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Author for correspondence:
Sheng-Feng Shen
e-mail: shensf@sinica.edu.tw

[†] These authors contributed equally to this work.

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Social rank modulates how environmental quality influences cooperation and conflict within animal societies

Mark Liu[1,†], Bo-Fei Chen[1,†], Dustin R. Rubenstein[2,3] and Sheng-Feng Shen[1]

[1]Biodiversity Research Center, Academia Sinica, Taipei 11529, Taiwan
[2]Department of Ecology, Evolution and Environmental Biology, and [3]Center for Integrative Animal Behavior, Columbia University, New York, NY 10027, USA

ML, 0000-0002-3124-4249; B-FC, 0000-0003-3005-8724; DRR, 0000-0002-4999-3723; S-FS, 0000-0002-0631-6343

Although dominance hierarchies occur in most societies, our understanding of how these power structures influence individual investment in cooperative and competitive behaviours remains elusive. Both conflict and cooperation in animal societies are often environmentally regulated, yet how individuals alter their cooperative and competitive investments as environmental quality changes remain unclear. Using game theoretic modelling, we predict that individuals of all ranks will invest more in cooperation and less in social conflict in harsh environments than individuals of the same ranks in benign environments. Counterintuitively, low-ranking subordinates should increase their investment in cooperation proportionally more than high-ranking dominants, suggesting that subordinates contribute relatively more when facing environmental challenges. We then test and confirm these predictions experimentally using the Asian burying beetle *Nicrophorus nepalensis*. Ultimately, we demonstrate how social rank modulates the relationships between environmental quality and cooperative and competitive behaviours, a topic crucial for understanding the evolution of complex societies.

1. Introduction

The idea that unfavourable environments promote cooperation in humans was first proposed over 2500 years ago by the Chinese military strategist Sun Tzu [1]. More recently, however, harsh or extreme environments have also been found to lead to increased ethnic unrest and civil war in human societies [2–9]. In other vertebrate societies, environmental uncertainty and harshness typically promote cooperation [10–12] and indirectly influence social conflict [13] over evolutionary timescales. Accumulating empirical evidence also suggests that social conflict in cooperative societies is often lower in adverse environments with harsh climate [14] or strong interspecific competition [15]. This pattern of reduced social conflict in harsh environments has been explained by the fact that the cost of engaging in social conflict is too high under adverse conditions [14,16]. Thus, although determining how environmental conditions influence individual levels of cooperation and conflict in social animals remains controversial, doing so is critical for not only understanding how environmental quality has shaped the evolution of animal societies, but also how those societies may respond to the increasing environmental variation associated with anthropogenic global change, including both climate warming and habitat fragmentation [13].

In addition to environmental factors, social factors play a critical role in shaping individual cooperative and competitive strategies. For example, dominance relationships can help reduce social conflict among group members [17–20], and high-ranking or privileged individuals tend to invest more in generating cooperative benefits than low-ranking individuals [21–24]. Yet, despite broad-scale taxonomic and geographic relationships between sociality and environmental

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harshness from phylogenetic comparative studies [10–13,25,26] and empirical evidence from long-term behavioural studies that cooperation improves fitness under poor environmental conditions [27,28], there is little empirical evidence demonstrating that social animals actually increase their investment in cooperation in harsh environments [29], or how they might achieve this given the existence of dominance hierarchies that help regulate social conflict. Thus, the relationships among environmental quality, dominance rank, and individual cooperative and competitive strategies remain largely unexplored, both empirically and theoretically.

Here, we construct a game theoretic model to investigate how environmental quality influences intraspecific cooperation and conflict among members of different social rank in a cooperatively breeding social group. Although our framework can be applied to any cooperatively breeding species that competes with both members of its own species as well as with other species for access to resources, our primary model is based on the natural history of the Asian burying beetle, *Nicrophorus nepalensis*, so that we can empirically test model predictions. In this system, beetles compete with blowflies (family Calliphoridae) for access to small vertebrate carcasses, their primary resource for reproduction [30–32]. Although some species of *Nicrophorus* beetles are predominantly solitary and aggressive to conspecifics, in *N. nepalensis*, multiple individuals often cooperate in carcass preparation and provide care for larvae [30–35], enabling them to outcompete blowflies for access to breeding resources [36,37]. Harsh or adverse environments can encompass either biotic—interspecific competition in the case of beetles, but also predation risk—or abiotic factors such as severe weather or resource scarcity [38,39]. Although we model environmental quality as levels of interspecific competition in the text to be consistent with the burying beetle system, we also consider environmental quality in terms of climatic variation in the electronic supplementary material.

