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ORIGINAL ARTICLE

Data-Based Analysis of Winner-Loser Models of Hierarchy Formation in Animals

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Abstract We review winner-loser models, the currently popular explanation for the occurrence of linear dominance hierarchies, via a three-part approach. (1) We isolate the two most significant components of the mathematical formulation of three of the most widely-cited models and rigorously evaluate the components' predictions against data collected on hierarchy formation in groups of hens. (2) We evaluate the experimental support in the literature for the basic assumptions contained in winner-loser models. (3) We apply new techniques to the hen data to uncover several behavioral dynamics of hierarchy formation not previously described. The mathematical formulations of these models do not show satisfactory agreement with the hen data, and key model assumptions have either little or no conclusive support from experimental findings in the literature. In agreement with the latest experimental results concerning social cognition, the new behavioral dynamics of hierarchy formation discovered in the hen data suggest that members of groups are *intensely* aware both of their own interactions as well as interactions occurring among other members of their group. We suggest that more adequate models of hierarchy formation should be based upon behavioral dynamics that reflect more sophisticated levels of social cognition.

Keywords Dominance hierarchy formation · Winner-loser models · Social networks · Social cognition · Linear hierarchies

1. Introduction

Linear dominance hierarchies occur in small groups across a broad range of species: insects, crustaceans, fish, birds, and mammals, including humans (Addison and Simmel, 1970; Barkan et al., 1986; Goessmann et al., 2000; Hausfater et al., 1982; Heinze,

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1990; Nelissen, 1985; Post, 1992; Savin-Williams, 1980; Vannini and Sardini, 1971; Wilson, 1975). In a linear hierarchy, one individual dominates all the others, i.e., is aggressive toward them, while receiving little aggression in turn; a second dominates all but the first, and so on. Mathematically, the relationships in a linear hierarchy can be described as a tournament graph (a complete oriented graph that contains no directed cycles) (Skiena, 1990). Hierarchical rank mediates many aspects of individuals' lives including physiology, reproduction, susceptibility to diseases, and access to scarce resources (Clutton-Brock et al., 1984; Ellis, 1995; Holekamp and Smale, 1993; Post, 1992; Raleigh et al., 1991; Sapolsky and Share, 1994).

In spite of their biological importance and their unique form as social structures, it is still not clear what accounts for the linear structure of dominance hierarchies. An earlier view assumed that these linear structures were simply reflections of linear rankings on attributes associated with dominance ability (e.g., some combination of traits like weight, aggressiveness, genotype, and hormonal profiles) that the animals had prior to joining a group (Beaugrand and Cotnoir, 1996; Cloutier et al., 1996; Drews, 1993; Ellis, 1995; Jackson, 1988; Jackson and Winnegrad, 1988; Slater, 1986; Wilson, 1975). However, theoretical work indicates that stringent, but not always recognized, mathematical requirements must be met in order for this view to be correct (Chase, 1974; Landau, 1951), and recent experimental work demonstrates that differences in prior attributes cannot generally account for linear structures (Chase et al., 2002).

The current view, which is based upon earlier studies of interaction sequences during hierarchy formation (Chase, 1982, 1985; Chase and Rohwer, 1987), suggests that linear hierarchy structures arise from series of pair-wise interactions involving winner and loser effects (Bakker et al., 1989; Bakker and Sevenster, 1983; Beacham, 1988; Beacham and Newman, 1987; Burke, 1979; Chase et al., 1994; Drummond, 2006; Drummond and Canales, 1998; Drummond and Osorno, 1992; Francis, 1983, 1987; Frey and Miller, 1972; Hsu and Wolf, 1999; Zucker and Murray, 1996). In a winner effect, an individual winning a contest increases its ability to win a subsequent contest; in a loser effect, an individual losing a contest decreases its ability to win a subsequent dominance encounter. A number of recent models incorporating these effects do produce highly linear structures (Beacham, 2003; Bonabeau et al., 1996, 1999; Dugatkin, 1997; Hemelrijk, 1999, 2000; Skvoretz et al., 1996). We have learned a great deal from these models, and they have motivated and advanced the study of the behavioral mechanisms that generate dominance hierarchies.

