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A Simple Behavioral Model Predicts the Emergence of Complex Animal Hierarchies

Takao Sasaki,[1,2,*,†] **Clint A. Penick,**[1,3,†] **Zachary Shaffer,**[1] **Kevin L. Haight,**[1] **Stephen C. Pratt,**[1] **and Jürgen Liebig**[1,‡]

1. School of Life Sciences and Center for Social Dynamics and Complexity, Arizona State University, Tempe, Arizona 85287; 2. Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, United Kingdom; 3. Department of Applied Ecology and Keck Center for Behavioral Biology, North Carolina State University, Raleigh, North Carolina 27695

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ABSTRACT: Social dominance hierarchies are widespread, but little is known about the mechanisms that produce nonlinear structures. In addition to despotic hierarchies, where a single individual dominates, shared hierarchies exist, where multiple individuals occupy a single rank. In vertebrates, these complex dominance relationships are thought to develop from interactions that require higher cognition, but similar cases of shared dominance have been found in social insects. Combining empirical observations with a modeling approach, we show that all three hierarchy structures—linear, despotic, and shared—can emerge from different combinations of simple interactions present in social insects. Our model shows that a linear hierarchy emerges when a typical winner-loser interaction (dominance biting) is present. A despotic hierarchy emerges when a policing interaction is added that results in the complete loss of dominance status for an attacked individual (physical policing). Finally, a shared hierarchy emerges with the addition of a winner-winner interaction that results in a positive outcome for both interactors (antennal dueling). Antennal dueling is an enigmatic ant behavior that has previously lacked a functional explanation. These results show how complex social traits can emerge from simple behaviors without requiring advanced cognition.

Keywords: dominance hierarchy, winner-loser effect, agent-based model, social insects, policing, reproductive conflict.

Introduction

Since Schjelderup-Ebbe (1922) first described the pecking order of chickens, there has been sustained interest in how animal interactions lead to the formation of dominance hierarchies. Like the pecking order, the most explored dominance structure has been the linear hierarchy, where each group member occupies a single rank and is subordinate to those ranked above them and dominant to those ranked below (Chase and Seitz 2011). However, not all hierarchies in nature are linear. For example, there are despotic hierarchies, where a single individual monopolizes power over a group of subordinates (Uhrich 1938; Kinsey 1976; Deslippe et al. 1990), and shared dominance structures, where multiple individuals occupy a single rank (Harcourt and de Waal 1992). Although linear and despotic hierarchies have received the most attention, shared dominance is commonly found in human groups (e.g., egalitarianism in hunter-gatherers; Cashdan 1980; Woodburn 1982; Harcourt and de Waal 1992; Boehm 2009) and other social animals (e.g., alliances and coalitions in primates [Harcourt and de Waal 1992; Watts 1998; Boehm 2009], lions [Bygott et al. 1979; Packer et al. 1991], dolphins [Connor et al. 1992, 2001], hyenas [Zabel et al. 1992], and mongooses [Waser et al. 1994]).

Theoretical models of hierarchy formation in vertebrates often take into account the advanced cognitive abilities of group members, such as individual recognition and memory of past interactions (Bond et al. 2004; Dugatkin and Earley 2004; Silk 2007). These abilities seem especially pertinent to shared hierarchy structures, including alliances and coalitions, where group members are involved in complex social relationships (Harcourt and de Waal 1992; Connor et al. 2001; Brosnan and de Waal 2002). However, shared hierarchies have also been observed in invertebrate species that lack these cognitive abilities, including social insects (Heinze et al. 1994; Hölldobler and Wilson 2009). Rather than advanced cognition of individual group members, complex collective patterns in social insects often arise from simple interactions among individuals (Bonabeau et al. 1997).

In this study, we investigated how complex dominance hierarchies could emerge in social insects without requiring advanced cognition. To this end, we developed an agent-

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[*] Corresponding author; e-mail: takao.sasaki@zoo.ox.ac.uk.

[†] These authors contributed equally to this work.

[‡] ORCID: Sasaki, http://orcid.org/0000-0002-4409-7655.

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based model, a computer simulation that can be used to explore how group-level patterns emerge from individual behaviors (Hogeweg and Hesper 1990; Bonabeau 2002), including the establishment of dominance hierarchies (Hemelrijk 1999; Bryson et al. 2007). Our model was closely based on empirical studies of the ant *Harpegnathos saltator*, whose workers establish a shared hierarchy for reproductive rights. Unlike most ant species, workers of *H. saltator* retain the ability to mate and reproduce. Workers initiate a tournament after the death of their queen or when her fertility wanes to establish a group of equally ranked reproductive individuals termed "gamergates" (Peeters and Hölldobler 1995; Liebig et al. 1999; Hölldobler and Wilson 2009). During tournaments, workers display three distinct agonistic interactions: dominance biting, physical policing, and antennal dueling (fig. A1; figs. A1–A6 and tables A1, A2 are available online).

