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Ecological Transitions in Grouping Benefits Explain the Paradox of Environmental Quality and Sociality

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ABSTRACT: Both benign and harsh environments promote the evolution of sociality. This paradox—societies occur in environments of such contrasting quality—may be explained by the different types of benefits that individuals receive from grouping: resource defense benefits that derive from group-defended critical resources versus collective action benefits that result from social cooperation among group members. Here, we investigate cooperative behavior in the burying beetle *Nicrophorus nepalensis* along an elevational gradient where environmental quality (climate and competition) varies with altitude. We show that climate (temperature) and competition (both intra- and interspecific) independently and synergistically influence sociality via different grouping benefits that vary along the gradient. At low elevations where interspecific competition for resources is intense, groups gain from the collective action benefit of increased interspecific competitive ability. In contrast, pairs have higher fitness at intermediate elevations where intraspecific competition for resources is greatest because resource defense is the key grouping benefit. However, groups and pairs have similar fitness at high elevations, suggesting that there is no grouping benefit in such physiologically challenging environments. Our results demonstrate that sociality is favored for different reasons under a range of environmental conditions, perhaps explaining why animal societies occur in environments of such contrasting quality.

Keywords: cooperation, mutual tolerance hypothesis, common enemy hypothesis, *Nicrophorus* spp., environmental quality, social evolution.

Introduction

A range of ecological (e.g., habitat, food, or nest site availability) and environmental factors (e.g., climatic variation) have been shown to influence the evolution of sociality (Jetz and Rubenstein 2011; Purcell 2011; Kocher et al. 2014; Guevara and Avilés 2015; Sheehan et al. 2015; Lukas and Clutton-Brock 2017; Lin et al. 2019). In general, constrained resources or limited breeding territories can lead to delayed dispersal and promote social living through the retention of offspring, a scenario referred to as habitat saturation or ecological constraints (Emlen 1982; Kokko and Ekman 2002). Yet both harsh, fluctuating environments, where resources are more variable and often limiting (Jeanne 1991; Kaspari and Vargo 1995; Jetz and Rubenstein 2011), as well as benign, stable environments, where resources are more constant (Soucy and Danforth 2002; Avilés et al. 2007; Gonzalez et al. 2013), have been found to promote the evolution of complex societies (Emlen 1982). This dichotomy has been referred to as the paradox of environmental quality and sociality (Shen et al. 2017).

To understand why sociality has evolved in environments of such contrasting quality, we must examine both the direct and the indirect benefits of grouping, something that requires considering the inclusive fitness benefits of not only current group members like parents (termed insiders) but also potential joiners like offspring (termed outsiders), individuals whose interests are rarely aligned (Giraldeau and Caraco 1993; Higashi and Yamamura 1993; Shen et al. 2017). According to insider-outsider conflict theory, social groups should be stable only when group productivity is greater than the sum of the expected direct fitnesses of each group member if they were to breed on their own (Giraldeau and Caraco 1993; Higashi and Yamamura 1993; Shen et al. 2017). Accordingly, outsiders should prefer to join a social group even when doing so lowers the

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per capita productivity of the group because an outsider's chance of obtaining the necessary resources to breed solitarily is low (e.g., under strong ecological constraints; Emlen 1982; Koenig et al. 1992). In other words, when the chances of obtaining resources necessary for breeding solitarily are low (e.g., because of high population density and strong intraspecific competition in benign environments), individuals are likely to either remain at home or join another existing group and jointly defend resources, despite the fact that their fitness payoff will be lower than when obtaining their own resources and breeding independently. This scenario represents a "best of a bad job" strategy because if resources become available, groups will often dissolve because subordinates prefer to breed on their own (Emlen 1982; Koenig et al. 1992; Komdeur et al. 2013). In contrast, insiders may share critical resources with other conspecifics and permit outsiders to join because of either (1) the high costs of excluding others from the group (i.e., a direct benefit) or (2) the benefits of providing mature offspring (i.e., an indirect benefit) a safe haven as a base to increase their survival and explore critical breeding resource outside of their natal territory (Kokko and Ekman 2002).

Insider-outsider conflict theory highlights the importance of shared resources in the evolution of animal societies. The sharing and group defense of common resources against intraspecific competitors—referred to as a resource defense benefit—facilitates the evolution of grouping of both related and unrelated individuals, particularly in stable (i.e., benign) environments where resources are more constant (Allee 1938; Alexander 1974; Shen et al. 2014, 2017). Additionally, stable environments may enable groups to persist for longer so that solitary pairs can produce offspring as workers to form social groups in subsequent breeding events (Field et al. 2010; Kocher et al. 2014). In contrast to these resource defense benefits that may be higher in benign environments, both related and unrelated animals in fluctuating (i.e., harsh) environments can derive a variety of collective action benefits from grouping and jointly working to enhance fitness (Shen et al. 2017) by increasing foraging (Yip et al. 2008) or nesting efficiency (Wcislo 1997; Michener 2000), by increasing competitive ability against interspecific competitors (Korb and Foster 2010), or by reducing predation risk (Lin and Michener 1972; Jeanne 1991). Although collective action benefits can also be related to resources, a key difference with resource defense benefits is that collective action benefits are more about obtaining resources rather than defending them from conspecifics.

Resolving the paradox of environmental quality and sociality and testing the hypothesis that sociality can be favored in different environments for very different reasons (i.e., because of different grouping benefits) requires studying a species whose social behavior varies predictably across an environmental gradient. Burying beetles (Silphidae, *Nicrophorus*) are ideal systems for testing the hypothesis that the benefits derived from living in groups differ in environments of contrasting quality because many species exhibit intraspecific variation in social behavior along environmental gradients (Scott 1998). All burying beetles use small vertebrate carcasses as the sole food source for their young, and in a number of species, parents provide care for young (Pukowski 1933; Trumbo 1992; Scott 1998; Rozen et al. 2008; Cotter and Kilner 2010; Capodeanu-Nägler et al. 2016). In extreme cases, a male and a female—and sometimes multiple individuals of each sex—cooperatively participate in carcass preparations (Scott 1998; Sun et al. 2014). Carcass preparation involves a variety of behaviors (e.g., cleaning, depilation, dragging, shaping, and burial of carcasses, removal of maggots, prevention of fungi or bacteria) that are likely to be important for eliminating both inter- and intraspecific competitors from utilizing the food resources (Scott 1998; Rozen et al. 2008; Shukla et al. 2018).

It has long been assumed that cooperative breeding by multiple male and female burying beetles occurs because vertebrate carcasses are rare bonanza resources, where the cost to insiders of excluding conspecific potential joining outsiders from sharing resources is too high (Wilson 1975). This mutual tolerance hypothesis—a type of resource defense grouping benefit—predicts that per capita reproductive output in groups will be consistently lower than that in pairs (Eggert and Müller 1992, 1997; Robertson et al. 1998; Komdeur et al. 2013). Additionally, grouping is more likely to occur when beetle densities are high, and higher-value resources are predicted to attract more individuals, resulting in larger groups. Empirical studies have also shown that although breeding success (i.e., total group productivity) was higher in groups than in solitary pairs (Sun et al. 2014), per capita productivity in groups was lower than in pairs (Trumbo 1992, 1995). However, recent work has shown that carcass sharing in group-living burying beetles may also make them better able to compete against natural enemies (e.g., blowflies or other interspecific intruders at carcasses) and achieve higher breeding success (Sun et al. 2014). This common enemy hypothesis—a type of collective action grouping benefit—predicts that both total and per capita productivity will be higher in groups than in pairs (Sun et al. 2014). Importantly, these studies suggest that, in addition to climatic conditions, interspecific competition against blowflies is also a crucial factor in determining resource availability and thus the quality of the environment for burying beetles (fig. S1; figs. S1–S7 are available online).

To test these alternative hypotheses for group formation (mutual tolerance vs. common enemy) and to determine how environmental quality—the interacting effects of climate and intra- and interspecific competition—influences the evolution of sociality in the Asian burying beetle *Nicrophorus nepalensis*, we performed a series of observational and experimental studies in the laboratory and along an ecological gradient in the field where temperature, population density (which influences competition), and the pressure of interspecific competition with blowflies vary with elevation (Sun et al. 2014; Chan et al. 2019; figs. 1*a*, S2). First, we determined how temperature and interspecific competition influence resource availability and rates of breeding success. Next, we quantified the distribution of natural group sizes and the differences in total and per capita productivity along the elevational gradient to explore how group size affects burying beetle reproductive success in environments of varying quality. Because of the inherent problem that environmental quality and group size often affect each other (i.e., groups in high-quality environments or with higher-quality resources tend to be larger; Koenig 1981), manipulating group size is essential for understanding the impact of environmental quality on grouping benefits. Therefore, we experimentally manipulated group size along the elevational gradient and quantified reproductive success (group size manipulation; fig. 1*a*). The common enemy hypothesis predicts that per capita productivity (i.e., number and mass of offspring) of groups should be higher than that of pairs in low-quality environments where blowfly competition is most intense (i.e., at low elevations; Sun et al. 2014; Chan et al. 2019) because of the collective action benefit of grouping. In contrast, the mutual tolerance hypothesis predicts that per capita productivity of groups will be lower than that of pairs in high-quality environments where blowfly competition is low (i.e., at intermediate elevations) because of the high cost of excluding other beetles from a carcass, a resource defense benefit of grouping.