In this paper, we evaluate winner-loser models as explanations for the occurrence of linear dominance hierarchies. We consider, as standards, three widely cited winner-loser models (Bonabeau et al., 1999; Dugatkin, 1997; Hemelrijk, 2000). Among the contributions of this body of work, the Bonabeau et al. and Hemelrijk models investigate the possibility that hierarchies may arise from simple, self-organizing processes involving feedback from previous wins and losses. Hemelrijk's model in particular explores the possibility of accounting for social complexity, such as spatial patterns among members of hierarchies and the propensity of animals of similar rank to engage in frequent aggression, on the basis of animals acting as agents following a few simple rules. Dugatkin's model shows how assessment of the costs and benefits of one's own resource holding power, and/or that of others, in the light of winner and/or loser effects can produce different kinds of hierarchy structures, including linear ones.

The papers describing these models suggest additional experimental and observational work to evaluate their formulations and to further unravel the mystery behind the formation of linear hierarchies. We now have a sufficient body of research on dominance with which to do so. In this paper, we test the mathematical formulations that these models use and the assumptions upon which the models rest. We find a lack of fit between the mathematical formulations and data for real animals forming hierarchies and that the assumptions concerning how animals form dominance relationships are not well supported by current experimental literature. In particular, the recent experimental evidence concerning eavesdropping, individual recognition, and transitive inference suggests that we need new models of hierarchy formation consistent with the sophisticated levels of social cognition in animals (Beecher and Campbell, 2005; Bond et al., 2003; D'Ettorre and Heinze, 2005; Earley and Dugatkin, 2002; Gherardi and Atema, 2005; Grosenick et al., 2007; Johnstone, 2001; Lai et al., 2005; Lazareva, 2004; McGregor, 2005; Oliveira et al., 2001; Paz-y-Mino et al., 2004; Tibbetts, 2002; Yurkovic et al., 2006). Thus motivated, we analyze data on hierarchy formation in hens to isolate specific features of hierarchy formation that should be considered in future models.

Although the three winner-loser models considered vary in some specifics, all share a common formulation. The models consist of three basic steps: step 1 determines the order in which pairs of animals meet; step 2 determines whether the selected pair (animals i and j) interact; step 3 determines the winner of the interaction and imposes winner/loser effects. Step 2 is governed by an interaction probability P_{ij}, and step 3 is governed by a winning/losing probability Q_{ij}. We shall refer to step 1 as the pairing component of the model and step 2 as the interaction component. Collectively, we refer to steps 1 and 2 as the pairing-interaction component. Step 3 will be referred to as the dominance component.

The dominance component of the models rests upon four common assumptions.

(A1) Individuals have dominance scores (alternatively referred to as "force" or "resource holding power") reflecting their past histories of winning and losing contests.

(A2) When two animals interact in a dominance contest, a specific mathematical formulation, based upon the difference in their scores, determines the probability that one or the other will win. The formulation varies from model to model.

(A3) The animals experience winner and loser effects in response to the outcomes of their contests; dominance scores are updated accordingly, in a specified manner. Individuals have equal dominance scores at the start of a simulation in order to demonstrate that winner and loser effects alone produce linear hierarchies.

(A4) Animals do not identify one another as individuals; consequently in subsequent meetings they are not influenced by memory of their previous encounters.

This paper is divided into four major parts. Part one evaluates assumptions A1 and A2 via comparison to experimental observations of interactions during hierarchy formation in 14 groups of Leghorn hens. First, we use the visualization technique known as music notation to compare a sample data record of interactions in one group of hens with simulated records from the models. This comparison provides a qualitative sense of the differences in the processes of interaction used by real animals versus those proposed by the models. In order to obtain rigorous quantitative comparison, we reformulate the models in terms of experimentally accessible quantities (so that they produce records of interaction that can be compared to experimental data) and then compare the pairing-interaction and the dominance components of the models with data extracted from the hen records. Part two reviews the experimental support in the literature for assumptions A3 and A4 of the dominance component of the models: the presence of winner and loser effects in groups, the lack of individual identification/absence of memory of previous encounters, and the use of the difference in dominance score values to determine winning probability. Part three presents several prominent features of hierarchy formation extracted from the hen data that have not previously (or only rarely) been described. The features include "bursting" (acts of repetitive aggression), "efficiency" (relative lack of counter-attacks), "rank emergence" (sequential rank differentiation), and the frequency of occurrence and stability of relationship configurations during hierarchy formation. The paper concludes with a discussion in which we suggest that the cumulative evidence of parts one through three indicates that group members are intensely aware of their own interactions, as well as interactions occurring among other members of their group, and that actions flowing from this awareness must be incorporated into any accurate account of hierarchy formation.