To test the predictions of our model, we manipulated the presence or absence of blowfly competition to experimentally determine how environmental quality influences the cooperative and competitive strategies of beetles of differing social rank. Burying beetles are well suited for studying the impacts of environmental quality on individual cooperative and competitive strategies because they exhibit flexible social behaviours [30,37,40,41] that are extremely sensitive to interspecific competition [29,36,37,42]. Carcass preparation involves a variety of behaviours (e.g. cleaning, depilation, dragging, shaping, burying carcasses, removing maggots, and preventing fungus or bacteria) that are important in eliminating the use of the resources by interspecific and sometimes intraspecific competitors [30,32,43]. By experimentally manipulating the group sizes of burying beetles along elevation gradients, we previously showed that beetles in large groups are more aggressive towards conspecifics in colder environments where the pressure of interspecific competition is lower, often engaging in fierce and even lethal fights with other beetles that result in a lower probability of breeding successfully than beetles in solitary pairs [36]. By contrast, in hotter environments, burying beetles cooperating with conspecifics were able to bury carcasses and evade competition from blowflies more quickly, ultimately achieving greater reproductive success than beetles in solitary pairs [36]. We also demonstrated experimentally that beetles are more cooperative at carcasses when blowfly maggots have begun to digest the tissue. This form of social cooperation appears to be triggered by a single chemical—dimethyl disulfide (DMDS)—cue emitted more rapidly from carcasses consumed by blowflies than from control carcasses [29]. Thus *N. nepalensis* provides a rare opportunity for performing well-controlled experiments to test how environmental quality influences individual levels of cooperative and competitive behaviours given that the key ecological driver of their social behaviour (i.e. fly competition) is easy to manipulate in the laboratory and field.

2. Material and methods

(a) Model description

We assume that each share of the group resource (G) that is contested by the two competing species is determined by the total cooperative investment (V_b) of all burying beetles (i.e. the sum of individual investments in the between-species tug-of-war) and the total investment (V_f) by blowflies in interspecific competition. Therefore, the share of resources for the beetle group is $V_b/(aV_f + V_b)$, where aV_f represents the pressure of interspecific competition from blowflies [29]. A higher ambient temperature (a) indicates a harsher environment for beetles because blowflies have a competitive advantage over beetles at warmer temperatures [36,37].

Since we are primarily interested in how dominance rank influences an individual's investments in intraspecific cooperation and conflict, we assume that the burying beetle's total cooperative investment (V_b) in the between-species tug-of-war against blowflies is equal to the sum of the individual investments in cooperation by the dominant (v_D) and by n subordinate group members (v_S), such that $V_b = v_D + n\ v_S$. We further assume that each individual's share of the group resource is determined by their within-group tug-of-war effort such that dominant and subordinates get a larger share when they exert greater competitive effort x_D and x_S, respectively, although with an increased personal cost in terms of decreased future fitness [14]. The share of the group resource is $x_D/(x_D + bnx_S)$ for the dominant and $bx_S/(x_D + bnx_S)$ for the subordinates. The dominant and the subordinates can vary in their competitive abilities in the within-species tug-of-war, something that is described by the scaling factor b, where $0 < b < 1$ [44,45]. The costs of investing in cooperation and conflict, which are assumed to be the same for the dominant and subordinates in the current breeding attempt, are described as accelerating future fitness cost functions [14,46]. For generality of the model, we did not assume any specific function between group size of the beetles and the pressure of interspecific competition. However, we did assume that investing in the within-group tug-of-war for resources will generate a cost of decreasing the value of the group resource for burying beetles, such that the group resource value G becomes $\left(G\dfrac{V_b[v_D,v_S,v'_S]}{aV_f + V_b[v_D,v_S,v'_S]} - x_D - n\ x_S\right)$.

In summary, the fitness functions of the blowflies (W_{fly}), the dominant beetle (w_D), and the subordinate beetles (w_S) are

$$w_{\text{fly}} = \left(G\frac{aV_f}{aV_f + V_b[v_D,v_S,v'_S]}\right) - c_f V_f^2, \tag{2.1}$$

$$w_D = \left(G\frac{V_b[v_D,v_S,v'_S]}{aV_f + V_b[v_D,v_S,v'_S]} - x_D - n\ x_S\right)\frac{x_D}{x_D + bn\ x_S} - (c_v v_D + c_x x_D)^2 \tag{2.2}$$

$$\begin{aligned} w_S = &\left(G\frac{V_b[v_D,v_S,v'_S]}{aV_f + V_b[v_D,v_S,v'_S]} - x_D - n\ (x_S + (n-1)x'_S)\right) \\ &\times \frac{bx_S}{x_D + b(x_S + (n-1)x'_S)} - (c_v v_S + c_x x_S)^2, \end{aligned} \tag{2.3}$$

where

$$V_b[v_D,v_S,v'_S] = v_D + v_S + (n-1)v'_S, \tag{2.4}$$

x'_S and v'_S represent the resident strategies, and x_S and v_S denote the rare mutant strategies in the population. The scaling factors c_f and c_v represent how the personal costs rise with increasing levels of investment in competition with blowflies and burying beetles, respectively. The term c_x denotes the rise in personal costs with the increasing levels of investment in social conflict. The evolutionarily stable levels of investment in intraspecific cooperation are V_f^*, v_D^*, and v_S^* for competing blowflies, the dominant beetle and the subordinate beetles, respectively. With investment in intraspecific social conflict, x_D^* and x_S^*, for a higher share of group resource for the group members, the inequality must then satisfy