While linear and despotic hierarchies may emerge from typical dominance behaviors (Dugatkin 1997; Hemelrijk 1999), the formation of shared dominance structures may require qualitatively different behavioral interactions. Typical dominance behaviors result in winner-loser effects, where winning or losing an interaction results in endocrine changes that influence an individual's performance in future interactions (Oyegbile and Marler 2005; Trainor et al. 2006; Oliveira et al. 2009; Rillich and Stevenson 2011). In contrast, antennal dueling does not result in a clear winner or loser (Hölldobler and Wilson 2009) and is performed most frequently among future dominants (Liebig et al. 2000; Penick et al. 2014). Rather than a winner-loser effect, antennal dueling may result in a winner-winner effect, where both individuals exhibit endocrine changes associated with winning an interaction. There is evidence that this may be the case in *H. saltator*, where dueling individuals exhibit an increase in dopamine, a neurohormone associated with dominance and reproduction in this species (Penick et al. 2014).

We used our model to test how different combinations of dominance interactions present in *H. saltator* could result in linear, despotic, or shared hierarchies. We predicted that a shared hierarchy would emerge only with the addition of antennal dueling, which we characterized as a winner-winner interaction. We then varied the outcome of dueling in our model to test whether a shared hierarchy could still emerge if dueling resulted in a loser-loser or a winner-loser interaction. To validate the model, we further conducted observations of actual *H. saltator* tournaments in the lab. Finally, we conducted a literature review of dominance hierarchies in other ant species to determine whether dueling was associated with shared dominance outside *H. saltator*. While our model was developed specifically to investigate dominance in social insects, we discuss how our model could apply to other species, including those where advanced cognition may play an additional role.

Methods

Focal Species

Our model was based on dominance interactions in colonies of the ant *Harpegnathos saltator*, whose workers establish a shared hierarchy for reproductive dominance. *Harpegnathos saltator* is a member of the ant subfamily Ponerinae and occurs throughout southern India and other tropical regions of southeast Asia (Jerdon 1854). In most ant species, workers are either sterile or only capable of producing male offspring from unfertilized eggs due to their inability to mate and store sperm (Hölldobler and Wilson 1990). Workers of *H. saltator*, however, have regained the ability to mate and can take on the reproductive role in their colony after the death of their queen (Peeters and Hölldobler 1995). New colonies are founded by a single queen that is usually replaced after several years by a group of reproductive workers (gamergates) that compete in a months-long tournament to establish a shared hierarchy. Once established, gamergates maintain their status through the production of a chemical fertility signal, and aggression is greatly reduced or absent (Liebig et al. 2000). Workers mate with their brothers inside the nest, and while both subordinate and dominant workers are often mated, only dominant individuals actively reproduce (Peeters et al. 2000). Workers engage in three primary dominance interactions during their tournaments—antennal dueling, dominance biting, and physical policing—which served as the basis for the dominance interactions used in our model (table 1).

Model Description

Agents had only one variable, social status (s), equivalent to the ovarian status in a worker of *H. saltator* (Liebig et al. 1999). Social status was modeled as a real number but could be used to categorize agents into two distinct classes: an individual with $s \leq 0$ would be classified as "subordinate," while an individual with $s > 0$ would be classified as a "potential dominant." An agent that became subordinate at any point during a simulation would remain subordinate through the end of that simulation.

An agent's social status gradually increased over time (i.e., individuals left alone would slowly increase their ovarian development), which naturally occurs when single *H. saltator* workers are isolated (Liebig et al. 1998). The growth rate (GR)—the increment of the agent's social status in each time step of the simulation—was expressed as $\text{GR} = \exp(-s/300)$ for $s > 0$ and as $\text{GR} = 0$ for $s \leq 0$ (fig. A2*A*). Under this function, a subordinate's social status does not change over time, while that of a potential dominant increases but eventually saturates. This function was based on empirically measured ovarian development in *H. saltator* workers after established dominant individuals were removed (fig. A3).

Table 1: Description of dominance interactions and implications for model parameters

Interaction	Description	Natural consequence	Model consequence
Dominance biting	Dominant bites subordinate and pushes head down one to several times	Subordinate loses dominance standing but may still become a gamergate	Potential dominant: +10, subordinate: –10
Physical policing	Subordinate bites and holds potential dominant	Potential dominant is reduced to complete subordinate	Potential dominant: loses all status points
Antennal dueling	Two potential dominants lunge back and forth, rapidly beating antennae	Both individuals continue dueling; there is no clear winner or loser	Both dominants: +1

Social status could also be changed as a consequence of interaction between agents. If two or more agents were sufficiently close (within one patch of each other), each of them had an opportunity to initiate an interaction. An agent's probability of initiation (P_{int}) was determined as $P_{\text{int}} = \exp(-s/30)$ for $s > 0$ and as $P_{\text{int}} = 0$ for $s = 0$. Thus, the probability of an interaction was determined solely by the initiator's social status: potential dominants ($s > 0$) became less likely to interact with others as their status increased (fig. A2*B*); subordinates ($s = 0$) never initiated interactions. This function produced a collective pattern that closely matched empirical observations (see "Results" for details). Once an agent decided to initiate, it would interact with a single agent chosen randomly from all those lying within one patch distance. After the interaction, the partners each moved one patch in opposite directions to avoid continuous interactions between the same agents.

