed by food deprivation but subsequently increases with prolonged deprivation, reflecting a complex and dynamic interplay between RHP and motivational urgency. These findings emphasize the importance of considering both condition and changing motivational states when predicting aggressive behavior and highlight the value of this system for future studies of behavioral plasticity and decision-making under resource scarcity.

Declarations

The authors declare no competing interests

Author Contribution

M.H. and J.D. designed the experiments. M.H. conducted the trials and collected data with help from undergraduate researchers. M.H. and O.W., and J.D. performed the analyses, wrote the manuscript text, and prepared the figures. All authors reviewed the manuscript.

Acknowledgement

We thank the Emily Hale, Austin Truong, and Regan Griffin for contributions to recording behavioral trials, especially. This work was supported by the National Science Foundation Graduate Research Fellowship, the Pat Tillman Foundation Pat Tillman Scholarship, the UTA William L. and Martha Hughes Scholarship, and the UTA Dissertation Grant, which collectively funded the doctoral education and research efforts of M. Herzog.

Data Availability

Data is provided within the manuscript or supplementary information files

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Tables

Table 1 Ethogram of behaviors used to score competitions

Behavior Type	Behavior	Code	Description
Aggressive	Attack	X	Initiates forceful contact with the opponent
Aggressive	Attack – Head	HC	Initiates forceful contact with the opponent's head
Aggressive	Attack – Body	BC	Initiates forceful contact with the opponent's body
Aggressive	Climb Over	CO	Approaches opponent from side or rear and climbs onto his dorsal area
Aggressive	Lift	L	Lifts opponent from substrate during combat
Aggressive	Flip	F	Flips opponent onto his back during combat
Aggressive	Chase	C	Pushes or chases opponent from the arena
Non-Aggressive	Approach	A	Initiates incidental contact with the opponent during normal exploratory movement
Non-Aggressive	Retreat	R	Flees from opponent or fighting area
Non-Aggressive	Travel	T	Moves from place to place without interacting with the opponent in the arena

Table 2 Summary Statistics and OLS Regression Results

	n	Mean (count)	SD	Min	Max
Aggression (Fed)	33	49.61	32.41	9	125
Aggression (Starved)	33	19.79	26.46	0	98
Travel (Fed)	33	85.27	39.78	9	175
Travel (Starved)	33	64.15	31.06	0	116

Aggression*	Coefficient	SE	t	p-value	95% CI Lower	95% CI Upper
Intercept	1.58	0.947	1.669	0.1	-0.312	3.472
Feeding Status	5.1	1.339	3.809	<0.001	2.424	7.776
Time	0.014	0.006	2.357	0.022	0.002	0.026
Status × Time	-0.014	0.009	-1.645	0.105	-0.031	0.003
Travel*						
Intercept	7.245	0.99	7.321	<0.001	5.267	9.223
Feeding Status	1.943	1.399	1.388	0.17	-0.854	4.74
Time	0.003	0.006	0.403	0.688	-0.01	0.015
Status × Time	-0.004	0.009	-0.48	0.633	-0.022	0.014

Model Summaries:

Aggression: $F(3, 62) = 11.32$, $p < 0.001$, $R^2 = 0.354$, Adjusted $R^2 = 0.323$

Travel: $F(3, 62) = 1.676$, $p = 0.181$, $R^2 = 0.075$, Adjusted $R^2 = 0.030$

* Ordinary Least Squares Regression was conducted on square-root-transformed counts of Aggression and Travel.

Table 3 Polynomial regression models for fed and starved beetles. Comparison of Akaike Information Criterion (AIC) values for linear, quadratic, and cubic regression models predicting square-root-transformed aggression in Fed and Starved groups. Lower values indicate better model fit.

Feeding Status	Linear	Quadratic	Cubic
Fed	148.3	149.1	150.1
Starved	156.6	158.3	158.0

Figures

Figure 1

Sexual dimorphisms between male (left) and female (right) *Gnatocerus cornutus*.