To further examine the relationship between environmental quality and the benefits of grouping experimentally, we heated mouse carcasses in the field to manipulate blowfly competition at the intermediate and high-elevation sites (heating treatment) where blowfly abundances are normally low (sensu Sun et al. 2014; fig. 1*a*). Importantly, previous work in this system has shown that heating carcasses increases blowfly abundance and activity and thus increases interspecific competition for access to carcass resources (Sun et al. 2014; Chan et al. 2019). Thus, our experiment allowed us to intensify interspecific competition pressure between flies and beetles at elevations with relatively low levels of natural interspecific competition without altering other environmental conditions. To ensure that any observed cooperation was the result of changes in social behavior and not simply changes in activity associated with differences in ambient temperature, we quantified social behavior by dividing the beetles' investment time into time spent (1) simply walking on the carcass and (2) conducting more complex and presumably more costly carcass preparation investment behaviors, including maggot and rotten tissue removal as well as carcass dragging, depilation, and burial. The common enemy hypothesis predicts that per capita productivity of beetle groups should be higher in groups than in pairs in the experimental heating treatment, whereas the mutual tolerance hypothesis predicts that per capita productivity should be lower in groups because heating a carcass reduces its value due to a faster rate of decomposition.

Finally, we identified the key determinant of breeding success and productivity at the high-elevation sites where temperatures are coldest. Given that blowfly competition is low at high elevations (Sun et al. 2014), it is perhaps puzzling to see lower productivity of pairs in these sites than those at intermediate elevations. However, our previous work suggested that it takes longer for *N. nepalensis* to discover carcasses at higher elevations (Sun et al. 2014; Chan et al. 2019), which appears to be the key mechanism preventing them from breeding successfully in this environment (Chan et al. 2019). Thus, in burying beetles there is potentially a third explanation—the physiological limit hypothesis—to explain group formation and cooperative behavior. To test this physiological limit hypothesis, we experimentally manipulated the arrival time of *N. nepalensis* on carcasses by placing a small piece of decomposing and odor-emitting meat near a carcass (odor treatment) to facilitate its rapid discovery (fig. 1*a*). In addition, since temperature could influence both *N. nepalensis*'s energetic costs of carcass preparation and the pressure of interspecific competition, we used a factorial design in the laboratory (fig. S2) to investigate the independent and synergistic effects of temperature and blowfly competition on breeding success in solitary pairs of *N. nepalensis*.

Material and Methods

Study System

This study was conducted in Nantou and Hualien counties, Taiwan (24°5′N, 121°10′E), along an elevational gradient composed primarily of uncultivated forest (fig. 1*b*). We conducted field experiments in four field seasons from 2012 to 2015. The data herein are related to those in a previously published study from this system (Sun et al. 2014) that demonstrated by examining and experimentally manipulating fly activity and abundance in relation to elevation and temperature that the probability of breeding successfully is higher for larger groups at low elevations. In the current study, we more directly quantify fitness (i.e., the number and body masses of beetle offspring)—something

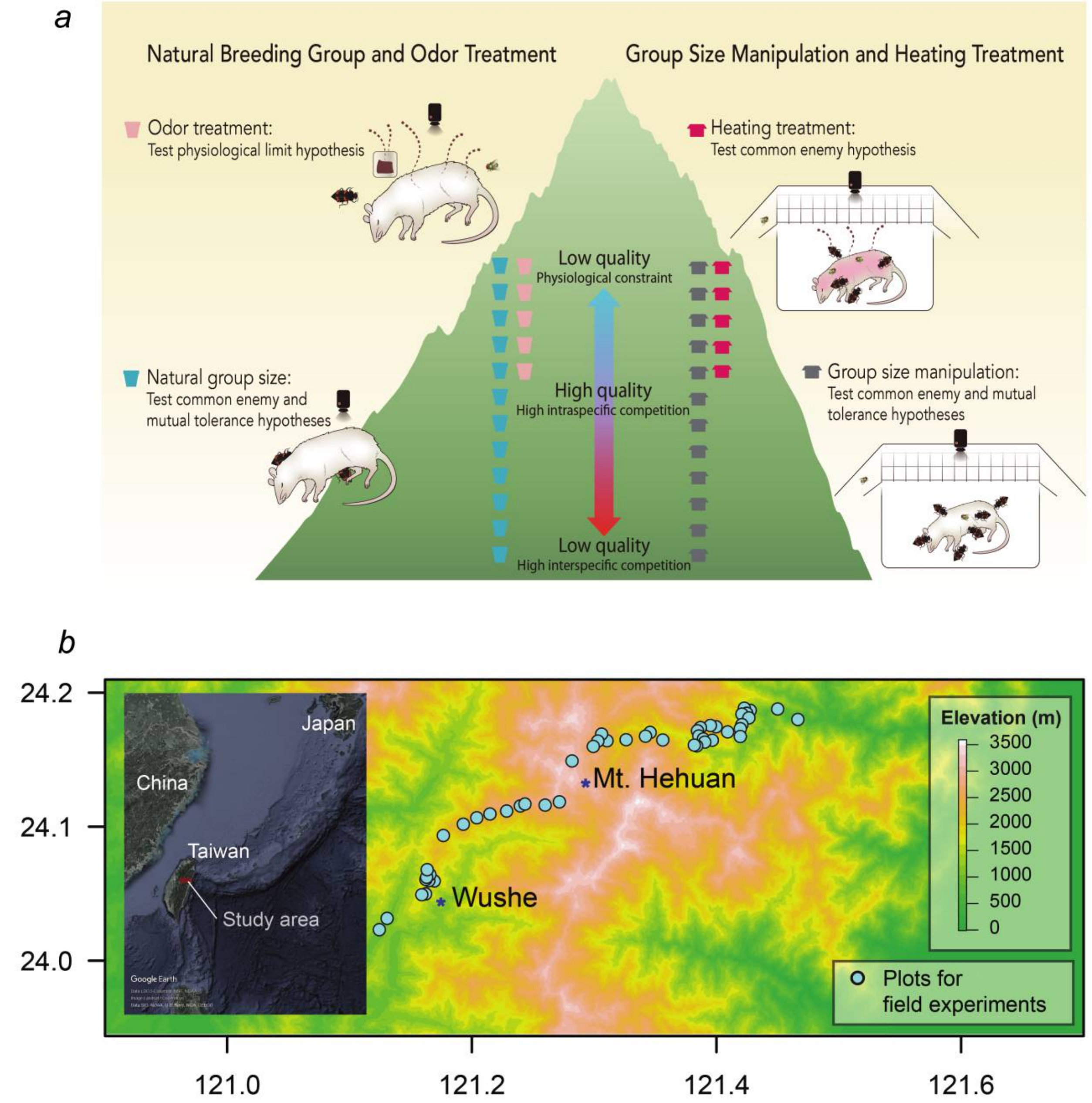

Figure 1: Summary of field experiments (*a*) and sites along the elevational gradient (*b*). In *a*, natural group sizes (*bottom left*) were quantified along the elevational gradient to investigate breeding performance. The odor treatment (*top left*) was used to test the physiological limit hypothesis at high elevations. The group size manipulation (*bottom right*) utilized breeding chambers to create pairs and groups in order to examine the benefits of grouping along the elevational gradient. The heating treatment (*top right*) was used to test the common enemy hypothesis at high elevations. The drawings in this figure are replicated in subsequent figures to indicate where the experiments occurred along the elevational gradient.

not determined in the previous study—at different elevations and in a carcass heating treatment. We also present new data to investigate how an odor treatment influences breeding success of *Nicrophorus nepalensis* at high elevations (quantified as the probability of breeding successfully, the arrival time on a carcass, and the total number of offspring produced). Additionally, a new set of lab experiments was used to investigate how temperature and interspecific competition independently or synergistically influence breeding success.

Natural Densities and Breeding Performance

To assess the density of *N. nepalensis* in the field, we hung pitfall traps ($n = 404$) baited with 100 ± 10 g of decomposing pork along the elevational gradient (ranging from 1,000 to 3,200 m). The apparatus consisted of a larger plastic container trap, a disk-shaped plastic landing pad, and a plastic roof. The baited pork was kept at room temperature for 4 days at the field station (Meifeng, 24°5′29″N, 121°10′33″E; elevation of 2,100 m and average daily temperature of 16°C in July) before deployment to minimize the potential for differential decomposition rates at different elevations. We counted the total number of beetles at each trap after four nights.

To assess the breeding performance of *N. nepalensis* in the field, fresh rat carcasses (75 ± 7.5 g) were placed in the center of soil-filled pots ($n = 459$) to attract local beetles to breed along the elevational gradient (ranging from 1,100 to 2,900 m). A previous study showed that 75 g is optimal for offspring production of a pair of *N. nepalensis* (Chan et al. 2019). The experimental pots were protected from scavengers with cages (30 cm × 30 cm × 30 cm) constructed of 2 × 2-cm wire mesh that excluded vertebrates but allowed both blowflies and beetles to access the carcass. Thermo data loggers were used to collect temperature data throughout the experimental period (for details, see Sun et al. 2014). The minimum daily temperature was used to represent the ambient thermal environment (sensu Sun et al. 2014). The natural group size of experimental pots was determined on the beetle's first arrival night. Since naturally arriving beetles were not individually marked, we counted the maximum number of beetles observed during three observed periods. An average of the three observed maximum group numbers was used to represent the natural group size of the experiment. We validated this method of group size estimation in the lab, where we could individually mark beetles, and found that although this method slightly underestimates actual group sizes, the two estimates are highly correlated (fig. S3). Finally, on the basis of our previous work (Sun et al. 2014), we analyzed data from only the breeding elevational range, defined as the range in which at least one pair or group of *N. nepalensis* bred successfully, which was separated into three equal quantiles for analysis: low (1,600–2,000 m), intermediate (2,000–2,400 m), and high (2,400–2,800 m) elevation.