Agents chose from three types of interaction corresponding to natural behaviors observed in *H. saltator*: dominance, policing, and antennal dueling (table 1; fig. A1). Dominance represented a typical agonistic behavior where one individual bites a subordinate and there is a clear winner and loser. In the model, the winner gained 10 points of social status, and the loser deducted 10 points. Policing corresponded to a natural behavior where a subordinate individual bites and holds a potential dominant for up to several hours (Liebig et al. 1999). Once an individual has been policed in *H. saltator*, her ovarian development is inhibited and reversed, and her chances of attaining gamergate status are greatly reduced if not completely eliminated (Penick et al. 2014). In the model, policed agents became subordinates (i.e., social status was lowered to 0). Finally, agents in our model could choose a reciprocal interaction that corresponded with antennal dueling (Heinze et al. 1994; Liebig et al. 1999). This behavior consists of multiple alternating bouts of rapid antennal beating back and forth between two individuals and does not result in a clear winner or loser (Heinze et al. 1994; Liebig et al. 1999; Gobin et al. 2001). For the model, we assumed that dueling produces a winner effect in both interacting agents, with each one gaining 1 point of social status (we tested this assumption in additional simulations described below).

An agent's choice of interaction depended on its own social status and that of its partner. If both were potential dominants and their social status differed by less than 30 points, they would engage in reciprocal dueling; if their status differed by 30 or more points, the agent with higher status would dominate the other one. Alternatively, if one partner was a potential dominant and the other a subordinate, the subordinate would police the potential dominant with a probability determined solely by the potential dominant's social status. Specifically, $P_{\text{policed}} = \exp(-s/15)$ for $s > 0$, and $P_{\text{policed}} = 0$ for $s = 0$, where s denotes the potential dominant's social status (fig. A2*C*). Thus, the higher the social status of a potential dominant, the less likely it was to be policed (see "Model Validation" below).

Subordinates and potential dominants followed different movement patterns in the model. During each time step, subordinates moved one patch in a random direction between –40 and +40 degrees; potential dominants moved one patch per time step as well, but they moved toward or within the area of the brood pile in the center of the simulated nest. This difference made dominant individuals more likely to interact with each other than with subordinates, which was similar to natural colonies of *H. saltator*, where dominant individuals aggregate near the brood pile (J. Liebig and C. A. Penick, personal observation).

Model Simulations. At the start of a simulation, 100 agents were randomly placed in an environment consisting of a 20 × 20 grid of patches with a central 2 × 2-patch region representing the brood pile. Each agent was randomly assigned a social status drawn from a normal distribution with a mean of 5 and a standard deviation of 3. This variation was similar to the natural condition in ants where individuals differ in their ability to activate their ovaries (Liebig et al. 1998) and the potential to become reproductive generally decreases with worker age (Tsuji and Tsuji 2005). An overview of the decision-making process is shown as a decision tree in figure A4.

To test the roles of dominance biting, physical policing, and antennal dueling in the establishment of a dominance hierarchy, we ran simulations under three conditions differing in the interactions available to agents: (1) only dominance, (2) dominance and policing, and (3) dominance, policing, and dueling. For each condition, we ran 100 simulations, each lasting 10,000 time steps. Because hierarchies usually became stable after 5,000 time steps, the duration was adequate to verify establishment of a hierarchy. At the end of each simulation, we measured the distribution of social status across agents. To compare the distribution across trials, social status was standardized in each simulation by dividing each agent's status by the highest status observed in that simulation.

Next, we varied the outcome of dueling to test whether it must result in a winner-winner effect for a shared hierarchy to emerge. We ran the model using the conditions described above but changed the outcome of dueling to either a loser-loser interaction (a decrease in social status of 1 point for both interactors) or a winner-loser interaction (a gain of 2 points for the winner and a decrease of 2 points for the loser). For the latter condition, we ran the simulation with and without policing. Each simulation ran 5,000 time steps and was repeated 100 times for each test.

Finally, we tested how variation in the strength of policing could influence hierarchy length by varying the number of status points deducted from a policed individual from 0 points (no policing) to 40 points at 1-point intervals. We then quantified the number of dominant individuals at the end of each simulation (number of individuals with social status > 0). Each simulation ran for 5,000 time steps and was repeated 100 times for each value of policing.