Figure 2

Arena and marking scheme for competition experiments. Competitions were conducted in 6-Well Cell Culture Plates (35mm diameter; lower image) with one male marked by a white spot on its elytra (top inset).

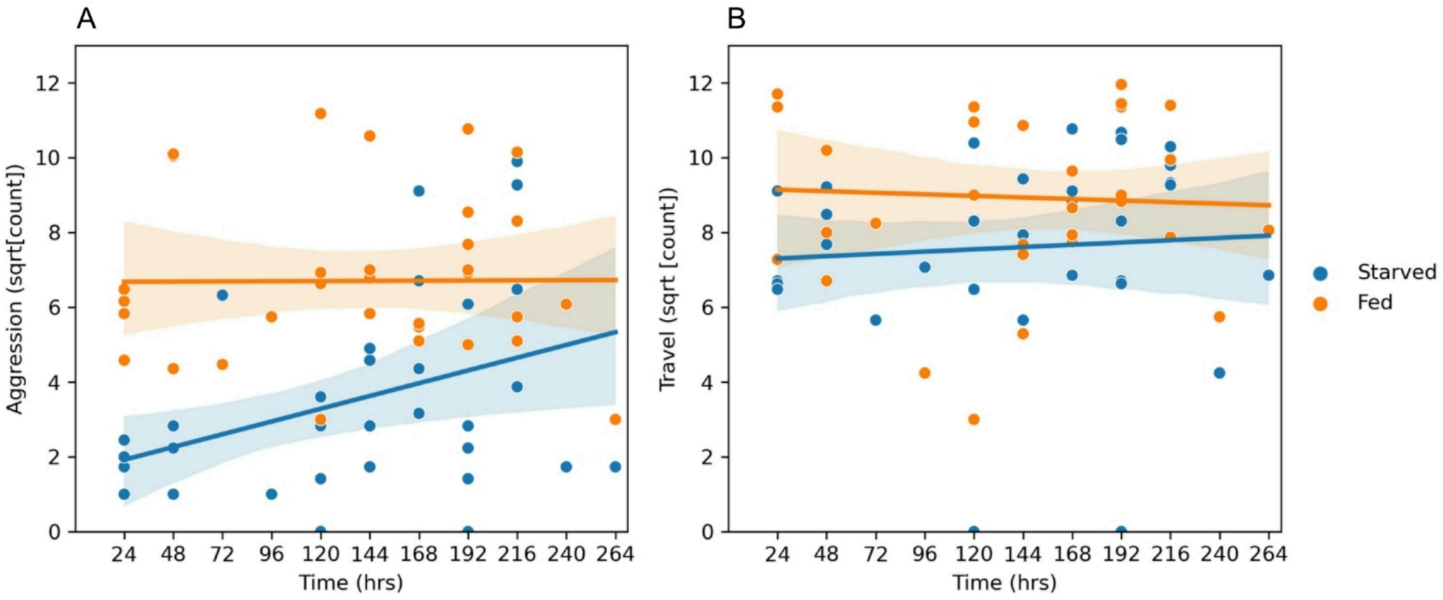

Figure 3

(A) Aggression was significantly affected by both status (starved versus fed), and the duration of food deprivation (time in hours). (B) Travel was not affected by either status or time indicating that changes in aggression are not explained by differences in general activity level. Y-axes show the square root of relevant behavior counts. Shaded areas are 95% confidence intervals.