Group Size Manipulation

To create pair and group treatments, we placed either two (one male and one female; $n = 53$ groups) or six (three males and three females; $n = 39$ groups) locally trapped beetles—caught at the same elevation at which they were released—in breeding chambers. These chambers were designed to limit access to additional beetles without impacting flight access to the carcasses (for details, see Sun et al. 2014). On the basis of a pilot study, we released beetles into the experimental chambers on different schedules to mimic arrival patterns at different elevations. Beetles were released into the chambers on day 2 at low elevations, on day 3 at intermediate elevations, and on day 4 at high elevations. After each trial was completed, the larvae at the third-instar stage were collected and weighed (±0.1 mg) individually using an electronic balance (Precisa XT 220A). Over the course of the group size manipulation in the breeding chamber experiment, a few beetles managed to enter or escape from the chambers, which caused slight variations in the mean group size: group size $= 2.03 \pm 0.10$ for the pairs (two beetles initially), and group size $= 5.29 \pm 0.19$ for the groups (six beetles initially) at the 23 sites along the elevational gradient. Pair and group breeding chambers were allocated in a pairwise manner such that two breeding chambers were placed no closer than 30 m apart at each site. Because of limited space to conduct the breeding chamber experiment in the mountainous terrain, we reused each site up to four times annually. However, different rounds of experiments at the same site were conducted at least 2 weeks apart.

Carcass Heating Treatment

To explore temperature-mediated cooperation in response to blowfly competition in situ, we manipulated carcass temperature by continuously heating each treatment carcass from below. A total of 24 heated carcass treatments (nine groups and 15 pairs) were deployed within the high-elevation range (from 2,039 to 2,814 m). The heating device was constructed with a series circuit of cement resistors (40 Ω) powered by Yuasa lead-acid batteries (6 V, 12 Ah). Heating treatments were paired with a control chamber (i.e., without a heating device) that was placed 30 m away. The heating treatment experiment used the same experimental apparatus that we used in the group size manipulation (described above). Although the heated carcass treatment created elevated soil temperatures (28.7° ± 0.71°C) relative to the control chambers at ambient temperatures (17.4° ± 0.31°C), the elevated soil surface temperatures were within the natural range at our low-elevation sites (15°–28°C).

Odor Treatment

We conducted field experiments with odor treatments to test whether the time it takes beetles to locate a carcass influences their breeding success at high elevations. The odor treatment experiment used the same experimental apparatus we used for assessing natural group sizes (described above). However, we placed an additional plastic bottle containing 50 g of predecomposed meat that emitted odor near the carcass to facilitate its rapid discovery. The meat was predecomposed at 16°C for 4 days before the experiment. The mouth of the bottle was covered with a fine wire mesh screen to prevent beetles from consuming the predecomposed meat. Each odor treatment was paired with a control treatment (i.e., without predecomposed meat), except for those in some small field sites that did not allow us to simultaneously conduct both treatments because of space limitations. A total of 25 odor and 25 control treatments were video recorded to quantify carcass arrival time, which was measured as the duration of time elapsed from when experiments were initiated until when a beetle arrived on the carcass. Since the goal of this experiment was to test carcass discovery rates, we excluded trials in which beetles did not come. Finally, breeding success was recorded if there were any offspring produced at the end of the experiment. We ran the experiment until the carcasses were fly-bloated or mummified, which took approximately 6 days.

Lab Temperature and Fly Competition Treatment

We conducted a series of lab experiments to more precisely examine how temperature and fly competition influence the breeding success of *N. nepalensis*. We used three temperature treatments (12°, 16°, and 20°C) to represent the mean temperatures at low, intermediate, and high elevations, with a daily fluctuation of 7°C (mean temperature ±3.5°C) that approximated the daily temperature fluctuation in the natural forest at our field sites. We prepared nursing boxes for burying beetles using 60 × 30 × 30-cm (length × width × height) plastic containers filled to a 20-cm depth with potting soil. The containers were placed into large Styrofoam boxes containing soil to help maintain the soil temperature. A pair of *N. nepalensis*, one male and one female, was released into each nursing box and provided with a 75 ± 7.5-g rat carcass. The entire apparatus was placed inside a growth chamber (model GRT-820HI, AC 220V, 7A; Yuh Chuen Chiou Industry) for temperature manipulation. To test the competitive effects of blowflies, half of the nursing boxes in each temperature treatment were supplemented with 10 g of maggots for 4 h before the release of the beetle pairs. Breeding behavior was monitored, and breeding success was recorded if there were any offspring produced at the end of the experiment. Carcass handling time was measured as the duration of time elapsed from when beetles were released until when a carcass was completely buried under the surface of the soil.

Behavioral Analyses

In total, 1,020 h of videos were analyzed from 89 replicates in the control breeding pots. A variety of social behaviors—including individual activities, social interactions, and investment in carcass processing—were recorded in the first 10 h (1900–0500 hours) after the first beetle arrived on the carcass using the Observer XT 14 (Noldus). We recorded walking and eating behaviors to quantify any activity or interactions that were unrelated to social conflict or social investment. Behaviors on the carcass on the first night of arrival were also analyzed hourly because social investment and conflict can change after initial arrival as the group forms.

Data Analysis

We analyzed our data using general linear models (GLMs) and generalized linear mixed models (GLMMs), depending on whether the experimental designs involved repeated sampling. Specifically, GLMs were used without repeated samplings of study sites, but GLMMs included site identification as a random factor to account for repeated sampling of study sites. We used different model families for response variables with different error structures: negative binomial for natural density and total offspring number (overdispersed count data), Gaussian for beetle arrival time at the carcasses, log-transformed natural group size of beetles (approximately normal data), and binomial for breeding success or failure (binary data). Since per capita offspring number (defined as the ratio between total offspring number and the number of females) did not fit directly to any model family, we modeled it by considering the total number of offspring as a negative binomial response with a log link by including the natural log of female number as an offset term. Independent variables of interest in the GLMs and GLMMs include elevation, minimum daily temperature, and type of experimental treatment. To facilitate model convergence, all continuous variables were standardized before analysis. Since the influences of elevation and temperature were not necessarily linear, we first modeled the potential nonlinear (i.e., unimodal) effects through including the quadric terms of these variables at the beginning of model fitting. We then removed nonsignificant ($P \geq .1$) quadric terms in the final models. Similarly, we included the interaction terms of interests, namely, the interactions among manipulative treatments (i.e., heating, odor, group size) and environmental gradients (i.e., elevation, temperature) at the beginning of model fitting. We then removed nonsignificant interaction terms for the final results. Using the R package car (Fox and Weisberg 2011), the statistical significance of models without interaction terms was obtained from type II sums of squares, whereas significance for models with interaction terms was obtained from type III sums of squares. Post hoc pairwise comparisons (Tukey tests) for categorical independent variables were conducted using the R package lsmeans (Lenth 2016). Finally, we conducted nonparametric Wilcoxon rank-sum tests for the analyses of total and per capita brood mass, since there was no proper error structure to fit the parametric GLM or GLMM tests. We averaged the total or per capita brood mass resulting from different experiments with the same treatment and at the same sampling sites, and we considered sites as the sampling unit for the Wilcoxon tests to solve the problem of repeated sampling and to provide relatively conservative statistical inferences. All statistical analyses were conducted in R version 3.2.3 (R Development Core Team 2015). The results are presented as means ± SE unless otherwise noted. Data have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.ncjsxksqt; Liu et al. 2019).

Results

Population Density and Natural Group Size

Natural group sizes initially increased as elevation increased to 2,200 m asl, where temperatures were moderate (~14°C), but then decreased as elevation continued to increase and temperature declined (fig. 2; table S1; tables S1–S10 are available online). Natural group size was positively correlated with population density (GLMM, $\chi^2_1 = 27.23$, $P < .001$), but the relationship varied along the elevational gradient (figs. 2*b*, S4). When restricting our analysis to the breeding elevational range, we found that natural group size was larger at low elevations (1,600–2,000 m) than at intermediate (2,000–2,400 m) or high (2,400–2,800 m) elevations when population density was above 10 beetles per trap (GLMM, $\chi^2_1 = 5.07$, $P = .024$, $n = 104$; fig. 2*b*).