Model Validation

We conducted observations of actual *H. saltator* tournaments in the lab to compare with results from our model simulations. Colonies of *H. saltator* were originally collected from southern India in Karnataka State between 1994 and 1999 (described in Peeters et al. 2000) and have been continuously bred in the lab since that time. Colonies were reared at a constant temperature of 25°C on a 12L∶12D cycle. Colonies were fed biweekly with live crickets (*Acheta domesticus*) and housed in plastic boxes (19 cm × 27 cm) with a dental plaster floor and preformed nest cavity covered by a glass plate (12 cm × 15 cm). We selected five colonies (median colony size: 84 individuals, range: 81–154) that each had a stable dominance hierarchy (i.e., no dominance biting or policing was observed). First, we identified gamergates based on behavioral observations (described in Liebig et al. 1999; Penick et al. 2011, 2014) and determined the ratio of gamergates to workers. We then removed all gamergates to induce a dominance tournament. To get comparable sizes across colonies, worker number was reduced in larger colonies so that colony size ranged between 69 and 80 workers. During tournaments, we quantified the frequency of dominance biting, policing, and antennal dueling during 5-min observation sessions each day for days 1–10 and once every other day for days 11–40 using ad lib. sampling between 2 and 5 h after lights were switched on. After 106 days, we determined the number of gamergates by identifying the individuals that continued to duel; we then dissected these individuals and confirmed that all of them had fully active ovaries (i.e., a succession of yolky oocytes in their ovarioles, including large and mature ones, which is a clear indication of gamergate status; see also Liebig et al. 1999).

Literature Review

We conducted a literature review of ant species that form linear, despotic, and shared hierarchies and cataloged the behaviors involved in dominance interactions. Hierarchy structure and presence/absence of dueling were mapped onto recent phylogenies (Moreau and Bell 2013; Schmidt 2013) and compared with patterns found in our model. We focused on species from the ant subfamilies Ponerinae and Ectatomminae and excluded cases where hierarchy structure or dominance behaviors were not clearly described. Terms for ant dominance interactions have not always been applied consistently in the literature, so we have defined "antennal dueling" here as a bidirectional interaction that involves bouts of rapid antennation back and forth between two or more individuals. This contrasts with "antennal boxing" or "antennal beating," which have been used to describe unidirectional bouts of rapid antennation directed by one individual toward another individual without reciprocation (e.g., Peeters and Tsuji 1993; Sommer et al. 1994; Monnin and Peeters 1999).

Model Package and Statistical Analysis

Our model was created in NetLogo, version 5.2.1 (Wilensky 1999), and is available at OpenABM (https://www.openabm.org/model/4841/version/1/view). Data were analyzed via the Kruskal-Wallis test and linear regression using the statistical package R, version 3.2.1. Both behavioral and model data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.sd370 (Sasaki et al. 2016).

Results

Emergence of Linear, Despotic, and Shared Hierarchies

When dominance biting was the only option in the model, a hierarchy emerged with dominant individuals distributed from the highest social position down to the level of subordinate workers, suggesting a near-linear structure (fig. 1*A*).