$$\left.\frac{\partial W_{\text{fly}}}{\partial V_f}\right|_{\substack{V_f = V_f^* \\ x_D = x_D^*, v_D = v_D^* \\ x_S = x_S^*, v_S = v_S^*}} = 0, \quad \left.\frac{\partial W_D}{\partial x_D}\right|_{\substack{V_f = V_f^* \\ x_D = x_D^*, v_D = v_D^* \\ x_S = x_S^*, v_S = v_S^*}} = 0, \left.\frac{\partial W_D}{\partial v_D}\right|_{\substack{V_f = V_f^* \\ x_D = x_D^*, v_D = v_D^* \\ x_S = x_S^*, v_S = v_S^*}} = 0$$

$$\left.\frac{\partial W_S}{\partial x'_S}\right|_{\substack{x_D = x_D^*, v_D = v_D^* \\ x'_S = x_S = x_S^*, v'_S = v_S = v_S^*}} = 0, \text{ and } \left.\frac{\partial W_S}{\partial v'_S}\right|_{\substack{x_D = x_D^*, v_D = v_D^* \\ v'_S = v_S = v_S^*, x'_S = x_S = x_S^*}} = 0.$$

Since we cannot obtain analytic solutions for the above equations, we use Mathematica v12.0 to solve for V_f^*, v_D^*, v_S^*, x_D^*, and x_S^* numerically.

(b) Beetle collection and maintenance

Experiments were conducted using *N. nepalensis* individuals from laboratory strains that originated from Meifeng, Nantou County, Taiwan (24°5′ N, 121°10′). We randomly paired beetles in 23 × 15.5 × 16 cm plastic boxes filled with 10 cm moist peat and supplied them with 75 ± 5 g of frozen and re-thawed dead rat (*Rattus norvegicus*) for reproduction. Emergent beetles were reared separately in 7.3 × 7.3 × 3.5 cm plastic boxes filled with 2 cm moist peat and fed dead superworms (*Zophobas morio*) once a week. All beetles were maintained in environmental chambers on a 14 L : 10 D photoperiod at 13.2–19.7°C to resemble the daily temperature fluctuation in the natural conditions at Meifeng where the laboratory strains originated. The age of the beetles used in the experiment ranged from 40 to 80 days because this is their optimal age for reproduction (S-F Shen, M Liu, B-F Chen 2020, unpublished data).

(c) Experimental design

All experiments were conducted in environmental chambers in the laboratory. To equalize the temperature of the experimental apparatus, boxes were filled with moist peat and put into the environmental chambers one day before the experiments began. For each experimental replicate, three unrelated male and three unrelated female beetles were randomly selected from different families. Each individual was uniquely marked with a Uni POSCA paint marker on the elytra and coated with Scorch® Super GlueGel for individual identification in videos. A precision scale was used to weigh each individual to the nearest 0.1 mg 2 h prior to the experiment in order to reduce the potential for disturbance by marking and weighing. All six marked beetles were placed into the experimental boxes in random order at the beginning of each experiment. Experimental boxes consisted of a smaller plastic container (23 × 15.5 × 13.5 cm filled with 13.5 cm freshly prepared moist peat) located inside a larger plastic container (45 × 34.5 × 25 cm filled with 13.5 cm moist peat) where a digital camera was fitted on the lid for behavioural recording. A metal cage of 2 × 2 cm mesh was placed around the small container to prevent beetles from moving the carcass outside the view of camera, but beetles could still move freely between the inner and outer areas. The blowfly treatment was conducted by exposing a 75 ± 5 g rat thawed carcass to blowflies in 32 × 32 × 32 cm fly cages for 50 h before the start of each experiment. Fly cages contained oriental latrine flies (*Chrysomya megacephala*) that emerged from 10 g pupa. We kept these blowflies in environmental chambers on a 14 L : 10 D photoperiod at 26°C. For control groups, carcasses in the same weight range were thawed at 4°C for 24 h before experiments began. Carcasses in either control or blowfly treatments were moved into the environmental chambers 8 h prior to the start of experiments. The carcasses receiving different treatments were relocated into the experimental apparatus 1 h before experiments began. Video recording started at the beginning of the experiments and ran continuously for 72 h if the beetles did not completely bury the carcass (under natural conditions, a carcass would be completely consumed by blowflies if beetles did not completely bury it within 72 h). In each experiment, 10 h of video recording from the beginning of the experiment (19:00–05:00) were used to analyse social conflict and cooperative investment using Observer® XT 14 (Noldus) software. In total, 1020 h of video recordings were used from 23 blowfly control and 23 blowfly treatment replicates.

