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LETTER

Interspecific Competition Reduces Energy Expenditure by Decreasing Intragroup Conflict in a Social Burying Beetle

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ABSTRACT

Assessing the physiological costs of sociality remains challenging due to complex interactions between environmental and social factors. To overcome this challenge, we integrated game theory with empirical research to examine how interspecific competition affects energy expenditure in the cooperatively breeding Asian burying beetle *Nicrophorus nepalensis*. Our nested tug-of-war model made two predictions: beetles facing interspecific competition would experience (1) lower physiological costs due to reduced investment in intragroup conflict, despite increased cooperative effort; and (2) decreasing physiological cost differences between dominance ranks. Using thermal imaging, we analysed body temperature as a proximal indicator of thermogenic effort during carcass work. Results supported our model's two key predictions: beetles competing with blowflies exhibited lower body temperatures, with less pronounced temperature differences between social ranks. Thus, reduced social conflict outweighs the energetic costs of increased cooperation in the face of external threats, providing insights into how environmental conditions shape energy allocation in social species.

1 | Introduction

Animals must allocate energy efficiently when facing both environmental challenges and social interactions within their group, including dominance contests, territorial defence, and cooperative activities (Viblanc et al. 2016; Emery Thompson 2017; Fisher et al. 2021). In harsh environments, animals often increase energy expenditure to maintain basic physiological function (e.g., thermogenesis or thermoregulation) to avoid detrimental effects on their metabolic processes (Morrison et al. 2008; Rezende and Bacigalupe 2015). Similarly, when resources are scarce or unpredictable, intensified competition leads to increased energy expenditure, often manifested in complex foraging or long-distance dispersal strategies (Berlincourt and Arnould 2015; Cozzoli et al. 2020). In social species, hierarchical structures within groups further complicate the distribution of physiological costs. High-ranking individuals often incur energetic costs to obtain and maintain dominance, while low-ranking individuals may expend energy when coping with challenges from dominant individuals or competing for higher social status (Abbott et al. 2003; Goymann and Wingfield 2004; Gesquiere et al. 2011). Notably, interspecific competition can differentially influence the physiological costs for individuals of different social ranks, as demonstrated in baboons (Sapolsky 1986) and cooperatively breeding superb starlings

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(Rubenstein 2007). However, unravelling the complex interplay between external competitive pressures and social factors on physiological state remains challenging, as these factors mutually shape the behaviour and physiological responses of individuals within a group (Takahashi et al. 2018; Fujii et al. 2019; Abdelall et al. 2020; Takahashi 2021).

Previous research indicates that when facing interspecific competition, social animals often reduce intragroup conflict and enhance cooperation (Rubenstein and Lovette 2007; Shen et al. 2012, 2017). However, the net effect of these behavioural shifts on individual physiological costs remains unclear. Reduced social conflict may lower related energy expenditure, while increased cooperative behaviour itself requires energy investment, especially in resource-competitive environments. Different species show varied physiological responses to external threats (Gunderson et al. 2017; Killen et al. 2021), complicating predictions about the combined impact of interspecific competition and social structure on individual physiological burden. Understanding this dynamic balance is crucial for elucidating the evolutionary costs of social living.

While research on the effects of competitive pressure and physiological costs has focused primarily on vertebrates (Creel et al. 2013; Culbert et al. 2018), studies in social insects have been relatively limited (Tibbetts and Huang 2010; Jandt et al. 2014; Tibbetts et al. 2018; Pandey et al. 2020), mainly due to technical challenges in insect hormone analysis. To overcome this limitation, we use relative body temperature (RBT)—the difference between body temperature and ambient temperature—as an indicator of physiological energy expenditure in insects. As ectotherms, insects have limited (Heinrich 2013; Colinet et al. 2015) though measurable thermoregulatory capacity (Heinrich 1974). For example, larger insects can raise their flight muscle temperature before taking off (Krogh and Zuthen 1941; Dorsett 1962), while some social insects warm their nests through collective body heat (Kleinhenz et al. 2003). These thermoregulatory behaviours not only mitigate extreme temperature effects but also enhance behavioural performance (Heinrich 1974; Kearney et al. 2009). Additionally, metabolic heat generated by insect activity directly increases body temperature, making higher RBTs indicative of greater energy expenditure (Krogh and Zuthen 1941; Dorsett 1962; Heinrich 1974). Thus, body temperature measurements provide a practical tool for studying energy expenditure in insects, one key axis in a suite of other relevant physiological costs (e.g., endocrine, immune, oxidative) that may also respond to competitor pressure.

Here, we investigate how the presence of interspecific competition (with blowflies) and intraspecific competition (with beetles of different social rank) jointly affect the energy expenditure in the cooperatively breeding Asian burying beetle *Nicrophorus nepalensis*. This species of beetle is known for both its cooperative behaviours in burying small carrion and communal brood care, with blowfly competition driving increased cooperation and reduced conflict within social groups (Sun et al. 2014). In this system, cooperation refers to a shift from carcass investment monopolised by dominant beetles to a more egalitarian contribution among all group members. Cooperation is defined as increased carcass preparation by subordinates, and includes a suite of behaviours including cleaning, depilating, removing maggots, and burying carcasses (Chen et al. 2020). Intraspecific competition intensifies when more aggressive interactions among same-sex conspecifics over access to the carcass occur, including wrestling, attacking, chasing, and fleeing behaviours (Chen et al. 2020).

We test two non-mutually exclusive hypotheses regarding the physiological costs during carcass preparation in burying beetles in relation to interspecific competition versus intraspecific conflict: if interspecific competition has a greater impact on energy expenditure, then beetles will expend more energy due to their increase in cooperative investment in response to stronger competitive pressure. Conversely, if intragroup social conflict more significantly influences energy expenditure, then beetles will expend lower energy costs due to their decrease in social conflict with the presence of interspecific competition. We employ an integrated theoretical and empirical approach to examine these hypotheses about interspecific competition and social conflict. For the theoretical component, we integrate Rubenstein and Shen's (2009) evolutionary game theory model of social stress and physiological costs with Reeve et al.'s (Reeve et al. 1998; Reeve and Hölldobler 2007) and Liu, Chen, et al.'s (2020) nested tug-of-war model describing interspecific and intraspecific competition dynamics. This theoretical integration enables us to predict how interspecific competitive environments affect energy allocation strategies and physiological burdens of individuals at different social ranks. We then use non-invasive thermal imaging to empirically quantify the RBT of beetles as a proxy of energy expenditure. This integrated approach helps reveal the physiological adaptation mechanisms of social insects under multiple competitive pressures, providing new theoretical and empirical frameworks for studying energy strategies in group-living organisms.

2 | Theoretical Model

2.1 | Model Description

We follow the model developed by Rubenstein and Shen (2009), which uses a tug-of-war framework to describe intragroup individual conflicts over resources. Following Liu, Chen, et al. (2020), we incorporate interspecific competition into this model because competition with blowflies is the most important factor affecting the social behaviours and reproductive success of burying beetles (Sun et al. 2014; Liu, Chan, et al. 2020). Thus, burying beetle individuals face nested tug-of-war dynamics in which they compete with interspecific competitors (blowflies) for resources while simultaneously engaging in intraspecific competition.

We assume that the resources obtained by burying beetles are determined by the total cooperative investment (V_b), which equals the sum of each beetle's cooperative investment ($V_b = v_A + v_B + v_G$) and the total investment of blowflies (V_f) in the interspecific tug-of-war for resources with value R. Thus, the resources obtained by the beetle group are $V_b/(a\ V_f + V_b)$, where $a\ V_f$ represents the pressure of interspecific competition from blowflies. The scaling factor (a) indicates a stronger competitive advantage for blowflies, which increases at higher temperatures where blowflies have been shown to gain greater competitive advantage over the beetles (Sun et al. 2014; Liu, Chan, et al. 2020). We also assume that the greater the investment in interspecific competition, the higher the individual personal cost.