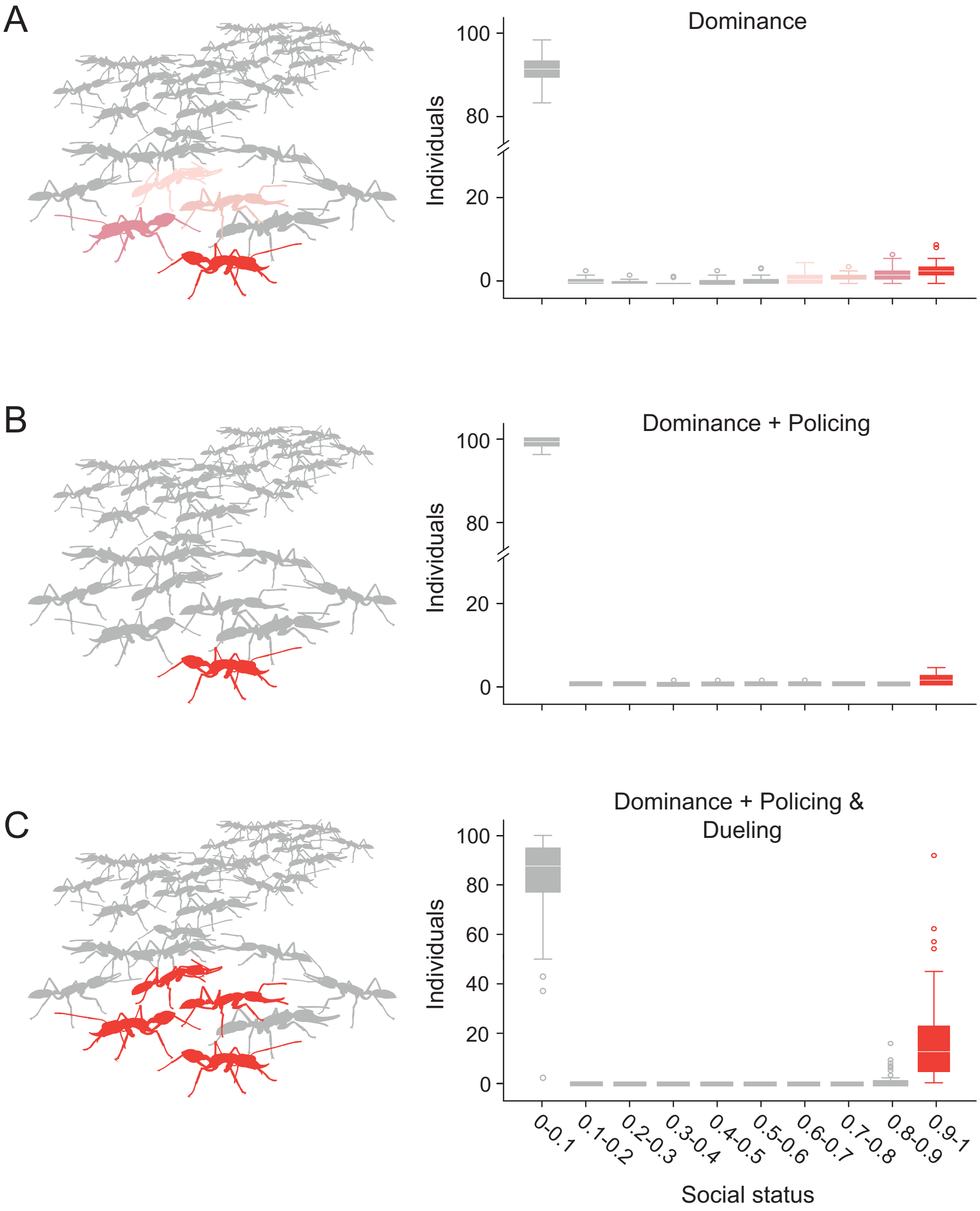

Figure 1: Three distinct hierarchies emerged from different combinations of dominance behaviors. *A*, When only dominance biting was present, a near-linear hierarchy emerged. *B*, When dominance biting and policing were present, a despotic hierarchy emerged with one dominant individual. *C*, When dueling was present with dominance biting and policing, a shared hierarchy emerged with multiple, equally ranked dominant individuals. Boxes delimit the first and third quartiles, the horizontal line indicates the median, and whiskers show the range (circles are outliers). The social status was standardized in each simulation by dividing each status by the highest status, which thus always had a value of 1.

The addition of policing resulted in a despotic hierarchy where only one individual was dominant and all others were subordinate (fig. 1*B*). When dueling was added, a shared hierarchy emerged with a small group of dominant individuals and all others subordinate (fig. 1*C*), which is the organizational structure that most closely matches that of *Harpegnathos saltator*.

Antennal Dueling as a Winner-Winner Effect

In line with predictions, only when dueling resulted in a positive outcome for both interactors (winner-winner effect) did a shared hierarchy emerge (fig. 2). If the outcome of dueling resulted in a negative outcome for both interactors (loser-loser effect), the hierarchy was destabilized, and no indi-

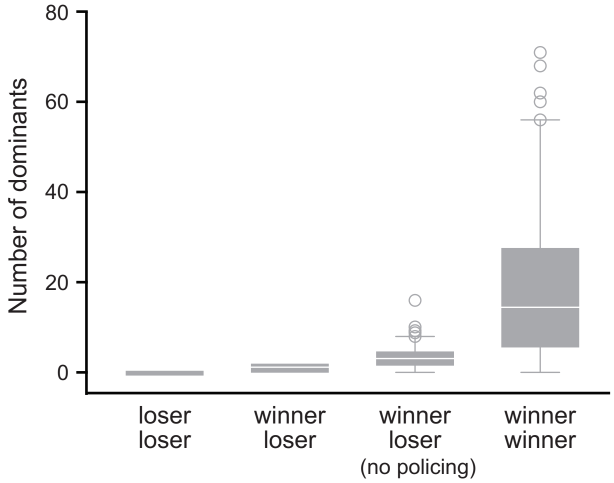

Figure 2: Antennal dueling as a winner-winner interaction. The number of individuals that achieved dominant status (social status between 0.9 and 1.0) when dueling was modeled as a loser-loser, winner-loser (with and without policing included), or winner-winner interaction. Only when dueling resulted in a positive outcome for both interactors did a shared hierarchy emerge with multiple dominant individuals of similar rank. Boxes delimit the first and third quartiles, the horizontal line indicates the median, and whiskers show the range (circles are outliers). The number of dominants in each trial differed between all treatments, with $p < .005$.

viduals became dominant. When the outcome was changed to a positive-negative interaction (winner-loser effect), this resulted in a despotic hierarchy with a single dominant individual when policing was present and a linear hierarchy when policing was absent. The number of dominant individuals (social status 0.9–1.0) differed between groups (Kruskal-Wallis: df $= 3$, $N = 400$, $H = 249.6$, $p < .0001$), and pairwise differences were all significant ($p < .005$; table A1).