(d) Behavioural analyses

Social conflict was defined as interactions (e.g. wrestles, attack, chases, and escapes) between same-Vsex individuals [29]. Two individuals grasping and biting each other was defined as a wrestle; an individual biting another individual was defined as an attack; a chase was defined as an individual rapidly running after another individual after any other interaction (e.g. wrestle, attack, or contact); an individual rapidly running away from another after any other interaction described above was defined as an escape (see also electronic supplementary material Videos in [29]). Since social conflicts occurred throughout the observation period, they were recorded for the entire 10 h (19:00–05:00). We calculated individual social conflicts as the total number of social conflicts divided by individual total investment time. We quantified the total time that each individual spent processing the carcass cooperatively by evaluating the cumulative time that each beetle spent inspecting carcasses, depilating rat hair, removing maggots and blowfly eggs, moving carcasses, and digging the peat surrounding carcasses [29]. The cooperative investment behaviours were sampled for 10 min in the middle of each 1 h period [29]. Therefore, the maximal investment time of each beetle was 100 min. The investment ratio was the ratio of the dominant individual's investments in either cooperation or conflict relative to the total investments of same-sex group members. After each trial, we recorded the degree of injury of each individual from 10 distinct body parts, including two antennae, six legs, and two elytra. We summed the number of injured body parts to create an injury index that ranged from 0 to 10.

(e) Determination of dominance hierarchies

We determined the hierarchical organization of dominance relationships among beetles using social network transitivity analysis [47,48]. The numbers of attacks and chases, as well as the roles of the behavioural actors or receivers, were used to construct the structure of the dominance hierarchies. In other words, beetles who initiated more attacks and/or chases were defined as high-ranking individuals. However, since social conflict also includes wrestles and escapes standardized by the total activity time, higher ranking individuals did not necessarily engage in higher levels of social conflict (or cooperation) than lower ranking individuals.

(f) Statistical analyses

Multivariate analyses were performed using generalized linear mixed models (GLMMs) to examine differences between the control and blowfly treatments in individual investment in cooperation and social conflict. Since six individuals were used in each replicate, group ID was included in the models as a random effect. We also included sex of the beetles as a covariate in the GLMMs but since its effect did not vary in blowfly treatment and control (i.e. no interaction between treatment and sex), it was excluded from the final model. All statistical analyses were performed in R using the packages stats, lme4, car, multcomp (http://cran.r-project.org), and glmmADMB (http://glmmadmb.r-forge.r-project.org) [49]. Additionally, we analysed the key biological parameters from the GLMMs using structural equation modelling (SEM) to determine how these factors influenced dominance hierarchy formation. The z-scores of body weight, pronotum width, and age of each individual were included in SEM. SEM was performed in R using the packages *MuMIn* (http://cran.r-project.org) and *piecewiseSEM* [50].

3. Results

(a) Model of environmental quality and intraspecific cooperation and conflict

We began by constructing an *n*-player game theoretic model of nested tug-of-war [44,51] to examine the tension between intraspecific cooperation and interspecific competition for resources (see Material and Methods for a detailed model description). In other words, a within-group tug-of-war between individuals of different social rank was nested within a between-species tug-of-war for the same resources. Greater pressure of interspecific competition represents a harsher environment in the model (see electronic supplementary material for a version of the model for harsh abiotic environments). In the within-group tug-of-war, each group member selfishly increases its share of the group resource G at the expense of lowering the total amount of the group resource (i.e. obtaining a larger share of a smaller pie). The group resource share that each individual receives in a within-group tug-of-war depends on each individual's investment in the within-group tug-of-war relative to the total investment of other group members [44,45]. However, the amount of group resource that each individual receives also depends on the group investment—the sum of the individual investments in the between-species tug-of-war. The higher the group investment in the between-species tug-of-war against interspecific competitors, the larger the group resource becomes (i.e. they create a bigger pie). Therefore, individuals face trade-offs between partitioning their effort into investing in cooperation to compete with other species for higher amounts of the total group resource (between-species tug-of-war) versus selfishly increasing their own personal share of a smaller group resource (within-group tug-of-war).

Our model shows that, as expected, in harsh environments with greater interspecific competition, individual beetles are not able to acquire as many resources as they can in benign environments (figure 1*a*). Although our model predicts that total investment in cooperation increases as environmental conditions become harsher (figure 1*b*), dominant beetles maintain relatively stable and high levels of cooperative investment across all environmental conditions, whereas subordinate beetles increase their investment in cooperation proportionally more than the dominant in harsh environments (figure 1*b*). This difference in cooperative investment between dominant and subordinate beetles in harsh environments occurs because the dominant can compete for a share of the group resource more efficiently than the subordinates, which enables the dominant to gain a greater share of the group resource for a relatively lower cost (since $b \leq 1$). Thus, dominant individuals invest more in cooperation than subordinates in benign environments where the pressure of interspecific competition is low (figure 1*c*), whereas subordinates invest proportionally more in intraspecific social conflict with each other (figure 1*d*). Moreover, both the dominant and subordinates invest less (in terms of absolute amount) in intraspecific social conflict. However, subordinates also increase their investment in cooperation in harsh environments where the pressure of interspecific competition is high in order to obtain (and share) a greater portion of the group resource. As a consequence, the dominant's investment ratio (i.e. the dominant's investment relative to the total investments of all group members) in cooperation is predicted to decrease as environmental conditions decline (figure 1*c*), while their investment in social conflict (relative to that of all group members) remains unchanged as environmental quality varies (figure 1*c*). Importantly, the results are qualitatively similar if we model environmental harshness as either a change in the degree of interspecific competition or as a change in climatic conditions (electronic supplementary material, figure S1).