Elevation, Group Size, and Reproductive Success

As we expected, there was no clear pattern of how natural group size influenced total and per capita and total productivity in terms of offspring number (figs. 3*a*, 3*b*, S5*a*, S5*b*; tables S2, S3), presumably because of the confounding effects of resource quality, population density, and group size, as found in other cooperatively breeding species (Koenig 1981). However, our experimental manipulation of group size along the elevational gradient demonstrated that per capita productivity in pairs and groups exhibited different trends along the elevational gradient. Specifically, the per capita number of offspring produced by pairs varied unimodally with elevation and peaked at intermediate elevations (fig. 3*c*; table S4b) and temperatures (fig. 3*d*; table S5b), whereas in groups it did not vary

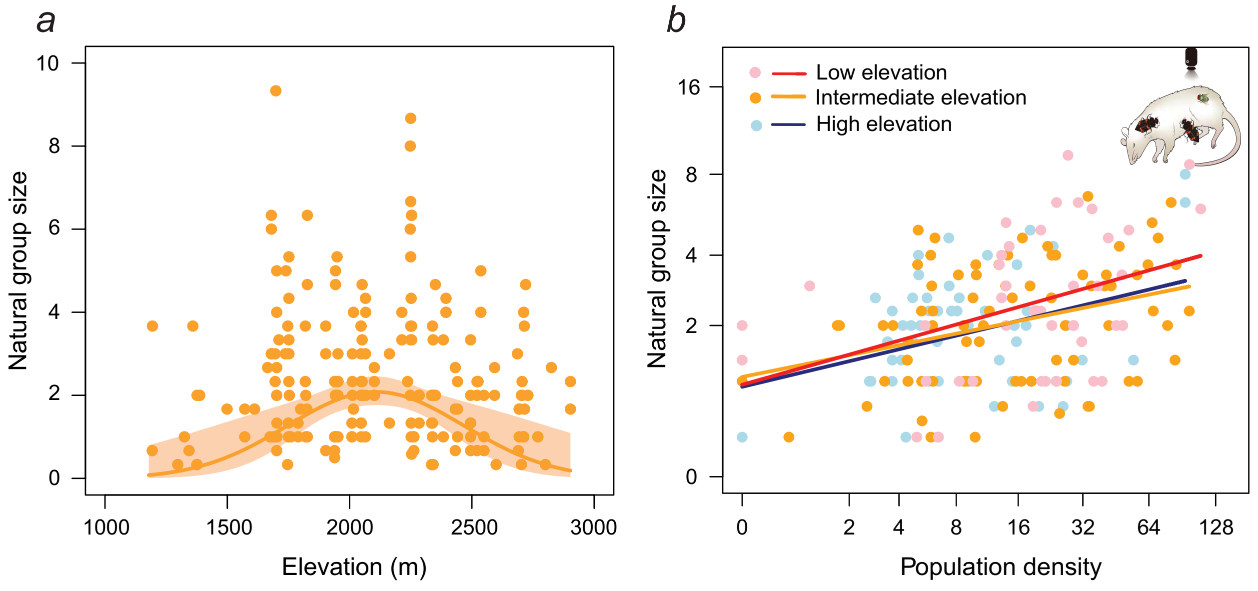

Figure 2: Relationships among elevation, population density, and natural group size in *Nicrophorus nepalensis*. *a*, Natural group size of *N. nepalensis* at different elevations. Points represent samples, the line represents the least squares mean, and the shaded area represents the 95% confidence interval expected from a generalized linear mixed model. *b*, Relationship between natural group size and population density (represented by the number of individuals caught in each hanging pitfall trap) at different elevations. Drawing corresponds to treatment illustrated in figure 1*a*.

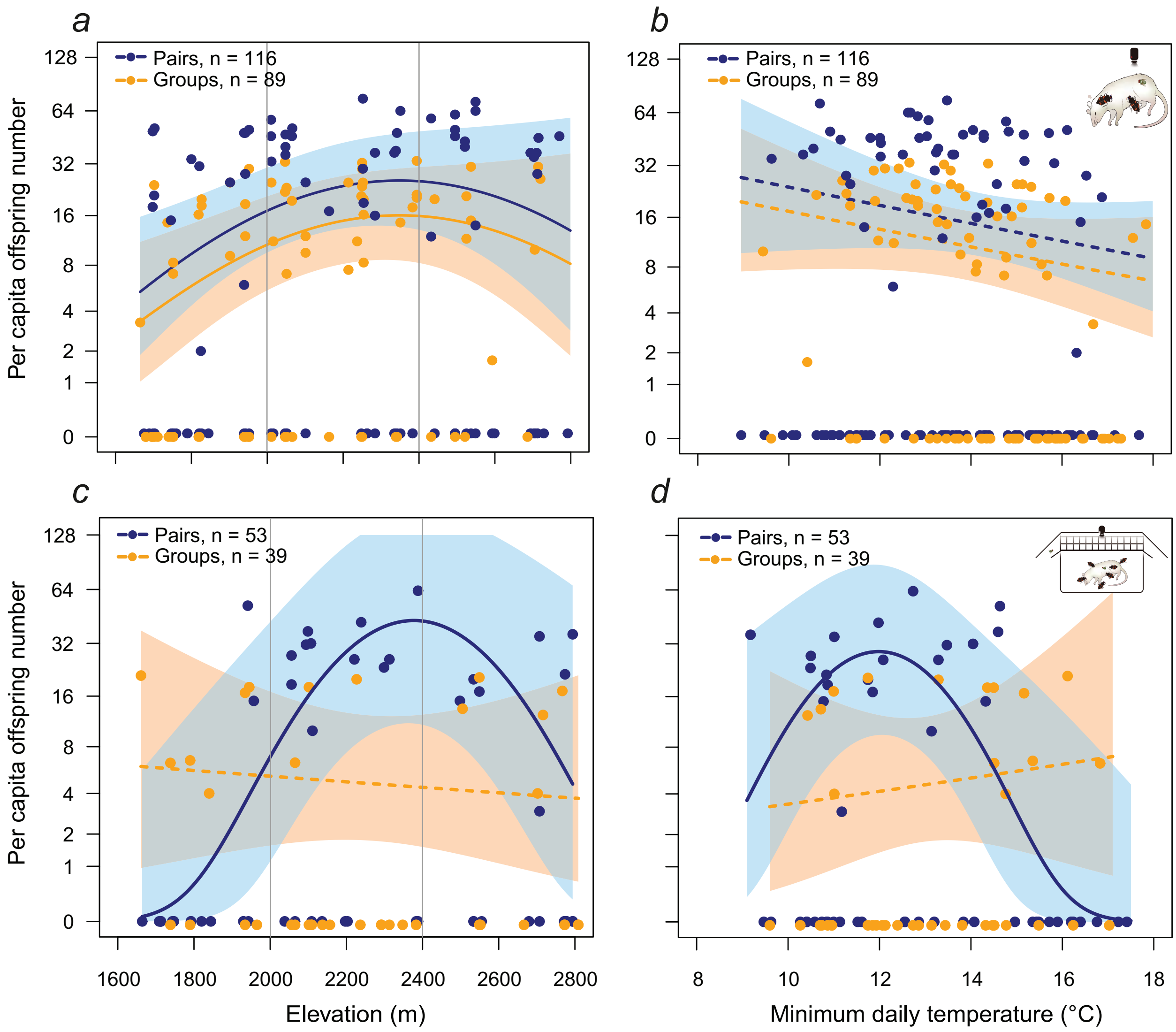

Figure 3: Per capita number of offspring produced in pairs and groups of *Nicrophorus nepalensis* at different elevations and temperatures in both natural pairs and groups and in the group size manipulation. Shown are per capita number of offspring produced in natural pairs and groups at different elevations (*a*) and temperatures (*b*) as well as per capita number of offspring produced in pairs and groups in the group size manipulation at different elevations (*c*) and temperatures (*d*). Lines represent least squares means, and shaded areas represent 95% confidence intervals expected from generalized linear mixed models. Dashed lines represent nonsignificant trends. Vertical lines indicate boundaries between elevational zones, which were determined by separating the breeding elevational range (defined as the elevations that at least one pair or group of *N. nepalensis* bred successfully) into equal quantiles. Drawings correspond to treatments illustrated in figure 1*a*.

with elevation (fig. 3*c*; table S4c) or temperature (fig. 3*d*; table S5c). When we divided the data set into elevational quantiles, we found that groups produced marginally greater per capita numbers of offspring than pairs at low elevations (Tukey pairwise comparison after GLMM, $z = 1.722$, $n = 26$, $P = .085$; fig. 3*c*), but pairs produced greater per capita numbers of offspring than groups at intermediate elevations (Tukey pairwise comparison after GLMM, $z = 2.05$, $n = 35$, $P = .040$; fig. 3*c*). However, pairs and groups produced similar per capita numbers of offspring at high elevations (Tukey pairwise comparison after GLMM, $z = 1.17$, $n = 31$, $P = .24$; fig. 3*c*). Similar patterns were observed in brood mass: groups had greater per capita brood mass than pairs at low elevations ($W = 17$, $n = 19$, $P = .021$; fig. S6*a*), but pairs had greater per capita brood mass than groups at intermediate elevations ($W = 159$, $n = 29$, $P = .009$; fig. S6*a*). Again, pairs and groups had similar per capita brood mass at high elevations ($W = 57$, $n = 20$, $P = .58$; fig. S6*a*). Finally, the total number of offspring produced per group showed similar patterns to the per capita offspring (fig. S5*c*, S5*d*; tables S6, S7), and the total brood mass produced per group showed patterns similar to those of the per capita brood mass (fig. S6*a*, S6*b*).