Strength of Policing and Hierarchy Length

As the strength of policing increased in our model, the length of the hierarchy (i.e., the number of dominant individuals) decreased (linear regression: $N = 21$, $F = 3{,}591$, $p < .0001$; fig. 3*A*). In all cases, the hierarchy was linear until policing resulted in a deduction of over 40 points, after which the hierarchy became despotic, with a single reproductive individual (fig. 3*B*). Variation in policing behavior is present in natural colonies (e.g., mutilation [Peeters and Higashi 1989] vs. biting and holding [Cuvillier-Hot et al. 2004*b*]) and may explain the different lengths of hierarchies observed in these species.

Model Validation

The frequency of dominance biting, policing, and dueling was similar in model simulations (fig. A5) compared to actual *H. saltator* tournaments (fig. A6). In general, there was a sharp increase in aggression at the start of a tournament, followed by an exponential decline. Dueling was the most common dominance behavior (85.7% of interactions in actual tournaments; 86.2% in model results), fol-

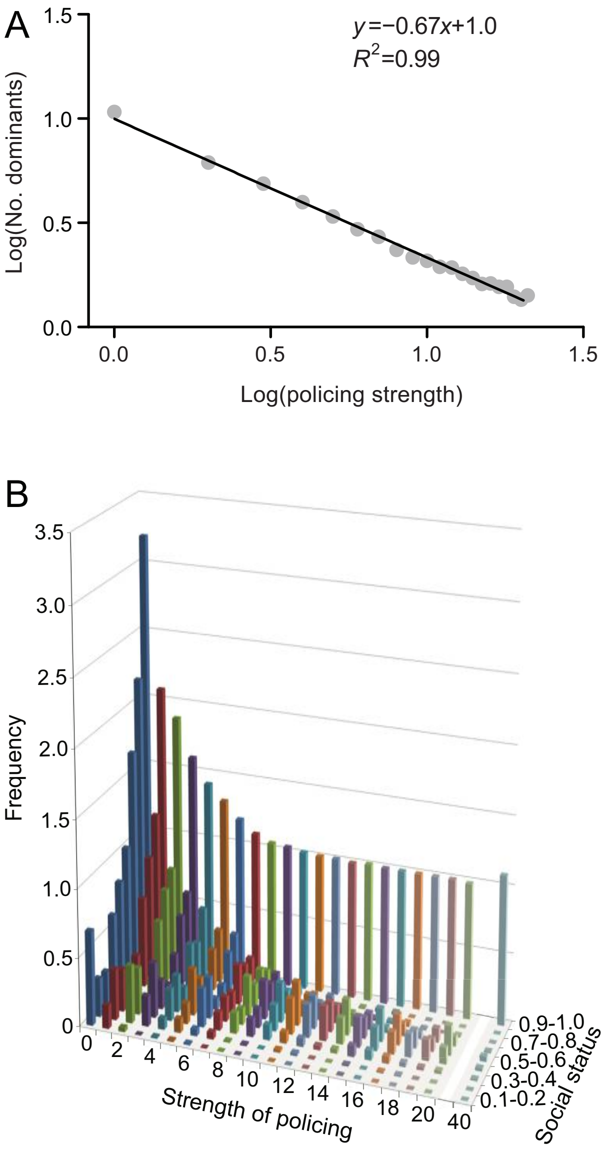

Figure 3: Influence of policing strength on hierarchy length. *A*, As the strength of policing increased, the number of dominants (social status greater than 0) decreased significantly. The graph plots log-transformed data; a value of 1 was added to all points for policing strength to eliminate 0 values. *B*, The frequency of individuals in each social status in a trial, with different values for policing strength (subordinates are not shown). The total number of individuals in the hierarchy declined with increased policing strength, eventually reaching a despotic hierarchy with only one reproductive (where policing strength was 40 or above).

lowed by dominance biting (10.3% and 10.0%) and policing (4.0% and 3.8%). Although when compared to the original size of the worker groups the proportion of newly established gamergates (median: 4%, range: 1%–10%) was lower than our simulated proportion (median: 12%), the gamergate proportion (median: 12%, range: 2%–21%) 3.5 months after gamergate removal was close to our simulated result. This was higher than the proportion of gamergates in colonies initially (median: 7.4%, range: 2.3%–8.4%). During our experimental period of 3.5 months, colony size dropped by 53%, which is consistent with laboratory life span of nonreproductive workers under absence of new worker production (median: 206 days; Haight 2012).