(b) Empirical test of model predictions in cooperatively breeding burying beetles

We began the empirical test of the model predictions by examining dominance hierarchies in experimentally created beetle social groups. *N. nepalensis* exhibited a clear dominance hierarchy (figure 2*a*) in which larger and older individuals were more likely to establish positions of high rank (figure 2*b*). Given this social hierarchy, we tested how environmental quality (i.e. levels of interspecific competition) influences cooperation and conflict among individuals of different rank by manipulating the presence of blowfly maggots on the carcass. As predicted by our model, we found that individuals of all ranks in the blowfly treatment invested more in cooperative carcass preparation than individuals of the same rank in the control treatment (figure 3*a*; table S1). As was also predicted by our model, subordinate individuals (beta and gamma) increased their investment in carcass preparation proportionally more than dominant individuals (alpha) in the blowfly treatment, but not in the control treatment (figure 3*a*,*b*; table S1). Additionally, social conflict between subordinates—defined as the number of conflict behaviours standardized by the total investment time, which controls for the fact that more interactions lead to higher conflict—was higher in the control than the blowfly treatment, but there was no difference in the dominant's level of social conflict between the two treatments (figure 3*b*; table S2). Consequently, the dominant's investment ratio in cooperation was higher in the blowfly than the control treatment (figure 4*a*, table S3), but the dominant's investment ratio in conflict did not differ between the treatments, results also predicted by our model (figure 4*b*; table S3). Finally, the pattern of individual injuries caused by fighting differed marginally between the blowfly and control treatments, such that subordinates had higher injury levels than the dominant in the control but not in the blowfly treatment, reflecting the differential degree of social conflict between the blowfly and control treatments (figure 5; table S4).

4. Discussion

Our game theoretic model makes two key predictions about how social rank influences the relationship between