Social Behavior

We found that time spent on complex carcass preparation behaviors increased with increasing daily minimum temperature in groups ($\chi^2_1 = 5.39$, $P = .02$, $n = 33$; fig. 4*a*) but not in pairs ($\chi^2_1 = 0.17$, $P = .68$, $n = 56$; fig. 4*a*). However, there was no significant relationship between walking time and daily minimum temperature in groups ($\chi^2_1 = 0.24$, $P = .60$, $n = 33$; fig. 4*b*) or in pairs ($\chi^2_1 = 0.79$, $P = .37$, $n = 56$; fig. 4*b*), suggesting that the increase in total investment time on carcasses in warmer environments was not caused by a simple increase in activity at warmer temperatures; it was instead driven by an increase in cooperative behavior.

Ecological Drivers of Grouping Benefits

Consistent with the common enemy hypothesis, a type of collective action grouping benefit, we found that the heating treatment differentially influenced per capita offspring number in pairs and groups (GLMM interaction: $\chi^2_1 = 4.98$, $n = 90$, $P = .026$; fig. 5*a*). That is, heated carcasses in pairs produced significantly fewer per capita offspring (Tukey pairwise comparison after GLMM, $z = 2.29$, $n = 52$, $P = .022$; fig. 5*a*) and smaller per capita brood masses than controls ($W = 245$, $n = 39$, $P = .006$; fig. S6*c*). In contrast, the heated carcass treatment in groups did not result in significantly fewer per capita offspring (Tukey pairwise comparison after GLMM, $z = 0.21$, $n = 38$, $P = .83$; fig. 5*a*) or smaller per capita brood masses ($W = 71$, $n = 29$, $P = .75$; fig. S6*c*). Additionally, the heating treatment also differentially influenced the total number of offspring produced in pairs and groups (GLMM interaction: $\chi^2_1 = 5.01$, $n = 90$, $P = .025$), which showed similar patterns to the total brood mass (fig. S6*d*).

Breeding Success at High Elevations

The odor treatment enabled beetles to find a carcass more quickly (fig. 5*b*; tables S8a, S9) and resulted in more beetles grouping on the carcass (fig. 5*c*). Therefore, the odor treatment increased the beetles' probability of breeding successfully (table S8b) and resulted in greater total and per capita offspring (fig. 5*d*; table S8c, S8d).

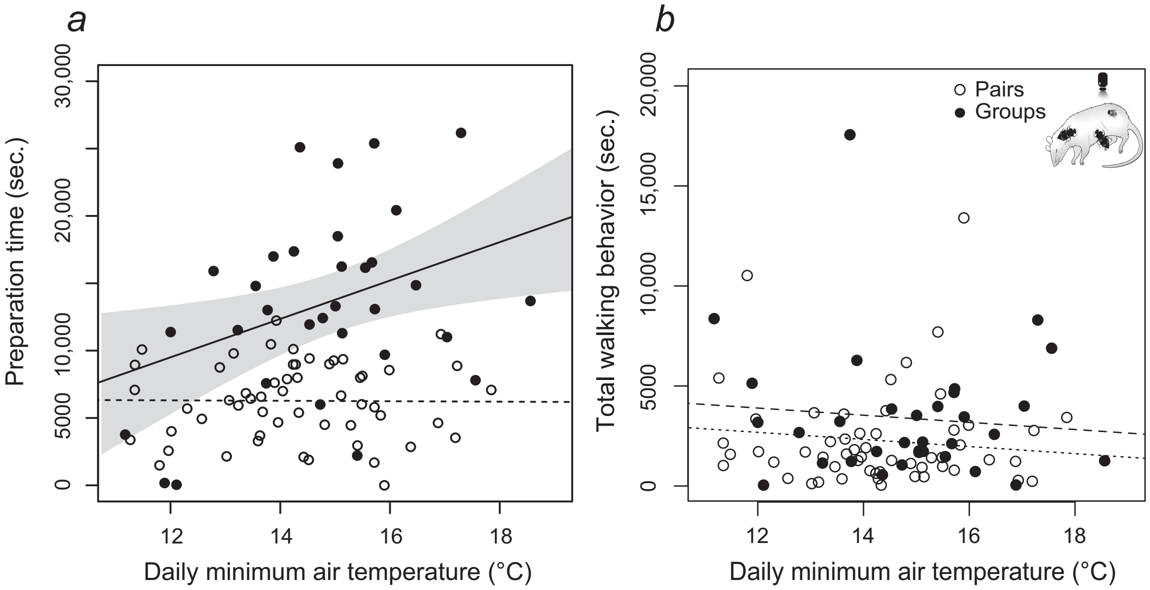

Figure 4: Complex carcass preparation and simple walking behaviors of *Nicrophorus nepalensis* during cooperative carcass preparation along the temperature gradient. Shown is the time that beetles spent on complex carcass preparation behaviors (*a*) and walking on the carcass (*b*) in relation to daily minimum air temperature in pairs and groups. Compared with pairs, individuals in groups spent more time on complex carcass preparation but not on walking as daily minimum air temperature increased, suggesting that the increase in total cooperative investment in warmer environments was not simply the result of increased activity at warmer temperatures. Lines represent least squares means (solid lines denote significant relationships, and dashed lines denote nonsignificant relationships), and the shaded area represents the 95% confidence interval expected from the generalized linear mixed model. Drawing corresponds to treatment illustrated in figure 1*a*. A color version of this figure is available online.

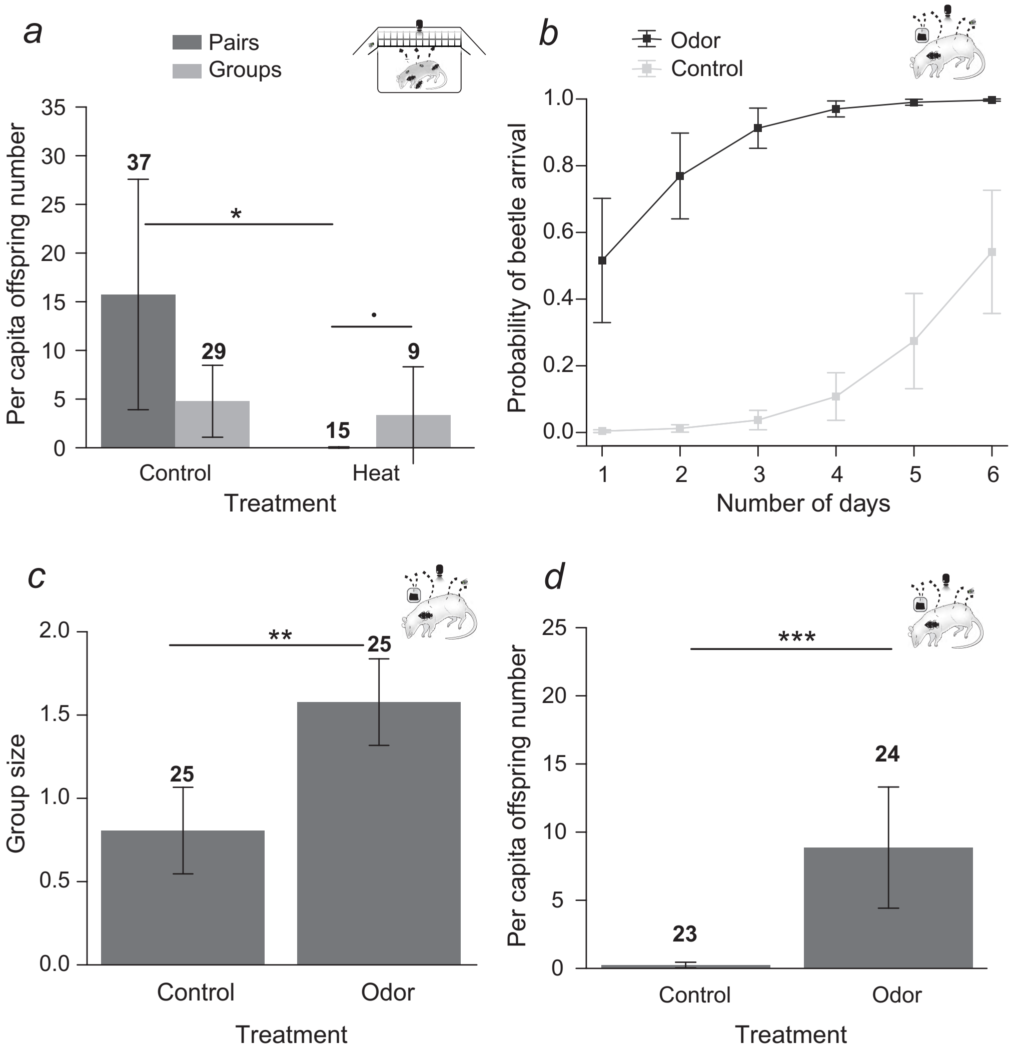

Figure 5: Per capita offspring number, total offspring number, and carcass arrival time in the heating and odor experimental treatments. *a*, Mean ± SE per capita number of offspring produced by pairs and groups of *Nicrophorus nepalensis* with and without heating treatments. *b*, Probability of beetle arrival. *c*, *d*, Group size (*c*) and per capita number of offspring produced (*d*) in the control and odor treatments. Samples sizes are given above each bar. Drawings correspond to treatments illustrated in figure 1*a*. A color version of this figure is available online.