Association between Antennal Dueling and Shared Hierarchies in Ants

Including *H. saltator*, antennal dueling was described in six ant species across three genera (*Harpegnathos*, *Gnamptogenys*, and *Rhytidoponera*; Ward 1983, 1986; Peeters and Hölldobler 1995; Gobin et al. 2001), and the presence of dueling was associated with a shared hierarchy in every case (fig. 4). For nine ant species that formed linear hierarchies (Oliveira and Hölldobler 1990; Ito and Higashi 1991; Ito 1993; Heinze and Hölldobler 1995; Liebig et al. 1997; Monnin and Peeters 1999; Monnin et al. 2003; Cuvillier-Hot et al. 2004*a*) and three that formed despotic hierarchies (Peeters and Higashi 1989; Peeters et al. 1992; Peeters and Tsuji 1993; Cuvillier-Hot et al. 2002; Cournault and Peeters 2012), no cases of dueling were reported (table A2). A similar behavior, antennal boxing, may occur in these species, but this behavior is unidirectional and involves a dominant individual boxing a subordinate (antennal boxing has been used in the past to describe behaviors we classify here as antennal dueling [Gobin et al. 2001]; we have recategorized this as antennal dueling when the behavior is bidirectional, as described for *H. saltator* by Heinze et al. [1994] and defined by Liebig et al. [2000]).

A despotic hierarchy was found in only one genus: *Diacamma*. In this genus, subordinate workers are physically mutilated to prevent reproduction, which is similar to strong policing in our model (but mutilation is performed by the unmutilated alpha worker against her subordinates in *Diacamma*). In one *Diacamma* species, most workers remain unmutilated and develop despotic hierarchies with policing and dominance biting involved (Cournault and Peeters 2012), while there are other cases where workers establish a linear hierarchy before an unmutilated alpha is produced (Sommer et al. 1993; Shimoji et al. 2014). Despite the diversity of dominance structures described in *Diacamma*, the presence of standard dominance behaviors and policing always leads to despotic or linear hierarchies, similar to our model outcomes.

Discussion

Complex dominance hierarchies have been described in societies of both vertebrate and invertebrate species. In ver-

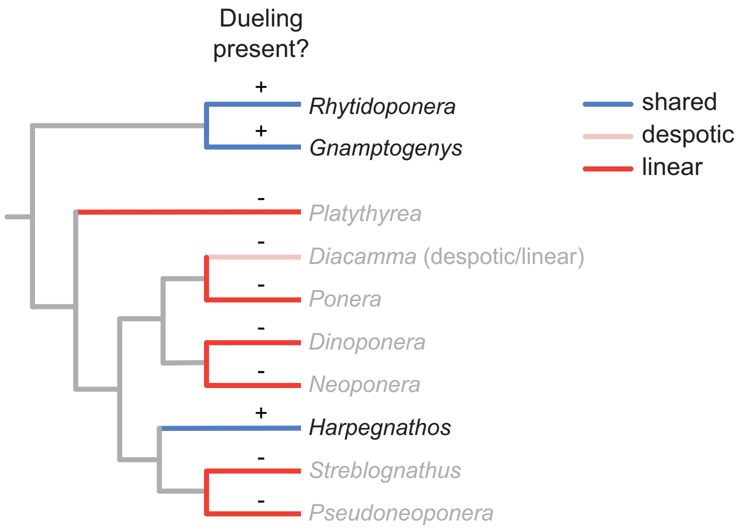

Figure 4: Relationship between ant hierarchy type (linear, despotic, or shared) and the presence/absence of dueling. Dueling was documented in three ant genera, all of which displayed shared dominance. Only one genus, *Diacamma*, displayed a despotic hierarchy, but colonies may initially pass through a linear stage before a single reproductive is established. Branch color indicates hierarchy structure, and the presence (plus sign) or absence (minus sign) of dueling is labeled. Phylogeny modified from Moreau and Bell (2013) and Schmidt (2013).

tebrates, these dominance relationships are thought to develop from interactions that require advanced cognition, but we show here that similar dominance structures could emerge from a mix of simple interactions found in social insects. This includes shared dominance, which emerged only when a winner-winner interaction was included in the model that resulted in a positive outcome for both interactors. This behavior corresponds with antennal dueling in ants, which differs from standard dominance interactions in that it does not result in a clear winner or loser. Winner-winner interactions like antennal dueling may provide an alternative path to shared dominance, compared with interactions that require advanced cognition.