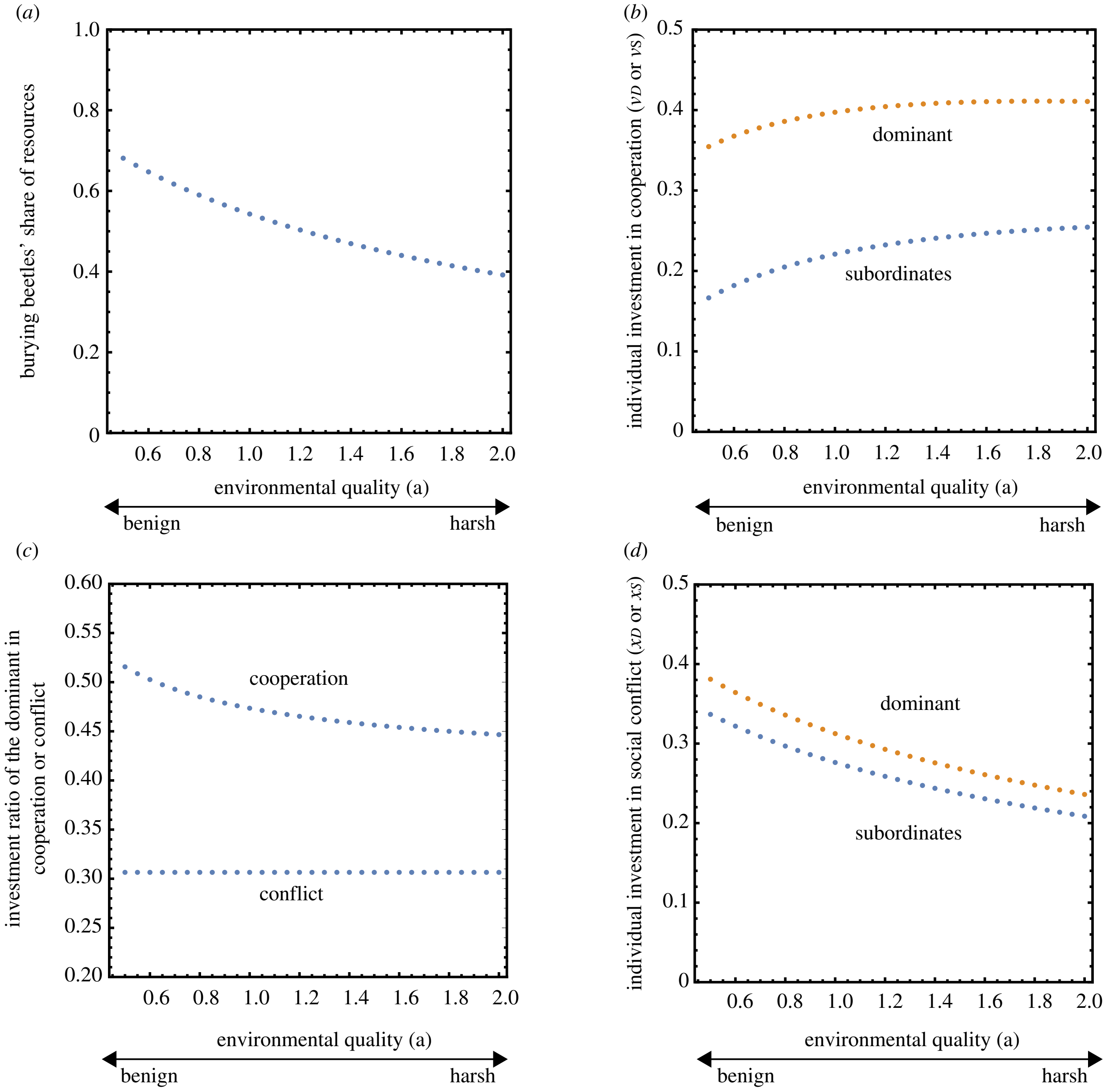

Figure 1. Results of game theoretic model of dominance hierarchies and intraspecific social conflict and cooperation. (*a*) The relationship between environmental quality and the beetle's share of resources (i.e. total group resource), (*b*) individual investments in cooperation (v_D or v_S), (*c*) the investment ratio between the dominants and subordinates in cooperation or conflict, and (*d*) individual investments in social conflict (x_D or x_S) in relation to environmental quality. Parameter values are $G = 3$; $b = 0.7$; $c_v = 0.5$; $c_x = 0.5$; $c_f = 1$; and $n = 2$. (Online version in colour.)

environmental quality and individual investment in intraspecific cooperative and competitive behaviour. First, our model predicts that total group investment in cooperation (i.e. independent of social rank) increases and social conflict decreases in harsh environments because (i) the interests of group members are more aligned when obtaining higher levels of the group resource from between-species tug-of-wars and (ii) doing so requires marginally more cooperative investment in poorer quality environments. This key prediction is consistent with the idea conceptualized in Sun Tzu's famous writings from more than 2500 years ago: 'For the men of Wu and the men of Yueh are enemies; yet if they are crossing a river in the same boat and are caught by a storm, they will come to each other's assistance just as the left hand helps the right' [1]. In harsh environments, reducing conflict is an intuitive outcome because the cost of intraspecific competition increases as environments become less habitable [14]. However, whether or not individuals actually increase their investment in cooperation in harsh environments depends on the marginal costs and benefits of the investment in cooperation, a topic we discuss in greater detail below.

Second, our model predicts that the subordinates' increased level of cooperative investment is crucial to reaching a greater total investment in cooperation in harsh environments. This can occur either due to stronger interspecific competition or to poorer abiotic conditions (see, electronic supplementary materials), since the marginal costs are exceedingly high for the dominant to increase its already substantial investment in cooperation to an even higher level in harsh environments. On the other hand, since low-ranking individuals invest less in cooperation than high-ranking individuals in benign environments, our model predicts that subordinates will increase their cooperative investment proportionally more than the dominant in harsh environments because the marginal costs for subordinates to increase their investment is relatively low. The effect of heterogeneous groups like the

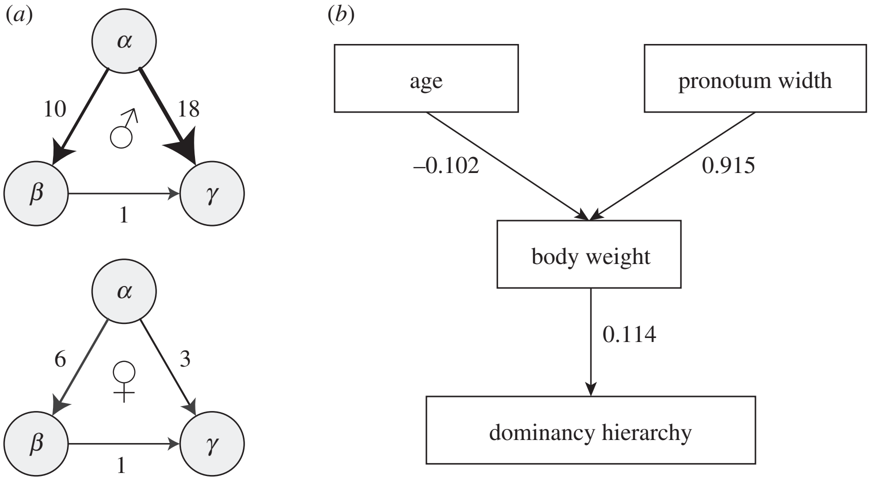

Figure 2. Dominance hierarchy within *N. nepalensis* groups. (*a*) Examples of within-group dominance networks in males and females. The arrows connecting group members of different social rank indicate the dominant-subordinate associations. The number next to each arrow indicates the net number of pairwise aggressive behaviours (attacks and chases). (*b*) Results of structure equation modelling (SEM) of factors influencing dominance hierarchy. The arrows indicate the hypothesized directional relationship between response and predictor factors. The number next to each arrow indicates the correlation coefficients between factors, and the solid line of the arrows indicates the *p-value* of each correlation coefficient is less than 0.01. Fisher. $c = 2$, $p = 0.7$. AIC = 20. $N = 275$.