Independent and Synergistic Effects of Temperature and Competition

Since both temperature and interspecific competition appear to influence fitness of *Nicrophorus nepalensis* in environments of varying quality along the elevational gradient, we used a factorial design in the laboratory to investigate their independent and synergistic effects on breeding success while controlling for an effect of the beetles' arrival time (fig. S2). As expected, the probability of solitary pairs breeding successfully when blowflies were present (i.e., high interspecific competition) was highest in the low-temperature treatment (12°C), followed by the intermediate (16°C) and high-temperature treatments (20°C; GLM, $\chi^2_1 = 13.85$, $n = 54$, $P < .001$; fig. 6*a*). Interestingly, even without blowfly competition, we still found that the probability of breeding successfully was highest in the low-temperature treatment, followed by the intermediate and high-temperature treatments (GLM, $\chi^2_1 = 23.68$, $n = 60$, $P < .001$; fig. 6*a*). Although the presence of blowflies decreased the probability of breeding successfully (GLM, $\chi^2_1 = 13.85$, $n = 114$, $P < .001$; fig. 6*a*), it took beetles more time to bury the carcass in the low-temperature treatment, followed by the intermediate and high-temperature treatments (GLM, $\chi^2_1 = 4.10$, $n = 82$, $P = .043$; fig. 6*b*). However, the presence or absence of blowflies did not

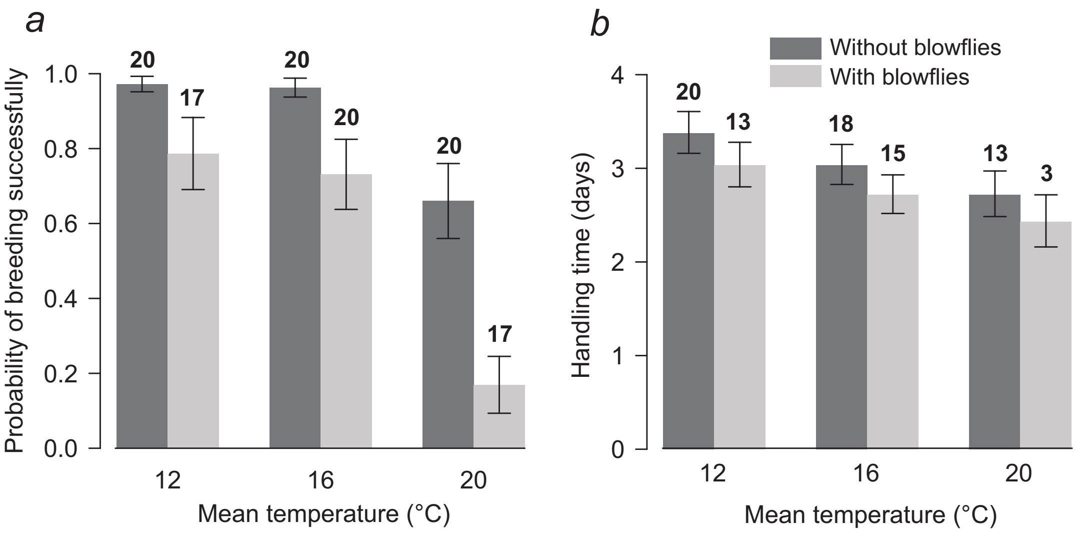

Figure 6: Probability of *Nicrophorus nepalensis* breeding successfully and carcass handling times of three different temperature treatments in the laboratory. *a*, Mean ± SE probabilities of breeding successfully in the experimentally manipulated mean temperature treatment. *b*, Mean ± SE carcass handling times of three different mean temperature treatment. The three temperature treatments (12°, 16°, and 20°C) represent the mean temperatures at low, intermediate, and high elevations, with a daily fluctuation of 7°C (mean temperature ± 3.5°C) that approximated the daily temperature fluctuation in the natural forest at our field sites. A color version of this figure is available online.

affect handling time of carcasses (GLM, $\chi^2_1 = 2.20$, $n = 82$, $P = .14$; fig. 6*b*).

Discussion

Our results demonstrate that climate (temperature) and competition (both intra- and interspecific) both independently and synergistically influence sociality by determining a continuum of environmental quality along an elevational gradient that shapes the ecological transitions in grouping benefits in *Nicrophorus nepalensis*. In other words, climatic differences that change gradually over an ecological gradient influence the potential benefits that individuals receive by forming groups because of differences in inter- versus intraspecific competition. In contrast to many other species where climate directly influences resource availability and cooperation (Shen et al. 2012; fig. S1*a*), in this system, temperature influences access to resources indirectly by mediating the degree of interspecific competition for carcasses against blowflies (which is higher in warmer temperatures at low elevations; fig. S1*b*), mediating the degree of intraspecific competition (beetle densities are higher at intermediate elevations; Chan et al. 2019), and influencing physiological constraints (which are higher at high elevations; Chan et al. 2019). Thus, we find support for the common enemy, mutual tolerance, and physiological limit hypotheses at different elevations. Although other species of competitors could in theory also influence cooperation and grouping in *N. nepalensis* (e.g., microorganisms could affect carcass decomposition rates, or mammalian carcass scavengers could affect carcass availability), we know that blowflies are critical competitors because experimental removal of blowfly competition in the field substantially increases *N. nepalensis* breeding success (Chan et al. 2019). Moreover, there was no elevational pattern of vertebrate scavengers visiting the carcasses we put out for the breeding experiments (based on the video recording data), suggesting no obvious elevational trend in their abundance (Chan et al. 2019).

Our results suggest that biotic and abiotic factors interact to influence environmental quality and social behavior in burying beetles. Therefore, environmental quality need not be synonymous with climate alone but instead should be defined by the key extrinsic factors—in this case, temperature and competition—that influence the population growth rate of a species. Therefore, low-quality (i.e., harsh) environments are those that have unsuitable climates, high levels of interspecific competition, high parasite or pathogen loads, or really any extrinsic factor that leads to low population density. Collective action benefits are generated by cooperative behavior that has evolved to cope with these types of extrinsic challenges (Shen et al. 2017). For burying beetles, such low-quality environments occur at both ends of the environmental gradient at hot and cold ambient temperatures (fig. S7). In support of the common enemy hypothesis, hot temperatures at low elevations favor the collective action benefit of greater competitive ability against natural enemies, as evidenced by the higher per capita productivity of groups. Indeed, our behavioral data also show that large natural groups of beetles spent more effort on complex carcass preparation in hotter environments (fig. S7*a*). Additionally, previous work has shown that individuals in experimentally created groups at this elevation invest more time in cooperative carcass processing and less time in social conflict (Sun et al. 2014). In contrast and in support of the physiological limit hypothesis, at high elevations—which appear to be the lowest-quality environments of all for beetles—cold temperatures not only reduce blowfly competition but also negatively impact the beetles' ability to locate and process carcasses, presumably because of temperature-driven effects on physiology (Chan et al. 2019). As a consequence, we do not see any grouping benefit in natural or experimentally manipulated groups at high elevations (fig. S7*c*).

In contrast, we define high-quality (i.e., benign) environments as those that have suitable climates, low interspecific competition, or low parasite or pathogen loads, which leads to high population density. In such environments, intraspecific competition for resources becomes the key determinant for individual fitness rather than interspecific competition. Thus, the resource defense benefit against intraspecific competition is the key mechanism underlying group formation in these types of environments (Shen et al. 2017). This scenario is often referred to as habitat saturation, where ecological constraints limit independent breeding and favor delayed dispersal of offspring in species that form kin groups (Emlen 1982; Koenig et al. 1992). In contrast to the low-quality environments at both extremes of the environmental gradient and in support of the mutual tolerance hypothesis, intermediate elevations with only moderate pressure from blowflies (Sun et al. 2014) appear to be the optimal (i.e., high-quality) environment for burying beetles. These intermediate temperature environments had both the highest beetle population densities along the elevational gradient (Chan et al. 2019) as well as the highest levels of intraspecific competition (Sun et al. 2014), presumably because of high population density. Therefore, for a potential joining outsider, the probability of obtaining a carcass elsewhere at this elevation is low (i.e., ecologically constrained), whereas for a solitary breeding insider pair, the cost of monopolizing and excluding all potential joiners is high. Tolerating at least some outsiders and allowing them to join the group in order to jointly defend the carcasses against other beetle outsiders—a prediction of the mutual tolerance hypothesis—is likely to be the resource defense benefit that drives grouping behavior at intermediate elevations (fig. S7*b*).

One potentially surprising result from our study was that per capita reproductive output at high-quality intermediate elevations differed between pairs and groups in the group size manipulation but not in natural collections. We anticipated this a priori because environmental quality and group size often affect each other in social species (Koenig 1981). It is important to realize, however, that since we placed three males and three females on each carcass in our group size manipulation—a number that is larger than the mean natural group size on the first day at this elevation—social conflict was also higher than in natural groups (Sun et al. 2014). This potentially explains why we found that pairs had higher per capita reproductive success than groups in our group size manipulation experiment but not in the natural groups at intermediate elevations. Several studies in *Nicrophorus* beetles have shown that individuals can recognize their mates and other group members (Steiger et al. 2008; Steiger and Müller 2010; Haberer et al. 2014; Keppner et al. 2017) as well as form dominance hierarchies (Eggert et al. 2008); B.-F. Chen, M. Liu, and S.-F. Shen, unpublished data). The fact that severe fights among individuals often occur near carcasses in other beetle species (Otronen 1988) as well as this one (B.-F. Chen, M. Liu, and S.-F. Shen, unpublished data) further indicates that carcasses cannot be freely accessed by every outsider and that resource defense is likely to be critical for burying beetles, particularly at intermediate elevations where interspecific competition is low but intraspecific competition is high.