In addition to interspecific competition with blowflies, burying beetles also face intraspecific competition for resources. For simplicity, we only consider competition among same-sex individuals and assume that burying beetle groups consist of three same-sex individuals, alpha, beta and gamma, in descending order of rank. We further assume that each individual's share of the group's resources is determined by their effort invested in the intragroup tug-of-war, such that when individuals exert greater competitive effort x_A, x_B, x_G, the individual's personal costs, such as energy costs, will also increase. The share of group resources is thus $x_A/(x_A+b\,x_B+c\,x_G)$ for alpha, $b\,x_B/(x_A+b\,x_B+c\,x_G)$ for beta, and $c\,x_G/(x_A+b\,x_B+c\,x_G)$ for gamma. In intragroup tug-of-war, alpha, beta and gamma can differ in their ability to compete, which can be described by the scaling factors b or c, where $b>c$ and $0<c<b\leqslant 1$ (Reeve et al. 1998; Shen and Reeve 2010). The costs of per unit investing in interspecific competition and intraspecific conflict are assumed to be the same for alpha, beta, and gamma, which is described as an accelerating function in terms of decreasing future fitness (Trivers 1972; Shen et al. 2012).

Following Rubenstein and Shen (2009), we use the cost functions $(k_{vA}\,v_A+k_{xA}\,x_A)^2$, $(k_{vB}\,v_B+k_{xB}\,x_B)^2$, and $(k_{vG}\,v_G+k_{xG}\,x_G)^2$ to represent the physiological cost of alpha, beta, and gamma. Since the physiological cost is the cumulative result of the individual's response to both interspecific and intraspecific competition, we explicitly build the physiological cost term as a function of the two levels of cooperative investment (v_A, v_B or v_G) and selfish effort (x_A, x_B, x_G), and we also consider individual body condition (k_{vi} and k_{xi}, where $i=A,B$ and G for alpha, beta and gamma respectively). We assume that more individual investment in intraspecific competition will reduce the amount of common resources, a standard tug-of-war model assumption. Thus, we can obtain the following fitness functions for blowfly (W_{fly}) and burying beetles of differing rank (W_A, W_B or W_G), as follows:

$$W_{fly} = \left(R \frac{a\,V_f}{a\,V_f + V_b\left[v_A, v_B, v_G\right]} \right) - k_f {V_f}^2$$

$$W_A = \left(R \frac{V_b\left[v_A, v_B, v_G\right]}{a\,V_f + V_b\left[v_A, v_B, v_G\right]} - x_A - x_B - x_G \right) \frac{x_A}{x_A + bx_B + cx_G} - \left(k_{VA}v_A + k_{xA}x_A\right)^2$$

$$W_B = \left(R \frac{V_b\left[v_A, v_B, v_G\right]}{a\,V_f + V_b\left[v_A, v_B, v_G\right]} - x_A - x_B - x_G \right) \frac{bx_B}{x_A + bx_B + cx_G} - \left(k_{VB}v_B + k_{xB}x_B\right)^2$$

$$W_G = \left(R \frac{V_b\left[v_A, v_B, v_G\right]}{a\,V_f + V_b\left[v_A, v_B, v_G\right]} - x_A - x_B - x_G \right) \frac{cx_G}{x_A + bx_B + cx_G} - \left(k_{VG}v_G + k_{xG}x_G\right)^2$$

The evolutionarily stable levels of investment in intraspecific cooperation are V_f^*, v_A^*, v_B^* and v_G^* for competing blowflies, the alpha, beta and gamma beetles, respectively. With investment in intraspecific social conflict, x_A^*, $x_B^*\,x_G^*$, for a higher share of group resource for the group members, the fitness functions must then satisfy

$$\left.\frac{\partial W_{fly}}{\partial V_f}\right|_{V_f=V_f^*,\, x_A=x_A^*, v_A=v_A^*,\, x_B=x_B^*, v_B=v_B^*, x_G=x_G^*, v_G=v_G^*} = 0$$

$$\left.\frac{\partial W_A}{\partial x_A}\right|_{V_f=V_f^*,\, x_A=x_A^*, v_A=v_A^*,\, x_B=x_B^*, v_B=v_B^*, x_G=x_G^*, v_G=v_G^*} = 0, \quad \left.\frac{\partial W_A}{\partial v_A}\right|_{V_f=V_f^*,\, x_A=x_A^*, v_A=v_A^*,\, x_B=x_B^*, v_B=v_B^*, x_G=x_G^*, v_G=v_G^*} = 0$$

$$\left.\frac{\partial W_B}{\partial x_B}\right|_{V_f=V_f^*,\, x_A=x_A^*, v_A=v_A^*,\, x_B=x_B^*, v_B=v_B^*, x_G=x_G^*, v_G=v_G^*} = 0, \quad \left.\frac{\partial W_B}{\partial v_B}\right|_{V_f=V_f^*,\, x_A=x_A^*, v_A=v_A^*,\, x_B=x_B^*, v_B=v_B^*, x_G=x_G^*, v_G=v_G^*} = 0$$

and

$$\left.\frac{\partial W_G}{\partial x_G}\right|_{V_f=V_f^*,\, x_A=x_A^*, v_A=v_A^*,\, x_B=x_B^*, v_B=v_B^*, x_G=x_G^*, v_G=v_G^*} = 0, \quad \left.\frac{\partial W_G}{\partial v_G}\right|_{V_f=V_f^*,\, x_A=x_A^*, v_A=v_A^*,\, x_B=x_B^*, v_B=v_B^*, x_G=x_G^*, v_G=v_G^*} = 0$$

Since we could not obtain analytic solutions for the above equations due to their complexity, we used Mathematica-v12.0 to solve for V_f^*, v_A^*, v_B^* and v_G^* and x_A^*, $x_B^*\,x_G^*$ numerically.

3 | Results

3.1 | Model Predictions of the Nested Tug-of-War Model

Our model shows that beetles receive fewer resources under high interspecific competitive pressure (larger a). Interestingly, our model also predicts that individuals experiencing intense interspecific competition have lower physiological costs compared to individuals in environments with minimal competition (Figure 1A). The model also highlights the influence of social factors, specifically individual rank, on physiological costs. Higher ranking individuals have higher physiological costs (alpha > beta > gamma), primarily because they invest more in cooperation against interspecific competitors compared to lower ranking individuals (Figure 1A).

Yet, even in environments with low interspecific competition, alpha individuals maintain relatively higher levels of cooperative investment than lower ranking beta and gamma individuals (Figure 1B). This occurs because under low competitive pressure, higher ranking individuals invest more in cooperation while being more efficient in intraspecific competition (Figure 1C). However, as interspecific competition intensifies, alpha individuals cannot easily increase their cooperative