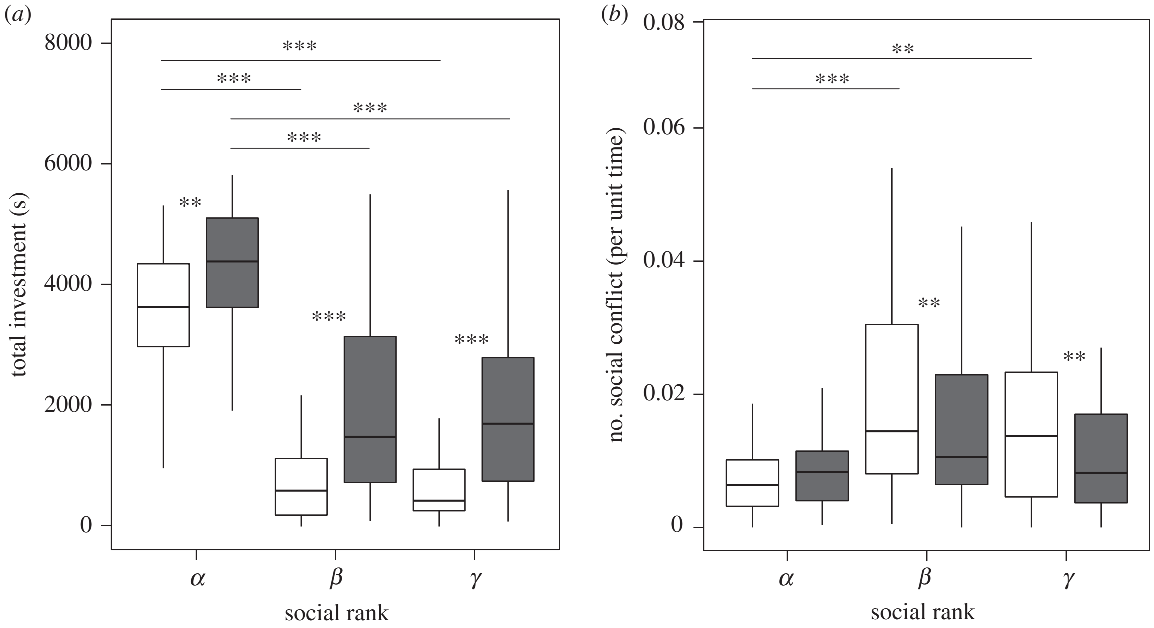

Figure 3. (*a*) Investment time per individual of each social rank in each group in the control (white) and blowfly (grey) treatments. (*b*) Individual conflict numbers for individuals of each social rank in the blowfly and control treatments. In each figure, $^{**}p \le 0.01$; $^{***}p \le 0.001$. In each figure, boxplot boundaries show quartiles; whiskers show 1.5 × interquartile range. Figures with data points are shown in electronic supplementary material, figure S2.

ones considered here is often modelled by assuming group members have different initial levels of resources, which influences their investment strategies. For example, Frank [52] found that individuals contribute to public goods proportionally to their initial levels of resources. However, unlike in Frank's model, we do not assume that individuals have different initial levels of resources. Instead, we only assume that the dominant can compete for a share of the group resource more efficiently than the subordinates ($b < 1$), and that they all experience the same costs of investing given their levels of cooperation and conflict. Therefore, our model can more directly explore how environmental conditions impact the investment strategies of both dominant and subordinate group members.

Both of the model's key predictions are supported by our empirical results because (i) the burying beetle's total investment in cooperation increases in harsh environments, largely because (ii) subordinates significantly increase their cooperative investments as environmental quality declines. Importantly, our model shows that free-riding (i.e. some subordinates remain part of the group but do not cooperate) is not an optimal strategy for subordinate beetles in harsh environments because their contribution is crucial to generating group benefits, which also explains the relatively low level of social conflict observed when environmental conditions are poor. Thus, subordinates are left with no better choice but to cooperate in the harsh environment, as proposed by Sun Tzu [1]. In burying beetles, if subordinates did not work as hard as the dominant in preparing carcasses by removing blowfly eggs and larvae, the carcass would likely be consumed by fly maggots and result in complete reproductive failure