Most studies examining evolutionary transitions from solitary to group living compare different species (Maynard Smith and Szathmary 1995; Bourke 2011; Calcott 2011; West et al. 2015). In this study, we found that within a single species that forms groups in environments of contrasting quality, cooperation can be favored by different grouping benefits in the different environments. This ecological transition in grouping benefits—from collective action to resource defense benefits along the elevational gradient—suggests that evolutionary transitions may be favored in a wider range of environmental conditions and thus could be more stable than previously recognized. It has long been known that stable but specialized resources constitute the ancestral ecological conditions that likely favored the evolution of group living because multiple individuals congregating around resources have opportunities to interact (Tallamy and Wood 1986; Johns et al. 2009). However, after initial group formation, the major challenge for the evolutionary transition to complex sociality—particularly for groups of unrelated individuals—is the maintenance of group stability as environmental conditions vary (Wilson 2008). Here we develop a general framework of ecological transitions in grouping benefits by showing that under different environmental conditions, the same type of resources can favor group living for very different reasons. Specifically, our results demonstrate the behavioral mechanism—a balance between enhancing the performance of the entire group and maximizing each individual's share of reproduction—that allows such ecological transitions to occur. In low-quality environments with hot temperatures, individuals cooperate to compete with a common enemy (i.e., blowflies); hence, interspecific competition is the key determinant of individual fitness in unfavorable environments where the collective action benefits of grouping are more apparent. However, in high-quality environments with intermediate temperatures, high beetle population density and strong ecological constraints cause intraspecific competition to be the key determinant of individual fitness in favorable environments where resource defense benefits are critical to group formation. Finally, in low-quality environments with cold temperatures, although blowfly competition is relatively low, our odor treatment demonstrated that the difficulty of discovering a carcass without the odor of rapidly decomposing meat is the key mechanism that explains the low productivity of both beetle pairs and groups in these suboptimal environments (see table S10). Our results—namely, the relative importance of inter- versus intraspecific competition in different environments—could also explain (1) how the seemingly paradoxical dichotomy of environmental quality (harsh vs. benign environments) that drives the evolution of group living in many species may arise because of intertwined relationships between abiotic (e.g., climate) and biotic factors (e.g. competition) that shape grouping benefits with different relative intensities in different environments (Lin et al. 2019); and (2) how individual strategies interact with ecological conditions to shape the evolutionary transition toward complex societies (Korb and Foster 2010; Jetz and Rubenstein 2011; Purcell 2011; Shen et al. 2012; Kocher et al. 2014; Guevara and Avilés 2015; Sheehan et al. 2015).

The general pattern that we observed of decreasing per capita productivity in larger groups has also been seen in many cooperatively breeding vertebrates (Koenig and Pitelka 1981; Stacey and Koenig 1990; Koenig and Dickinson 2004) and eusocial insects, where it is referred to as Michener's paradox (Michener 1964; Kramer et al. 2014). The typical explanation for Michener's paradox has been that larger groups can increase the predictability (i.e., reduce the variance) of foraging success but at the cost of lowering the mean per capita food intake due to the limitation of food resources for species that are central place foragers because workers need to travel further to find food and then return to their nest (Wenzel and Pickering 1991; Naug and Wenzel 2006). However, because the per capita productivity of burying beetles is mainly determined by carcass size and not the costs of locating food (and even when locating carcasses for reproduction, they do not return to a central nest; Emlen 1982; Field et al. 2010; Helms and Cahan 2012), the explanation for Michener's paradox in eusocial insects is insufficient to explain the pattern observed here. Instead, we hypothesize that the shortage of breeding resources and hence the individual reproductive costs of competing with intraspecific competitors promotes the formation of groups, even if it leads to a reduction in per capita fitness in high-quality environments (see also Eggert and Müller 1992). Thus, our study provides an alternative explanation for resolving Michener's paradox that is likely to apply to other social insects that show decreasing per capita productivity with an increase in group size.

In conclusion, we show that environments of contrasting quality can favor the evolution and maintenance of grouping behavior, even for the same species. Importantly, this result contrasts with what is often observed in other facultative cooperatively breeding insects that show flexibility in social organization (i.e., being social in some contexts and nonsocial in others) in response to temporal or spatial environmental variation (Emlen 1982; Field et al. 2010; Helms and Cahan 2012). Instead, we see this difference in *N. nepalensis* because individuals can flexibly adjust their cooperative and competitive strategies in response to hetero- and conspecifics, and thus a social group can be stable in different environments for very different reasons. Ultimately, our results demonstrate that animal societies can be favored under a wide range of environmental conditions where the benefits of grouping differ, perhaps explaining the paradox of why sociality occur in environments of such contrasting quality. Our work also helps to resolve the long-standing puzzle of the adaptive significance of sociality among burying beetles (Eggert and Müller 1992, 1997; Robertson et al. 1998; Komdeur et al. 2013) by considering both the costs and the benefits of group living across an environmental gradient. This approach of studying ecological transitions in grouping benefits could help to more broadly explain the inconsistent patterns of group size effects on reproductive success observed in many other social animals (Avilés et al. 2007; Silk 2007; Wcislo and Tierney 2009; Purcell 2011; Kocher et al. 2014) as well as why animal societies evolve in such different types of environments (Jeanne 1991; Kaspari and Vargo 1995; Soucy and Danforth 2002; Avilés et al. 2007; Jetz and Rubenstein 2011; Gonzalez et al. 2013).

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Literature Cited

Alexander, R. D. 1974. The evolution of social behavior. Annual Review of Ecology and Systematics 5:325–383.

Allee, W. C. 1938. The social life of animals. Norton, New York.

Avilés, L., I. Agnarsson, P. A. Salazar, J. Purcell, G. Iturralde, E. C. Yip, K. S. Powers, and T. C. Bukowski. 2007. Altitudinal patterns of spider sociality and the biology of a new midelevation social *Anelosimus* species in Ecuador. American Naturalist 170:783–792.

Bourke, A. F. G. 2011. Principles of social evolution. Oxford University Press, Oxford.

Calcott, B. 2011. Alternative patterns of explanation for major transitions. Pages 35–51 *in* B. Calcott and K. Sterelny, eds. The major transitions in evolution revisited. MIT Press, Cambridge, MA.

Capodeanu-Nägler, A., E. M. Keppner, H. Vogel, M. Ayasse, A.-K. Eggert, S. K. Sakaluk, and S. Steiger. 2016. From facultative to obligatory parental care: interspecific variation in offspring dependency on post-hatching care in burying beetles. Scientific Reports 6:29323.

Chan, S.-F., W.-K. Shih, A.-Y. Chang, S.-F. Shen, and I.-C. Chen. 2019. Contrasting forms of competition set elevational range limits of species. Ecology Letters 22:1668–1679.

Cotter, S. C., and R. M. Kilner. 2010. Sexual division of antibacterial resource defence in breeding burying beetles, *Nicrophorus vespilloides*. Journal of Animal Ecology 79:35–43.

Eggert, A.-K., and J. K. Müller. 1992. Joint breeding in female burying beetles. Behavioral Ecology and Sociobiology 31:237–242.

———. 1997. Biparental care and social evolution in burying beetles: lessons from the larder. Pages 216–236 *in* J. C. Choe and B. J. Crespi, eds. The evolution of social behavior in insects and arachnids. Cambridge University Press, Cambridge.

Eggert, A.-K., T. Otte, and J. K. Müller. 2008. Starving the competition: a proximate cause of reproductive skew in burying beetles (*Nicrophorus vespilloides*). Proceedings of the Royal Society B 275:2521–2528.

Emlen, S. T. 1982. The evolution of helping. I. An ecological constraints model. American Naturalist 119:29–39.

Field, J., R. J. Paxton, A. Soro, and C. Bridge. 2010. Cryptic plasticity underlies a major evolutionary transition. Current Biology 20:2028–2031.

Fox, J., and S. Weisberg. 2011. An R companion to applied regression. Sage, Thousand Oaks, CA.

Giraldeau, L. A., and T. Caraco. 1993. Genetic relatedness and group size in an aggregation economy. Evolutionary Ecology 7:429–438.

Gonzalez, J.-C. T., B. C. Sheldon, and J. A. Tobias. 2013. Environmental stability and the evolution of cooperative breeding in hornbills. Proceedings of the Royal Society B 280:20131297.

Guevara, J., and L. Avilés. 2015. Ecological predictors of spider sociality in the Americas. Global Ecology and Biogeography 24:1181–1191.

Haberer, W., S. Steiger, and J. K. Müller. 2014. Dynamic changes in volatile emissions of breeding burying beetles. Physiological Entomology 39:153–164.

Helms, K., and S. H. Cahan. 2012. Large-scale regional variation in cooperation and conflict among queens of the desert ant *Messor pergandei*. Animal Behaviour 84:499–507.

Higashi, M., and N. Yamamura. 1993. What determines animal group size? insider-outsider conflict and its resolution. American Naturalist 142:553–563.

Jeanne, R. L. 1991. The swarm founding Polistinae. Pages 191–231 *in* K. G. Ross and R. W. Matthews, eds. The social biology of wasps. Cornell University Press, Ithaca, NY.