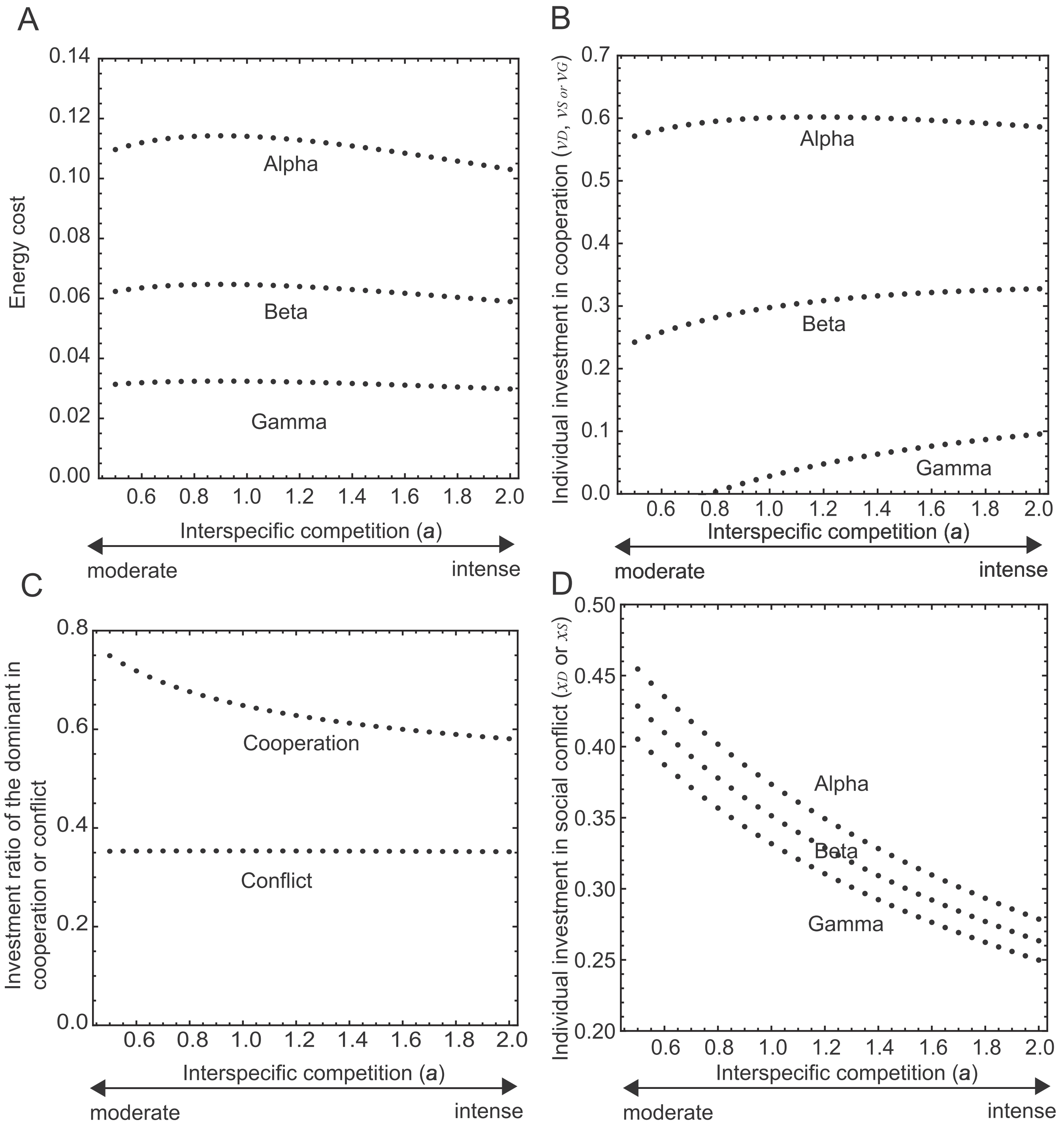

FIGURE 1 | Results of game-theoretic model of dominance hierarchies, physiological cost $(c_v\ v_i + c_x\ x_i)^2$ and intraspecific social conflict and cooperation. (A) The relationship between physiological cost and interspecific competition, (B) individual investments in cooperation (v_i), (C) the investment ratio between the dominants and subordinates in cooperation $(v_A/(v_A + b\ v_B + c\ v_G))$ or conflict $(x_A/(x_A + b\ x_B + c\ x_G))$, and (D) individual investments in social conflict (x_i) in relation to interspecific competition, where $i = A$, B or G. Parameter values are $G = 3$; $b = 0.7$; $c = 0.5$; $c_v = 0.5$; $c_x = 0.5$; $c_f = 1$.

investment because they already invest significantly even under low competitive pressure. Conversely, lower ranking individuals (beta and gamma), due to their lower baseline investment, can obtain relatively higher benefits by increasing their cooperative investment under strong interspecific competition (Figure 1B). Therefore, when interspecific competition is strong, the cooperative investment of dominant and subordinate individuals becomes more similar (Figure 1B).

The model also predicts that as interspecific competition increases, all individuals reduce their investment in social conflict (Figure 1D), resulting in lower individual physiological costs. This unexpected result suggests that the reduction in social conflict outweighs the increase in cooperative investment, resulting in overall lower physiological costs for individuals under strong interspecific competition. Note that a model using resource availability as a proxy for competition intensity yields the same qualitative results as the interspecific competition model (see Liu, Chen, et al. 2020, appendix for details).

3.2 | An Empirical Test in Burying Beetles

We used burying beetles to test the key predictions of our theoretical model regarding the effects of interspecific competition and social factors on the energetic costs of social organisms. In our laboratory experiment, social groups of burying beetles consisting of three males and three females were provided with a rat carcass, allowing us to examine the cooperative and competitive behaviours exhibited by individuals of different ranks in the social group. Specifically, we examined the effect of interspecific competition on the energetic costs experienced by individuals of different ranks by manipulating the presence or absence of blowfly competition.

3.3 | Interspecific Competition and Energetic Costs

The empirical results confirmed the prediction from the theoretical model that individuals experience lower energetic costs when facing interspecific competition pressure. We found that the RBT of beetles increased rapidly during the first few hours of the experiment and then gradually decreased in both the control (Figure 2A, Figure S1, Table S1) and blowfly treatments (Figure 2B, Figure S2, Table S2). However, the mean RBT in the blowfly treatment was lower than in the control (LM, $F=5.81$, $n=262$, $p=0.017$; Figure 2C), and it took less time to reach the maximum RBT (LM, $F=8.23$, $n=257$, $p=0.004$; Figure 2D). This means that the body temperature of the beetles in the blowfly treatment started to decrease earlier than in the control. Both results support the key prediction of our model that energetic costs, as represented by RBT, are lower when facing interspecific competition than in environments with no competition.

3.4 | Social Rank and Energetic Costs

Consistent with our second model prediction, the empirical results showed that higher ranking beetles had higher energetic costs compared to lower ranking beetles, but the trend differed between the control and the blowfly treatments. In the control, the RBTs of higher ranking individuals were greater than those of lower ranking individuals (LM, social rank ($\beta-\gamma$), $t(256)=2.38$, $n=262$, $p=0.047$; social rank ($\alpha-\gamma$), $t(256)=4.27$, $n=262$, $p<0.001$) (Figure 3), but there was no significant difference between the RBTs of higher and lower ranking individuals in the blowfly treatment (LM, social rank ($\alpha-\beta$), $t(256)=1.71$, $n=262$, $p=0.203$; social rank ($\beta-\gamma$), $t(256)=-0.08$, $n=262$, $p=0.997$;