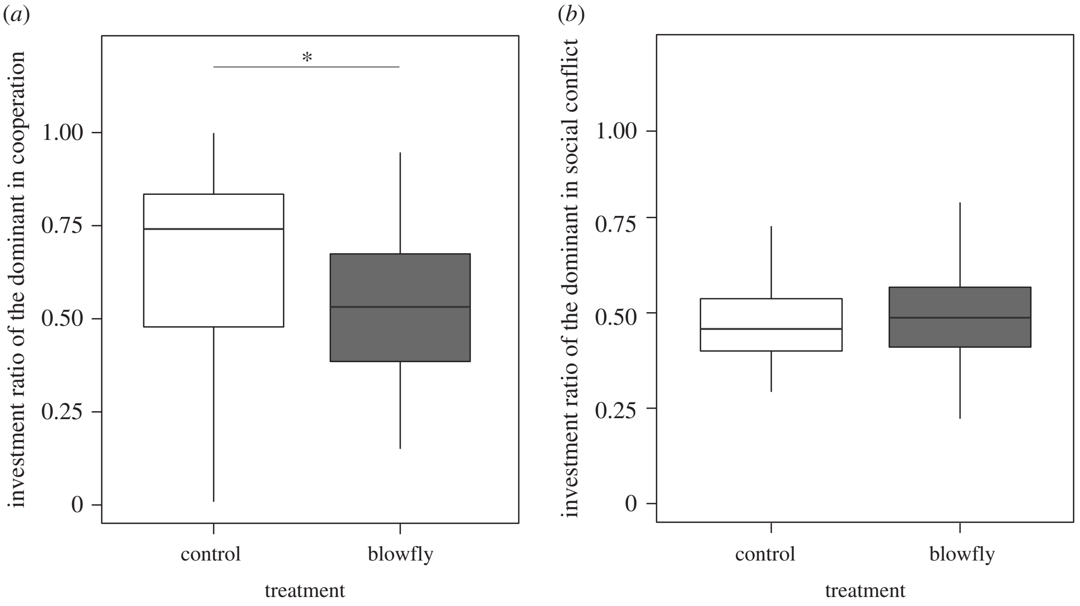

Figure 4. Investment ratio of the dominant individual in relation to the subordinates in (*a*) cooperation and (*b*) social conflict in each group in the control (white) and blowfly (grey) treatments. In each figure, *$p < 0.05$. In each figure, boxplot boundaries show quartiles; whiskers show 1.5 × interquartile range. Figures with data points are shown in electronic supplementary material, figure S3.

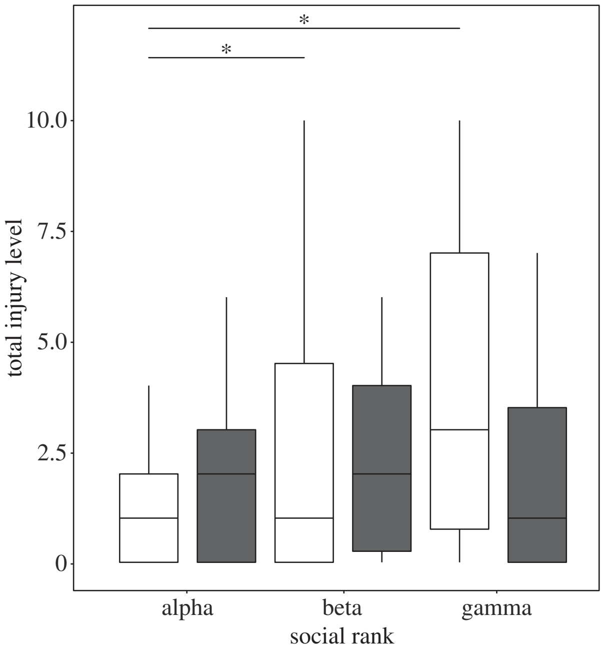

Figure 5. Injury levels of individuals of each social rank in the control (white) and blowfly (grey) treatments. *$p < 0.05$. Boxplot boundaries show quartiles; whiskers show 1.5 × interquartile range. A figure with data points is shown in electronic supplementary material, figure S4.

for all of the beetles in the group [29,36,37]. Thus, all beetles—independent of social rank—would fail to breed successfully when blowfly competition is strong.

More generally, our model provides a framework for understanding how environmental quality influences collective action problems in heterogeneous groups (i.e. groups whose members vary in social rank, investment costs, or share of collective goods). One of the most intriguing predictions of collective action theory is the 'exploitation of the great by the small', which means that the largest beneficiary of the collective goods (i.e. the group resource) bears a disproportionately large burden in its production [21,53]. Indeed, we found, both theoretically and empirically, that high-ranking individuals invest proportionally more in cooperative investment than low-ranking individuals in benign environments, as proposed by collective action theory. However, since subordinates do not work as hard as dominants in benign environments, they essentially act as insurance in case of a decline in environmental quality, only helping to contribute more to generate group benefits when needed. In other words, our results likely explain why high-ranking or privileged individuals within a group tolerate seemingly free-riding low-ranking individuals that tend to do little under normal conditions. In many eusocial insect societies, for example, 'lazy workers', or those that do not work as hard as other individuals in the group [54,55], may be tolerated by other group members because they provide insurance during unfavourable environmental conditions, such as periods of high intergroup conflict [56,57] or food shortage [58]. The same phenomena may also occur in cooperatively breeding birds [59,60]. Since dominance hierarchies are an almost universal phenomenon in animal societies [20], studying how social rank modulates the relationships between environmental quality and cooperative and competitive investments will be crucial not only for understanding the evolution and maintenance of complex societies, but also how societies will respond to rapid shifts in environmental conditions in an age of anthropogenic global change [13].

Data accessibility. Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.5tb2rbp1s [61].

Authors' contributions. All authors designed and performed the research and analysed the data. S.F.S. constructed the theoretical model. M.L., D.R.R. and S.F.S. wrote the paper.

Competing interests. We declare we have no competing interests.

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