Jetz, W., and D. R. Rubenstein. 2011. Environmental uncertainty and the global biogeography of cooperative breeding in birds. Current Biology 21:72–78.

Johns, P. M., K. J. Howard, N. L. Breisch, A. Rivera, and B. L. Thorne. 2009. Nonrelatives inherit colony resources in a primitive termite. Proceedings of the National Academy of Sciences of the USA 106:17452–17456.

Kaspari, M., and E. L. Vargo. 1995. Colony size as a buffer against seasonality: Bergmann's rule in social insects. American Naturalist 145:610–632.

Keppner, E. M., M. Prang, K. C. Engel, M. Ayasse, J. Stökl, and S. Steiger. 2017. Beyond cuticular hydrocarbons: chemically mediated mate recognition in the subsocial burying beetle *Nicrophorus vespilloides*. Journal of Chemical Ecology 43:84–93.

Kocher, S. D., L. Pellissier, C. Veller, J. Purcell, M. A. Nowak, M. Chapuisat, and N. E. Pierce. 2014. Transitions in social complexity along elevational gradients reveal a combined impact of season length and development time on social evolution. Proceedings of the Royal Society B 281:20140627.

Koenig, W. D. 1981. Reproductive success, group size, and the evolution of cooperative breeding in the acorn woodpecker. American Naturalist 117:421–443.

Koenig, W. D., and J. L. Dickinson. 2004. Ecology and evolution of cooperative breeding in birds. Cambridge University Press.

Koenig, W. D., and F. A. Pitelka. 1981. Ecological factors and kin selection in the evolution of cooperative breeding in birds. Pages 261–280 *in* R. D. Alexander and D. W. Tinkle, eds. Natural selection and social behavior: recent research and new theory. Chiron, New York.

Koenig, W. D., F. A. Pitelka, W. J. Carmen, R. L. Mumme, and M. T. Stanback. 1992. The evolution of delayed dispersal in cooperative breeders. Quarterly Review of Biology 67:111–150.

Kokko, H., and J. Ekman. 2002. Delayed dispersal as a route to breeding: territorial inheritance, safe havens, and ecological constraints. American Naturalist 160:468–484.

Komdeur, J., M. J. Schrama, K. Meijer, A. J. Moore, and L. W. Beukeboom. 2013. Cobreeding in the burying beetle, *Nicrophorus vespilloides*: tolerance rather than cooperation. Ethology 119:1138–1148.

Korb, J., and K. R. Foster. 2010. Ecological competition favours cooperation in termite societies. Ecology Letters 13:754–760.

Kramer, B. H., I. Scharf, and S. Foitzik. 2014. The role of per-capita productivity in the evolution of small colony sizes in ants. Behavioral Ecology and Sociobiology 68:41–53.

Lenth, R. V. 2016. Least-squares means: the R package lsmeans. Journal of Statistical Software 69:1–33.

Lin, N., and C. D. Michener. 1972. Evolution of sociality in insects. Quarterly Review of Biology 47:131–159.

Lin, Y.-H., S.-F. Chan, D. R. Rubenstein, M. Liu, and S.-F. Shen. 2019. Resolving the paradox of environmental quality and sociality: the ecological causes and consequences of cooperative breeding in two lineages of birds. American Naturalist 194:207–216.

Liu, M., S.-F. Chan, D. R. Rubenstein, S.-J. Sun, B.-F. Chen, and S.-F. Shen. 2019. Ecological transitions in grouping benefits explain the paradox of environmental quality and sociality. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.ncjsxksqt.

Lukas, D., and T. Clutton-Brock. 2017. Climate and the distribution of cooperative breeding in mammals. Royal Society Open Science 4:160897.

Maynard Smith, J., and E. Szathmary. 1995. The major transitions in evolution. Oxford University Press, New York.

Michener, C. D. 1964. Reproductive efficiency in relation to colony size in hymenopterous societies. Insectes Sociaux 11:317–341.

———. 2000. The bees of the world. Johns Hopkins University Press, Baltimore, MD.

Naug, D., and J. Wenzel. 2006. Constraints on foraging success due to resource ecology limit colony productivity in social insects. Behavioral Ecology and Sociobiology 60:62–68.

Otronen, M. 1988. The effect of body size on the outcome of fights in burying beetles (*Nicrophorus*). Annales Zoologici Fennici 25:191–201.

Pukowski , E. 1933. Ökologische Untersuchungen an *Necrophorus* F. Zeitschrift fur Morphologie und Ökologie der Tiere 27:518–586.

Purcell, J. 2011. Geographic patterns in the distribution of social systems in terrestrial arthropods. Biological Reviews 86:475–491.

R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Robertson, I. C., W. G. Robertson, and B. D. Roitberg. 1998. A model of mutual tolerance and the origin of communal associations between unrelated females. Journal of Insect Behavior 11:265–286.

Rozen, D., D. Engelmoer, and P. Smiseth. 2008. Antimicrobial strategies in burying beetles breeding on carrion. Proceedings of the National Academy of Sciences of the USA 105:17890–17895.

Scott, M. P. 1998. The ecology and behavior of burying beetles. Annual Review of Entomology 43:595–618.

Sheehan, M. J., C. A. Botero, T. A. Hendry, B. E. Sedio, J. M. Jandt, S. Weiner, A. L. Toth, and E. A. Tibbetts. 2015. Different axes of environmental variation explain the presence vs. extent of cooperative nest founding associations in *Polistes* paper wasps. Ecology Letters 18:1057–1067.

Shen, S.-F., E. Akçay, and D. R. Rubenstein. 2014. Group size and social conflict in complex societies. American Naturalist 183:301–310.

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., S. L. Vehrencamp, R. A. Johnstone, H.-C. Chen, S.-F. Chan, W.-Y. Liao, K.-Y. Lin, and H.-W. Yuan. 2012. Unfavourable environment limits social conflict in *Yuhina brunneiceps*. Nature Communications 3:885.

Shukla, S. P., C. Plata, M. Reichelt, S. Steiger, D. G. Heckel, M. Kaltenpoth, A. Vilcinskas, and H. Vogel. 2018. Microbiome-assisted carrion preservation aids larval development in a burying beetle. Proceedings of the National Academy of Sciences of the USA 115:11274–11279.

Silk, J. B. 2007. The adaptive value of sociality in mammalian groups. Philosophical Transactions of the Royal Society B 362:539–559.

Soucy, S. L., and B. N. Danforth. 2002. Phylogeography of the socially polymorphic sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). Evolution 56:330–341.

Stacey, P. B., and W. D. Koenig. 1990. Cooperative breeding in birds: long term studies of ecology and behaviour. Cambridge University Press, Cambridge.

Steiger, S., and J. K. Müller. 2010. From class-specific to individual discrimination: acceptance threshold changes with risk in the partner recognition system of the burying beetle *Nicrophorus vespilloides*. Animal Behaviour 80:607–613.

Steiger, S., K. Peschke, and J. K. Müller. 2008. Correlated changes in breeding status and polyunsaturated cuticular hydrocarbons: the chemical basis of nestmate recognition in the burying beetle *Nicrophorus vespilloides*? Behavioral Ecology and Sociobiology 62:1053–1060.

Sun, S.-J., D. R. Rubenstein, B.-F. Chen, S.-F. Chan, J.-N. Liu, M. Liu, W. Hwang, P.-S. Yang, and S.-F. Shen. 2014. Climate-mediated cooperation promotes niche expansion in burying beetles. eLife 3: e02440.

Tallamy, D. W., and T. K. Wood. 1986. Convergence patterns in subsocial insects. Annual Review of Entomology 31:369–390.

Trumbo, S. T. 1992. Monogamy to communal breeding: exploitation of a broad resource base by burying beetles (*Nicrophorus*). Ecological Entomology 17:289–298.

———. 1995. Nesting failure in burying beetles and the origin of communal associations. Evolutionary Ecology 9:125–130.

Wcislo, W. T. 1997. Behavioral environments of sweat bees (Halictinae) in relation to variability in social organization. Pages 316–332 *in* J. C. Choe and B. Crespi, eds. The evolution of social behaviour in insects and arachnids. Cambridge University Press, Cambridge.

Wcislo, W. T., and S. M. Tierney. 2009. The evolution of communal behavior in bees and wasps: an alternative to eusociality. Pages 148–169 *in* J. Gadau and J. Fewell, eds. Organization of insect societies from genome to sociocomplexity. Harvard University Press, Cambridge, MA.

Wenzel, J. W., and J. Pickering. 1991. Cooperative foraging, productivity, and the central limit theorem. Proceedings of the National Academy of Sciences of the USA 88:36–38.

West, S. A., R. M. Fisher, A. Gardner, and E. T. Kiers. 2015. Major evolutionary transitions in individuality. Proceedings of the National Academy of Sciences of the USA 112:10112–10119.

Wilson, E. O. 1975. Sociobiology: the new synthesis. Harvard University Press, Cambridge, MA.

———. 2008. One giant leap: how insects achieved altruism and colonial life. Bioscience 58:17–25.

Yip, E. C., K. S. Powers, and L. Avilés. 2008. Cooperative capture of large prey solves scaling challenge faced by spider societies. Proceedings of the National Academy of Sciences of the USA 105:11818–11822.

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