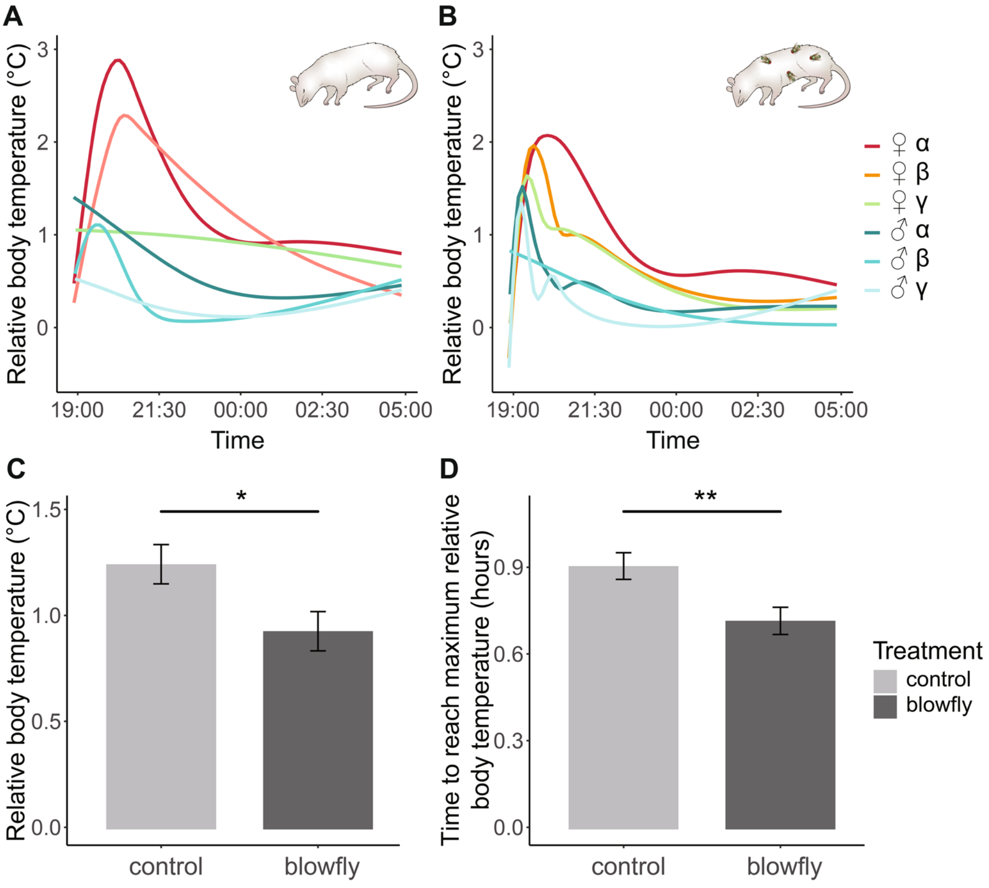

FIGURE 2 | Results of the generalised additive model (GAM) analysis of the temporal trend of relative body temperature for individuals of different sexes and ranks in the (A) control and (B) blowfly treatment. The results of the (C) mean relative body temperature of individuals and (D) mean time to maximum relative body temperature in the control and blowfly treatments. Alpha is the highest ranking, beta is the second ranking, and gamma is the lowest ranking individual. *$p \leq 0.05$; **$p \leq 0.01$. Error bars indicate ±1 standard error (SE) of the model-fitted mean.

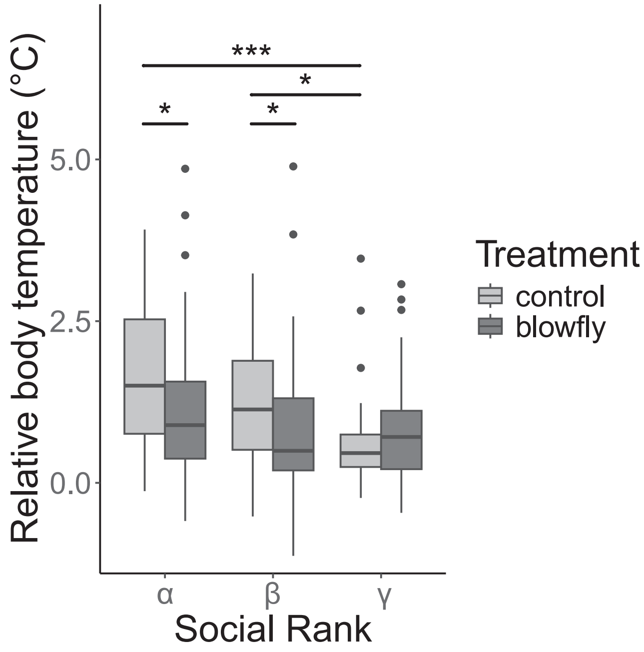

FIGURE 3 | Mean relative body temperature for individuals of different rank in the blowfly and control treatments. The lower, middle, and upper boundaries of each box plot represent the 1st, 2nd (median), and 3rd quartiles, respectively. The black dots represent data that are more than 1.5 times different from the range of the 1st and 3rd quartiles. * $p \leq 0.05$; *** $p \leq 0.001$.

social rank ($\alpha-\gamma$), $t(256)=1.52$, $n=262$, $p=0.283$) (Figure 3). We also found that the RBT in the control was greater than that in the blowfly treatment for the highest-ranking individual (LM, $t(256)=2.33$, $n=262$, $p=0.021$) and the middle ranking individual (LM, $t(256)=1.99$, $n=262$, $p=0.048$) (Figure 3). The lack of marked differences in mean RBT between ranks in the blowfly treatment is consistent with the model's prediction that the energetic costs of higher-ranking individuals when facing interspecific competition will be closer to those of lower ranking individuals than under conditions of no competition.

The RBTs of burying beetles showed distinct temporal trends between the first half of the night (19:00–23:59) and the second half (00:00–5:00), as shown in Figure 2A,B. Based on this, we divided the temperatures into these two periods for further analysis. In the first half of the night, we found that the RBTs of individuals in the control and blowfly treatments were similarly high (LM, $F=3.78$, $n=257$, $p=0.053$) (Figure S3A). We also found that during the first half of the night, mean RBT was significantly different between the highest and lowest ranking individuals in the control treatment (LM, social rank ($\alpha-\gamma$), $t(128)=4.02$, $n=131$, $p<0.001$) (Figure S4A). No such differences in RBT were found between ranks in the blowfly treatment (Figure S4C). However, in the second half of the night, the RBT of individuals in the control treatment was higher than that in the blowfly treatment (LM, $F=9.21$, $n=169$, $p=0.003$) (Figure S3B). In the control treatment, the mean RBT of high rank individuals was significantly higher than that of beta and gamma individuals (LM, social rank ($\alpha-\beta$), $t(76)=2.77$, $n=79$, $p=0.019$; social rank ($\alpha-\gamma$), $t(76)=2.47$, $n=79$, $p=0.041$) (Figure S4B). However, in the blowfly treatment, only the highest-ranking individual had a higher RBT than the lowest-ranking individual (LM, social rank ($\alpha-\gamma$), $t(87)=3.09$, $n=90$, $p=0.007$) (Figure S4D).

3.5 | Energetic Costs Associated With Cooperative and Competitive Behaviour

Next, we determined how social factors (i.e., the cooperative and intraspecific competitive strategies of individuals of different rank) influence social behaviours and energy expenditure in the presence or absence of interspecific competition. We analysed the temporal trends in burying beetle investment in time spent cooperatively preparing rat carcasses (Figure S5) and the number of intraspecific competitive interactions (Figure S6), as well as the relationships between beetle cooperative and competitive behaviours and their relative body temperatures. Because conflict behaviours occur primarily in the first half of the night, and cooperative investments in carcass preparation are more frequent during this time, we present results for the first half of the night (results for the second half of the night can be found in the Supporting Information).

Our results indicate that RBT covaried with the energetic costs of performing cooperative and intraspecific conflict behaviour of an individual. In both the control group (LM, $F=7.41$, $n=122$, $p=0.007$) (Figure 4A) and the blowfly treatment (LM, $F=7.56$, $n=123$, $p=0.007$) (Figure 4B), RBT was positively associated with cooperative investment. Furthermore, our analysis of the amount of cooperative investment revealed that the average cooperative investment in the blowfly treatment was higher than in the control (LM, $F=29.4$, $n=264$, $p<0.001$) (Figure 4C). However, the comparison of individual conflict frequency and RBT showed a significant positive relationship between the number of conflicts and RBT in the control (LM, $F=6.03$, $n=122$, $p=0.016$) (Figure 4D), but not in the blowfly treatment (LM, $F=3.68$, $n=123$, $p=0.058$) (Figure 4E). Interestingly, we also found that the number of conflicts was significantly lower in the blowfly treatment compared to the control (LM, $F=9.53$, $n=260$, $p=0.002$) (Figure 4F). Together, these behavioural results are consistent with the patterns observed in the RBT measurements. To further validate these findings, our structural equation modelling confirmed that RBT is primarily influenced by social interactions (cooperative investment and conflict behaviours) rather than ambient temperature (Figure 5).