When dueling was not included in the model, either a linear or a despotic hierarchy emerged, depending on which of the other two interactions was present. Dominance biting represented a standard winner-loser interaction that produced a linear hierarchy when it was the only interaction included in the model. This was consistent with previous models that have investigated winner-loser interactions in the context of hierarchy formation (Dugatkin 1997; Beacham 2003; Dugatkin and Earley 2004; Hock and Huber 2009). When physical policing was added to the model, it shifted the hierarchy toward despotism to a degree that depended on the relative strength of policing. Policing is distinct from dominance biting in that a subordinate individual bites and holds a potential dominant, sometimes also called "immobilization" behavior (Kawabata and Tsuji 2005), which decreases their social status (the social status of the subordinate remains unchanged). When policing resulted in the complete loss of social status for a policed individual, a despotic hierarchy emerged with a single dominant. This is similar to the establishment of a despotic hierarchy in ants of the genus *Diacamma*, where subordinate individuals are physically mutilated to prevent reproduction (an extreme form of policing; Peeters and Higashi 1989; Peeters et al. 1992; Sommer et al. 1993). When the strength of policing was relaxed, a linear hierarchy emerged, with an increase in hierarchy length associated with a decrease in policing strength. In ant species that display differences in hierarchy length (Monnin et al. 2003), variation in policing strength could serve as a proximate mechanism to regulate the number of individuals in a hierarchy.

The addition of antennal dueling to the model produced a shared hierarchy, but only when dueling resulted in a positive outcome for both interactors (i.e., a winner-winner effect). If the outcome of dueling was changed to produce either a winner-loser or a loser-loser effect, a shared hierarchy no longer emerged. Like standard winner-loser effects, winner-winner effects may be mediated by endocrine changes that affect an individual's performance in future interactions (Oyegbile and Marler 2005; Trainor et al. 2006; Oliveira et al. 2009; Rillich and Stevenson 2011). In *Harpegnathos saltator*, dopamine could potentially serve this role. High dopamine levels are correlated with dominance and reproduction in *H. saltator*, and dopamine levels rise in individuals that begin dueling (Penick et al. 2014). In contrast, dopamine levels fall in response to policing, which may represent a loser effect.

The connection between antennal dueling and shared dominance was supported by observations of hierarchies in other ant species. Antennal dueling has been documented outside of *H. saltator* in species found in two ant genera (*Gnamptogenys* and *Rhytidoponera*) that also establish shared hierarchies (Ward 1983, 1986; Gobin et al. 2001). When mapped onto the current ant phylogeny, antennal dueling and shared hierarchies appear to have evolved together at least two times independently. In contrast, antennal dueling was not found in ant species that form linear or despotic hierarchies. Species that do not form shared hierarchies may display antennal boxing, a behavior similar to dueling, but antennal boxing is performed by a dominant individual toward a subordinate and resembles a standard winner-loser interaction (Hölldobler and Wilson 2009). This is also true for wasps that establish linear hierarchies, where common behaviors used in dominance tournaments (e.g., biting, sting threats, and falling fights) also resemble standard winner-loser interactions (Ross and Matthews 1991).

To our knowledge, this is the first study investigating winner-winner effects in the context of hierarchy formation. In *H. saltator*, antennal dueling is a ritualized agonistic interaction that is likely derived from antennal boxing. The aggressive nature of dueling differs from behaviors in vertebrates that promote shared dominance, such as negotiation and bargaining behaviors (McNamara et al. 1999; Binmore 2010; Cant 2011), which tend to reduce aggression. Instead, dueling allows dominant individuals to express aggression without inducing a cost to the receiving individual. Research on wasps has found that aggression may stimulate ovarian activity, and dominant wasps that are prevented from engaging in aggressive interactions take longer to begin laying eggs (Lamba et al. 2007). If a similar relationship between aggression and ovarian activity is present in ants, then dueling may help stimulate reproductive activity in rising dominant individuals that engage in frequent dueling with each other.

So what might winner-winner interactions look like in other animal species? Using antennal dueling as a model, we propose three criteria: winner-winner interactions (1) should be performed in the context of dominance tournaments, (2) should not result in a clear winner or loser, and (3) should not impose a net cost on the receiver. In ants, our literature review showed that antennal dueling may function as a winner-winner effect in at least two unrelated groups, and similar antennal beating behaviors occur in wasps, though their function has not been associated with emergence of shared dominance (Jeanne 2009; Suryanarayanan et al. 2011). While not yet formally studied, agonistic behaviors in vertebrate groups also meet some of our criteria, such as ritualized aggression in the form of threat displays (Hurd and Enquist 2001). Future studies of dominance interactions in animals should consider the potential of winner-winner interactions in other systems as well as additional mechanisms that could lead to shared dominance.

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Indian jumping ant workers (*Harpegnathos saltator*) policing their nest mate. Photo credit: Clint A. Penick.