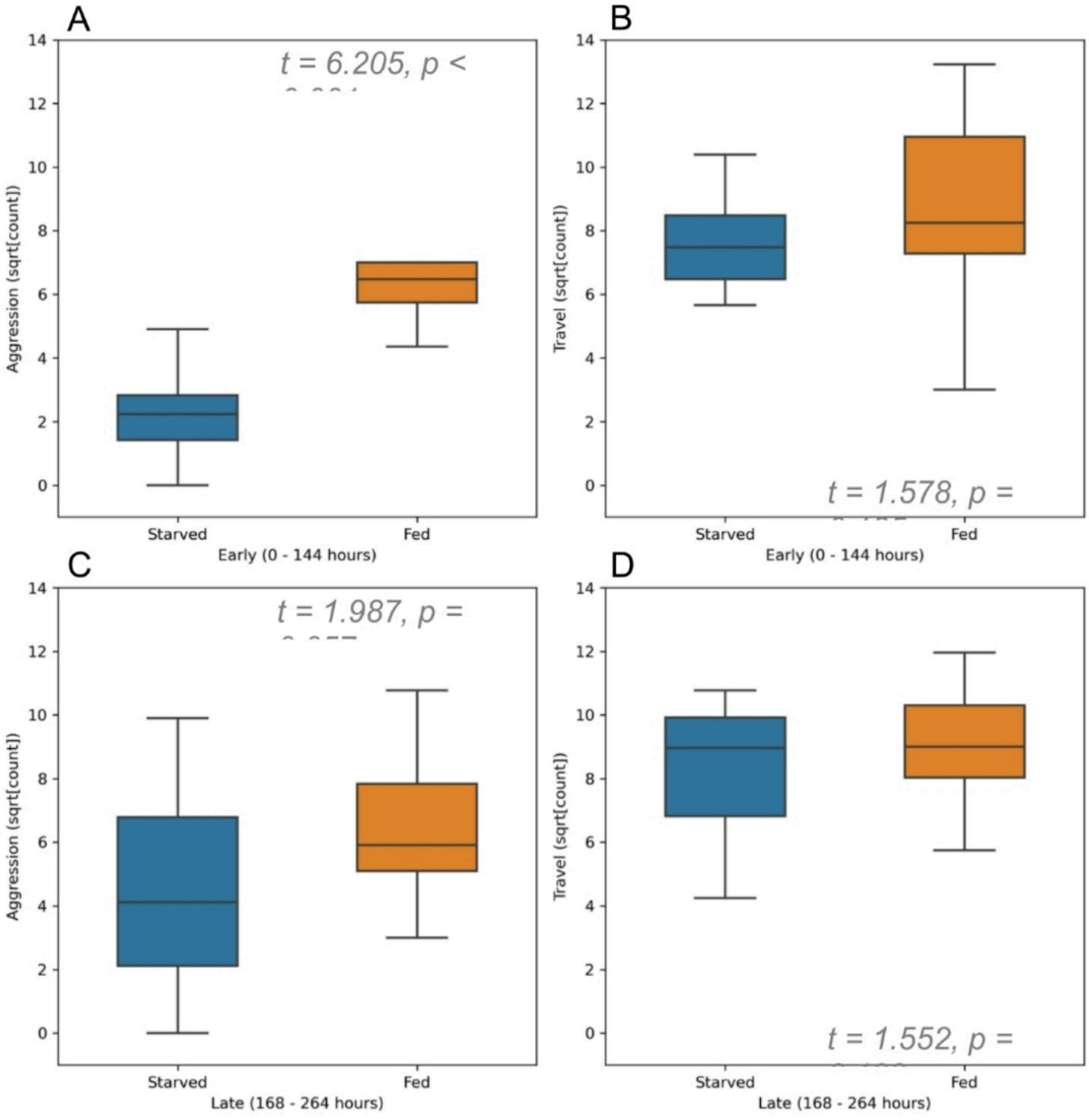

Figure 4

Starved males (blue) were significantly less aggressive than fed males (orange) over the first half of the experiment (A). Owing to increasing aggression over time, aggression levels were not different between

starved and fed over the second half of the experiment (C). Travel did not differ between starved and fed males during either period (B,D), indicating that differences in aggression are not due to differences in general activity level.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementaryTableS1.csv