4 | Discussion

Our game-theoretic model makes two key predictions about how interspecific competition affects the physiological costs of individuals of different social rank. First, it predicts that individuals experience lower energetic costs in more competitive environments—where interspecific competition is intense—because they reduce investment in intraspecific social conflict. Conversely, in less competitive environments, where interspecific pressure from competitors is weak, individuals invest more in social conflict, leading to higher energetic costs. Second, while higher ranking individuals generally incur greater energetic costs than lower ranking individuals, the difference between ranks is smaller in highly competitive environments. This

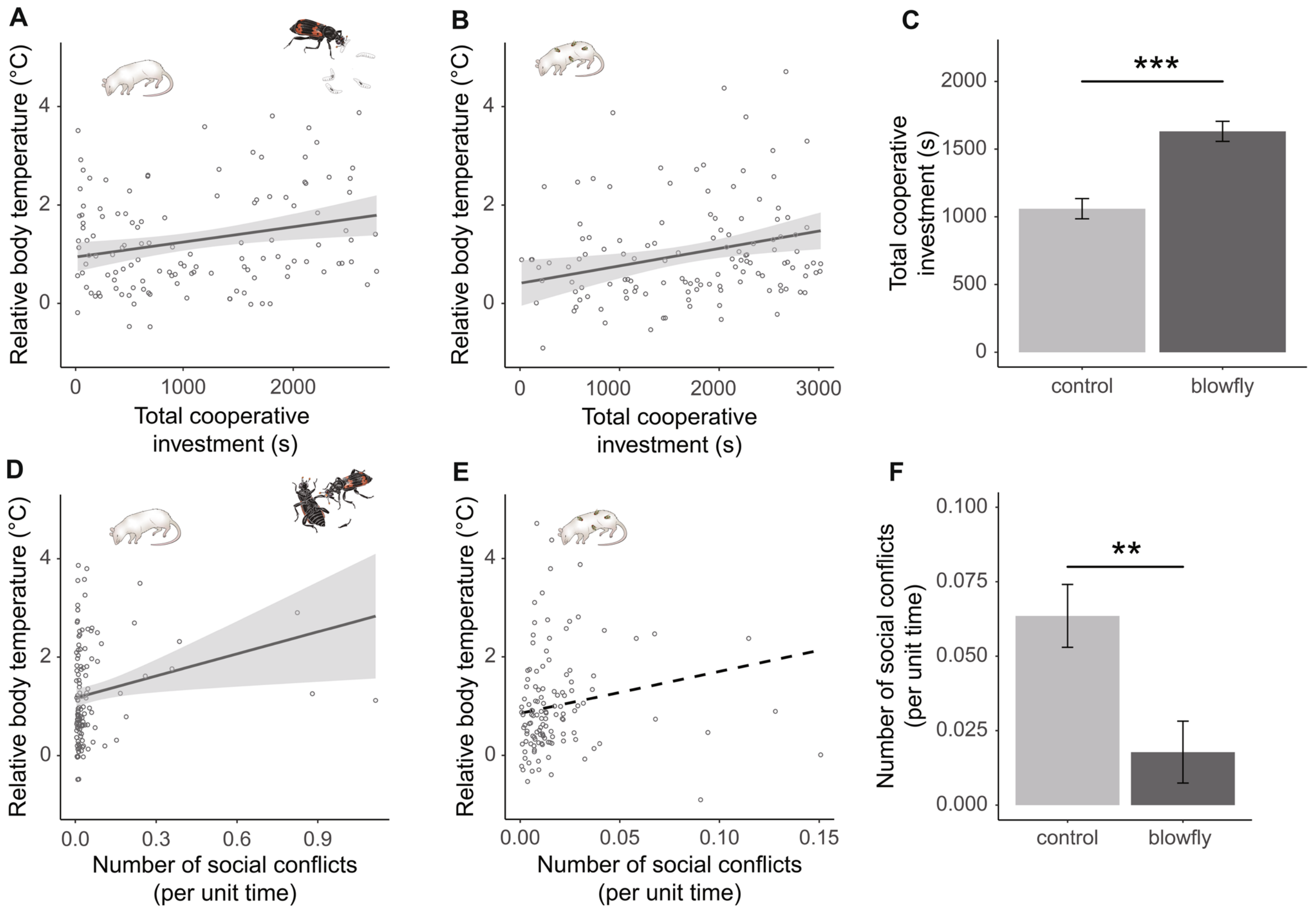

FIGURE 4 | Cooperative and conflict behaviours in the first half of the night. Individuals' investment time in cooperation in relation to relative body temperature in (A) the control and (B) the blowfly treatments. (C) The results of the mean investment time of individuals in the control and blowfly treatments. The relationships between number of social conflicts (per unit time) and relative body temperature in (D) the control and (E) the blowfly treatments. (F) The results of the mean number of social conflict (per unit time) in the control and blowfly treatments. The solid black lines represent significant relationships. The grey blocks are the 95% confidence intervals. **$p \leq 0.01$; ***$p \leq 0.001$. Error bars indicate ±1 standard error (SE) of the model-fitted mean.

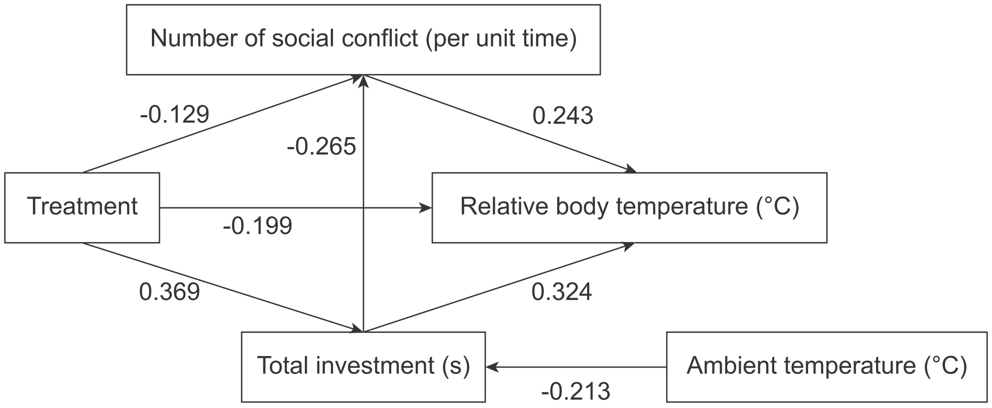

FIGURE 5 | Piecewise structural equation model (SEM) linking *treatment* (blowfly competition vs. control), *total cooperative investment* (s), *number of social conflicts* (events per unit time), *ambient temperature* (carcass surface temperature, °C), and *relative body temperature* (RBT; thorax—carcass surface temperature, °C). Arrows show standardised path coefficients (β); solid lines = $p < 0.05$, dashed = not significant. Model fit: Fisher's $C = 3.852$, $p = 0.426$, $n = 275$. Units: RBT and ambient temperature in °C; cooperative investment in seconds; conflicts as counts per unit time. Full model specification is in Methods S6.

is because increased interspecific competition aligns individual interests and reduces within-group conflict. Our empirical results support both predictions when costs are operationalised as RBT—indexed energetics: (1) beetles exposed to blowfly competition had lower mean RBTs compared to the control group where interspecific competition was absent; and (2) the temperature differences between social ranks were smaller under blowfly competition than in the control treatment.

These seemingly counterintuitive predictions can be explained by considering how interspecific competition affects the cooperative and competitive behaviours of individuals of different rank. The energetic costs of higher ranking individuals are higher than lower ranking individuals in environments with minimal interspecific competition because higher ranking individuals invest more in fighting against intraspecific competitors for common resources. Conversely, the lower social conflict under strong interspecific competition leads to lower energetic costs of all individuals because the interests of individuals cooperating against interspecific competitors are more aligned when facing strong interspecific competition. Similar patterns have been observed in intergroup competition across various social species. For instance, in primate societies such as those of baboons and chimpanzees, intense between-group conflicts often lead to an increase in within-group cohesion and reduced intragroup aggression because members prioritise collective defence over internal disputes (Sapolsky 1986; Braga Goncalves et al. 2022). In banded mongooses, encounters with neighbouring groups have been shown to increase affiliative behaviours within the group, while also reducing within-group antagonism because individuals strengthen social bonds to cope with external threats (Thompson et al. 2017; Preston et al. 2021). These observations of intergroup competition parallel our findings on interspecific competition, suggesting that our model may have broader applications in understanding how external competitive pressures affect individual physiological states across different types of social organisation. However, since energetic costs are determined by both cooperative investment and social conflict, our previous models and experimental results show that an increase in the level of low ranking individuals' cooperative investment is crucial to achieving a greater total cooperative investment against interspecific competitors (Liu, Chan, et al. 2020). High ranking individuals already invest heavily in cooperation when facing interspecific competition. Thus, the additional cost for them to increase this investment is substantial. In contrast, low ranking individuals tend to invest less in cooperation than their high ranking group members in environments with minimal competition. However, under strong interspecific competition, these low-ranking individuals are more likely to increase their cooperative investment, presumably because the marginal cost for them to do so is less, as we show in the model. As a result, under strong competitive conditions, the energetic costs for low ranking individuals become more comparable to those of high ranking ones.

Although elevated body temperature could also arise from alternative processes, including post-prandial heat and environmental warming of the carcass (e.g., maggot-mass thermogenesis), the directional predictions of these alternatives do not match our data. Since blowfly larvae are readily preyed upon by burying beetles (*Nicrophorus* spp.; Potticary et al. 2024) and are actively encountered and removed by *N. nepalensis* (Sun et al. 2014; Chen et al. 2020), an ingestion-driven mechanism would predict higher RBT when edible maggots are present. Moreover, maggot masses typically raise internal carcass temperatures (Johnson et al. 2013; Aubernon et al. 2019), which would tend to elevate beetle temperatures via passive warming. Taken together, if either intake-driven assimilation or carcass heating dominated, one would therefore predict higher RBT in the blowfly treatment than in the control. Contrary to this prediction, we observed lower mean RBT under blowfly treatment despite higher cooperative activity. This pattern is inconsistent with feeding-heat or passive warming and instead supports our interpretation that interspecific competition reduces intragroup conflict and lowers per-capita thermogenic effort during cooperation. We therefore interpret RBT as a proximal indicator of the thermogenic cost of cooperative work rather than increased digestion or passive warming.

For ectotherms, higher RBTs generally indicate greater energy expenditure if all else is equal (Heinrich 1974; Harrison et al. 1996). Our results demonstrate a strong association between the RBT of burying beetles and their cooperative and competitive behaviours. That is, the higher the level of individual investment in cooperation or conflict, the higher their RBT (Figures 4 and 5). These results suggest that for burying beetles, the degree of RBT increase (relative to the baseline temperature of the environment) represents the energetic cost of their coping strategies to predictable and unpredictable challenges to the environment. Similar to studies in vertebrates, studying animal physiology can yield valuable insights beyond behavioural observations alone (Creel 2001; Sapolsky 2005; Mehta and Josephs 2010; Maguire et al. 2021). Our results highlight the significance of RBT in understanding the physiological consequences of social life. Specifically, we show that the energetic cost of social conflict outweighs that of cooperative investment, as evidenced by the greater impact of social conflict on RBT (Figures 4 and 5). While previous research in vertebrates, such as baboons, has demonstrated lower glucocorticoid levels in subordinate individuals under adverse environments because of reduced social interactions (Sapolsky 1986), our study on burying beetles reveals that higher ranking individuals become more tolerant of lower ranking individuals, thus reducing social conflict and resulting in lower energetic cost. Conversely, in superb starlings, lower ranked individuals exhibited higher glucocorticoid levels in harsher environments, indicating a greater influence of environmental stressors on energetic costs (Rubenstein 2007). Obviously, further investigations in ectotherms are necessary to understand the relative significance of environmental and social stressors on the energetic cost of social species.

Our study focuses on *N. nepalensis* competing with blowflies, but the mechanism that we identify should apply in principle to any systems where (i) an external competitor raises the marginal benefit of group cooperation (e.g., defence or rapid resource processing) more than that of within-group contest, and (ii) individuals can reallocate effort across cooperation and conflict. Under such conditions, competitor presence is predicted to reduce within-group conflict and compress rank differences in energetic costs, even as cooperative effort increases. A hypothetical example would be carcass-using beetle species beyond *N. nepalensis* (e.g., *Nicrophorus vespilloides*, *Nicrophorus orbicollis*). Except for burying beetles, few systems have been shown to meet both criteria, so we state generality cautiously and emphasise beetles as the most immediate test system.

In summary, our findings reveal the complex interactions between environmental and social factors in influencing the physiological status of social organisms. Previous studies suggest that harsh environmental conditions reduce conflict (Shen et al. 2012) or increase cooperation (Chen et al. 2020) in burying beetles. Given the intricate interplay of these factors, studies of the physiological effects of environmental conditions on social animals reveal heterogeneous results across species (Gunderson et al. 2017; Killen et al. 2021). We believe that studying body temperature changes in socially ectothermic animals using non-invasive thermal imaging offers a promising direction of research in behavioural ecophysiology. At the same time, our approach quantifies energy expenditure using relative body temperature and does not directly index other physiological costs. Future work could integrate thermal profiling with endocrine markers (e.g., juvenile hormone), oxidative-stress biomarkers, and immune metrics to assess whether reductions in intragroup conflict under interspecific competition generalise beyond thermal energetics.

5 | Materials and Methods

5.1 | Experimental Design

In each experimental replicate, three unrelated male and three unrelated female beetles were randomly selected from different families to avoid kinship effects on their behaviour. Beetles were introduced into the experimental chamber after marking. The experimental chamber consisted of a large peat-filled box (45 × 34.5 × 25 cm) containing a small peat-filled box (23 × 15.5 × 13.5 cm) enclosed by an iron-mesh barrier to keep the carcass within the camera view. Overhead digital and thermal cameras recorded behaviour and body temperature continuously (see Methods S2 for detailed procedures).

5.2 | Experimental Procedure

Prior to the blowfly treatment, rat carcasses (75 ± 5 g) were pre-exposed to *Chrysomya megacephala*, a natural carrion fly competitor and the main interspecific competitor of *Nicrophorus nepalensis* (Sun et al. 2014). All carcasses were equilibrated to the environmental chamber temperature for 8 h before being placed in the arena. Control carcasses of the same mass were handled identically without flies. Behavioural videos were recorded from 19:00 until the carcasses were completely buried, or for 72 h if the beetles did not bury the carcasses (under natural conditions, lack of burial within 72 h would likely result in carcasses being consumed by blowflies; Chen et al. 2020). Infrared videos were recorded from 19:00 to 05:00 the next day. We established 23 nests per treatment (see Methods S3 for detailed procedures).

We used FLIR ThermaCAM Researcher 2.10 to extract body temperature from the thermal imaging videos. For each recording, the maximum temperature value in the beetle's mid and posterior thorax was considered its body temperature for that time interval. Our camera recorded temperatures at four time intervals: 19:00–21:00, 22:00–23:00, 01:00–02:00, and 04:00–05:00. The data were sampled every 3 min between 19:00 and 21:00, and every 10 min during the other periods. We also recorded the average surface temperature of the rat carcasses to determine the ambient temperature at each sampling time. By subtracting the ambient temperature from the beetle body temperature, we obtained the RBT for each beetle.

5.3 | Behavioural Analyses

We used The Observer XT 14 (Noldus) to record social behaviour, including conflict and investment in carcass preparation, during the first 10 h (19:00–05:00). Among same-sex individuals, we identified four distinct interactions as social conflicts: wrestling, attacking, chasing, and fleeing. Social conflicts occurred randomly, so they were recorded over the entire 10-h period. To assess investment, we summed the time each beetle spent cleaning, depilating, dragging, shaping, burying carcasses, removing maggots, and preventing fungus or bacteria. We sampled investment behaviour for 10 min each hour, resulting in a maximum investment time of 100 min per beetle. For more details and sample video clips of each behaviour (see Chen et al. 2020).

5.4 | Determination of Dominance Hierarchies

To determine dominance hierarchies among beetles, we used social network transitivity analysis (Shizuka and McDonald 2012; Liu, Chen, et al. 2020). This approach examines connections between individuals based on attacks and chases, considering both actor and recipient roles to construct an accurate dominance hierarchy.

5.5 | Statistical Analyses

For behavioural data, cooperative investment time and number of conflicts were calculated as the sum of hourly data, with 10 data points collected per beetle per night. To represent relative temperature trends, data from all individuals of the same sex and rank were combined using a generalised additive model (Wood 2017) with the gam function from the mgcv package version 1.9-3. To estimate smoothed lines representing changes in cooperative investment time and social conflict over time, we used local regression with the gam function in R. We analysed data in three time intervals: full night (19:00–05:00), first half (19:00–23:59), and second half (00:00–05:00). RBT was calculated by averaging all data points in the selected time interval, whereas cooperative investment time and conflicts were calculated as the sum of data values for the selected time interval. To test whether cooperative and conflict behaviours covaried with physiology, we fitted separate linear models by treatment (control, blowfly) and by time windows. All analyses were performed with R version 4.5.1 (R Core Team 2022).

Author Contributions

Conceptualization: S.-F.S. Methodology: B.-F.C., S.-J.S., M.L., D.-P.C. and S.-F.S. Investigation: B.-F.C., Y.-C.L., D.R.R., M.L., D.-P.C. and S.-F.S. Analyses: Y.-C.L. and B.-F.C. Visualisation: Y.-C.L. Funding acquisition: S.-F.S. Supervision: S.-F.S. and D.R.R. Writing – original draft: S.-F.S. and Y.-C.L. Writing – review and editing: D.R.R., S.-F.S., Y.-C.L., B.-F.C. and A.R.

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Data Availability Statement

The data that support the findings of this study are openly available in the GitHub repository thermal_EcologyLetters at https://github.com/yuhinas/thermal_EcologyLetters (https://doi.org/10.5281/zenodo.17769641).

Peer Review

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References

Abbott, D. H., E. B. Keverne, F. B. Bercovitch, et al. 2003. "Are Subordinates Always Stressed? A Comparative Analysis of Rank Differences in Cortisol Levels Among Primates." *Hormones and Behavior* 43: 67–82.

Abdelall, E. S., Z. Eagle, T. Finseth, et al. 2020. "The Interaction Between Physical and Psychosocial Stressors." *Frontiers in Behavioral Neuroscience* 14: 63.

Aubernon, C., V. Hedouin, and D. Charabidze. 2019. "The Maggot, the Ethologist and the Forensic Entomologist: Sociality and Thermoregulation in Necrophagous Larvae." *Journal of Advanced Research* 16: 67–73.

Berlincourt, M., and J. P. Arnould. 2015. "Influence of Environmental Conditions on Foraging Behaviour and Its Consequences on Reproductive Performance in Little Penguins." *Marine Biology* 162: 1485–1501.

Braga Goncalves, I., A. Morris-Drake, P. Kennedy, and A. N. Radford. 2022. "Fitness Consequences of Outgroup Conflict." *eLife* 11: e74550.

Chen, B.-F., M. Liu, D. R. Rubenstein, et al. 2020. "A Chemically Triggered Transition From Conflict to Cooperation in Burying Beetles." *Ecology Letters* 23: 467–475.

Colinet, H., B. J. Sinclair, P. Vernon, and D. Renault. 2015. "Insects in Fluctuating Thermal Environments." *Annual Review of Entomology* 60: 123–140.

Cozzoli, F., M. Shokri, G. Ligetta, et al. 2020. "Relationship Between Individual Metabolic Rate and Patch Departure Behaviour: Evidence From Aquatic Gastropods." *Oikos* 129: 1657–1667.

Creel, S. 2001. "Social Dominance and Stress Hormones." *Trends in Ecology & Evolution* 16: 491–497.

Creel, S., B. Dantzer, W. Goymann, and D. R. Rubenstein. 2013. "The Ecology of Stress: Effects of the Social Environment." *Functional Ecology* 27: 66–80.

Culbert, B. M., K. M. Gilmour, and S. Balshine. 2018. "Stress Axis Regulation During Social Ascension in a Group-Living Cichlid Fish." *Hormones and Behavior* 103: 121–128.

Dorsett, D. 1962. "Preparation for Flight by Hawk-Moths." *Journal of Experimental Biology* 39: 579–588.

Emery Thompson, M. 2017. "Energetics of Feeding, Social Behavior, and Life History in Non-Human Primates." *Hormones and Behavior* 91: 84–96.

Fisher, D. N., R. J. Kilgour, E. R. Siracusa, et al. 2021. "Anticipated Effects of Abiotic Environmental Change on Intraspecific Social Interactions." *Biological Reviews* 96: 2661–2693.

Fujii, S., M. K. Kaushik, X. Zhou, M. Korkutata, and M. Lazarus. 2019. "Acute Social Defeat Stress Increases Sleep in Mice." *Frontiers in Neuroscience* 13: 322.

Gesquiere, L. R., N. H. Learn, M. C. M. Simao, P. O. Onyango, S. C. Alberts, and J. Altmann. 2011. "Life at the Top: Rank and Stress in Wild Male Baboons." *Science* 333: 357–360.

Goymann, W., and J. C. Wingfield. 2004. "Allostatic Load, Social Status and Stress Hormones: The Costs of Social Status Matter." *Animal Behaviour* 67: 591–602.

Gunderson, A. R., B. Tsukimura, and J. H. Stillman. 2017. "Indirect Effects of Global Change: From Physiological and Behavioral Mechanisms to Ecological Consequences." *Integrative and Comparative Biology* 57: 48–54.

Harrison, J. F., J. H. Fewell, S. P. Roberts, and H. G. Hall. 1996. "Achievement of Thermal Stability by Varying Metabolic Heat Production in Flying Honeybees." *Science* 274: 88–90.

Heinrich, B. 1974. "Thermoregulation in Endothermic Insects: Body Temperature Is Closely Attuned to Activity and Energy Supplies." *Science* 185: 747–756.

Heinrich, B. 2013. *The Hot-Blooded Insects: Strategies and Mechanisms of Thermoregulation*. Springer Science & Business Media.

Jandt, J. M., E. A. Tibbetts, and A. L. Toth. 2014. "Polistes Paper Wasps: A Model Genus for the Study of Social Dominance Hierarchies." *Insectes Sociaux* 61: 11–27.

Johnson, A. P., K. M. Mikac, and J. F. Wallman. 2013. "Thermogenesis in Decomposing Carcasses." *Forensic Science International* 231: 271–277.

Kearney, M., R. Shine, and W. P. Porter. 2009. "The Potential for Behavioral Thermoregulation to Buffer "Cold-Blooded" Animals Against Climate Warming." *Proceedings of the National Academy of Sciences of the United States of America* 106, no. 10: 3835–3840. https://doi.org/10.1073/pnas.0808913106.

Killen, S. S., D. Cortese, L. Cotgrove, J. W. Jolles, A. Munson, and C. C. Ioannou. 2021. "The Potential for Physiological Performance Curves to Shape Environmental Effects on Social Behavior." *Frontiers in Physiology* 12: 754719.

Kleinhenz, M., B. Bujok, S. Fuchs, and J. Tautz r. 2003. "Hot Bees in Empty Broodnest Cells: Heating From Within." *Journal of Experimental Biology* 206: 4217–4231.

Krogh, A., and E. Zuthen. 1941. "The Mechanism of Flight Preparation in Some Insects." *Journal of Experimental Biology* 18: 1–10.

Liu, M., S.-F. Chan, D. R. Rubenstein, S.-J. Sun, B.-F. Chen, and S.-F. Shen. 2020. "Ecological Transitions in Grouping Benefits Explain the Paradox of Environmental Quality and Sociality." *American Naturalist* 195: 818–832.

Liu, M., B.-F. Chen, D. R. Rubenstein, and S.-F. Shen. 2020. "Social Rank Modulates How Environmental Quality Influences Cooperation and Conflict Within Animal Societies." *Proceedings of the Royal Society B: Biological Sciences* 287: 20201720.

Maguire, S. M., R. DeAngelis, P. D. Dijkstra, A. Jordan, and H. A. Hofmann. 2021. "Social Network Dynamics Predict Hormone Levels and Behavior in a Highly Social Cichlid Fish." *Hormones and Behavior* 132: 104994.

Mehta, P. H., and R. A. Josephs. 2010. "Testosterone and Cortisol Jointly Regulate Dominance: Evidence for a Dual-Hormone Hypothesis." *Hormones and Behavior* 58: 898–906.

Morrison, S. F., K. Nakamura, and C. J. Madden. 2008. "Central Control of Thermogenesis in Mammals." *Experimental Physiology* 93: 773–797.

Pandey, A., U. Motro, and G. Bloch. 2020. "Juvenile Hormone Interacts With Multiple Factors to Modulate Aggression and Dominance in Groups of Orphan Bumble Bee (*Bombus terrestris*) Workers." *Hormones and Behavior* 117: 104602.

Potticary, A. L., M. C. Belk, J. C. Creighton, et al. 2024. "Revisiting the Ecology and Evolution of Burying Beetle Behavior (Staphylinidae: Silphinae)." *Ecology and Evolution* 14: e70175.

Preston, E. F. R., F. J. Thompson, S. Ellis, S. Kyambulima, D. P. Croft, and M. A. Cant. 2021. "Network-Level Consequences of Outgroup Threats in Banded Mongooses: Grooming and Aggression Between the Sexes." *Journal of Animal Ecology* 90: 153–167.

R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Reeve, H. K., S. T. Emlen, and L. Keller. 1998. "Reproductive Sharing in Animal Societies: Reproductive Incentives or Incomplete Control by Dominant Breeders?" *Behavioral Ecology* 9: 267–278.

Reeve, H. K., and B. Hölldobler. 2007. "The Emergence of a Superorganism Through Intergroup Competition." *Proceedings of the National Academy of Sciences of the United States of America* 104: 9736–9740.

Rezende, E. L., and L. D. Bacigalupe. 2015. "Thermoregulation in Endotherms: Physiological Principles and Ecological Consequences." *Journal of Comparative Physiology B* 185: 709–727.

Rubenstein, D. R. 2007. "Stress Hormones and Sociality: Integrating Social and Environmental Stressors." *Proceedings of the Royal Society B: Biological Sciences* 274: 967–975.

Rubenstein, D. R., and I. J. Lovette. 2007. "Temporal Environmental Variability Drives the Evolution of Cooperative Breeding in Birds." *Current Biology* 17: 1414–1419.

Rubenstein, D. R., and S.-F. Shen. 2009. "Reproductive Conflict and the Costs of Social Status in Cooperatively Breeding Vertebrates." *American Naturalist* 173: 650–662.

Sapolsky, R. M. 1986. "Endocrine and Behavioral Correlates of Drought in Wild Olive Baboons (*Papio anubis*)." *American Journal of Primatology* 11: 217–227.

Sapolsky, R. M. 2005. "The Influence of Social Hierarchy on Primate Health." *Science* 308: 648–652.

Shen, S.-F., S. T. Emlen, W. D. Koenig, and D. R. Rubenstein. 2017. "The Ecology of Cooperative Breeding Behaviour." *Ecology Letters* 20: 708–720.

Shen, S.-F., and H. K. Reeve. 2010. "Reproductive Skew Theory Unified: The General Bordered Tug-of-War Model." *Journal of Theoretical Biology* 263: 1–12.

Shen, S.-F., S. L. Vehrencamp, R. A. Johnstone, et al. 2012. "Unfavourable Environment Limits Social Conflict in *Yuhina brunneiceps*." *Nature Communications* 3: 1–7.

Shizuka, D., and D. B. McDonald. 2012. "A Social Network Perspective on Measurements of Dominance Hierarchies." *Animal Behaviour* 83: 925–934.

Sun, S.-J., D. R. Rubenstein, B.-F. Chen, et al. 2014. "Climate-Mediated Cooperation Promotes Niche Expansion in Burying Beetles." *eLife* 3: e02440.

Takahashi, A. 2021. "Social Stress and Aggression in Murine Models." In *Neuroscience of Social Stress*, 181–208. Springer International Publishing.

Takahashi, A., M. E. Flanigan, B. S. McEwen, and S. J. Russo. 2018. "Aggression, Social Stress, and the Immune System in Humans and Animal Models." *Frontiers in Behavioral Neuroscience* 12: 56.

Thompson, F. J., H. H. Marshall, E. I. K. Vitikainen, and M. A. Cant. 2017. "Causes and Consequences of Intergroup Conflict in Cooperative Banded Mongooses." *Animal Behaviour* 126: 31–40.

Tibbetts, E. A., M. L. Fearon, E. Wong, Z. Y. Huang, and R. M. Tinghitella. 2018. "Rapid Juvenile Hormone Downregulation in Subordinate Wasp Queens Facilitates Stable Cooperation." *Proceedings of the Royal Society B: Biological Sciences* 285: 20172645.

Tibbetts, E. A., and Z. Y. Huang. 2010. "The Challenge Hypothesis in an Insect: Juvenile Hormone Increases During Reproductive Conflict Following Queen Loss in Polistes Wasps." *American Naturalist* 176: 123–130.

Trivers, R. L. 1972. "Parental Investment and Sexual Selection." In *Sexual Selection and the Descent of Man, 1871–1971*, edited by B. G. Campbell, 136–179. Aldine-Atherton.

Viblanc, V. A., C. Saraux, J. O. Murie, and F. S. Dobson. 2016. "Kin Effects on Energy Allocation in Group-Living Ground Squirrels." *Journal of Animal Ecology* 85: 1361–1369.

Wood, S. N. 2017. *Generalized Additive Models: An Introduction With R*. 2nd ed. Chapman and Hall/CRC.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** ele70300-sup-0001-AppendixS1.docx.