2. Part one: accuracy of the models' predictions to experimental data

We begin part one with some necessary preliminaries. We: (1) describe the collection of the hen data; (2) define the *dominance index* used throughout the paper as the experimentally determinable measure of dominance; and (3) reformulate the relevant mathematical detail of the three winner-loser models in terms of experimentally accessible quantities to enable comparison of model predictions with the hen data.

2.1. Experimental data

Details concerning the subjects, experimental design, data collection, and apparatus can be found in Chase (1982). Briefly, two observers working in alternate 1.5 hour shifts for 6 hours a day over 2 days recorded *every aggressive interaction involving physical contact* in 14 groups, each of four Leghorn hens, from the moment of introduction through the formation of stable linear hierarchies. The aggressive interactions were recorded as one of three types: "peck," "jump (onto)," and "claw." Of the 7,257 recorded interactions, 6,922 (95.4%) were pecks, 303 (4.2%) were jumps, and 32 (0.4%) were claws. *Since the vast majority involved pecks*, *for brevity during the rest of this article*, *we will refer to all the recorded interactions simply as pecks*. When not being observed, the hens were separated by opaque partitions in their common cage. We assembled the groups of hens using an incomplete block design such that no two individuals were grouped more than once, all individuals in a group had previously been in the same number of groups, and all hens were in the same number of experimental groups. We refer to the groups as Q1 through Q16 (with groups Q5 and Q13 missing).

2.2. Dominance index

The relative dominance of individuals in a group was deduced from determination of the dominance index,

$$X_i(t) = D_i(t)/\big(D_i(t) + S_i(t)\big), \tag{1}$$

where $D_i(t)$ is the number of observed physical interactions—pecks—up through time t that animal i has won (i.e., the number of encounters in which it has attacked another animal), and $S_i(t)$ is the number of interactions it has lost (i.e., the number of encounters in which it has been attacked by another animal). $X_i(t)$ measures the fraction of interactions experienced by animal i in which it has emerged as a winner. It is an experimentally measurable dominance indicator, not to be confused with the dominance score (force, resource holding parameter) which is used in the winner-loser models as a fundamental parameter of an individual. *Hen rank in each observed group is inferred from relative* X_i *values under apparent* "*steady state*" *conditions*. (In the experiments, rank differentiation was apparent by the end of 2 days of observation, therefore, the hen emerging with the largest value of X_i after 2 days was considered the rank 1 individual, etc.) Dominance assignments based upon this index agree with the alternative way of assigning ranks based on the number of individuals dominated in a group (the rank 1 individual dominates all the others, etc.). Note from (1) that $X_i(0)$ is undefined—for convenience, we assume $X_i(0) = 0.5$ for all individuals.

2.3. The mathematical formulations

The mathematical formulations of winner-loser models are developed in terms of a fundamental attribute (variously referred to as a "force," "dominance score," or "resource holding power") held by individuals. While theoretically attractive, researchers have not proposed techniques for measuring this attribute (as far as we are aware). A critical step in our analysis of the models has been to relate this attribute to the experimentally measured variables $D_i(t)$ and $S_i(t)$. We therefore briefly review the mathematical formulation of each model, examine the model parameterizations, and rework the models in terms of our experimental variables in order to compare the models' predictions with the experimental data.

The Bonabeau model (*Bonabeau et al.,* 1999): This model uses a "force" variable, $F_i(t)$, to characterize the time development of the dominance ability of an animal as a result of its record of wins and losses in earlier contests. The model can be succinctly described as follows:

- The pairing component has two versions. In version one, the pairs are repeatedly chosen randomly. While the authors of this model do not clarify the random process, we infer that successive pairings were chosen independently with uniform probabilities. In version two, the pairs interact in round-robin fashion, i.e., each individual is matched against every other individual and this procedure is continually repeated. Either version is a particular implementation of an equi-likelihood pairing component.
- The interaction component is governed by a probability of interaction between animals i and j at time t, modeled as a product of sigmoid functions,

$$P_{ij}(t) = Y_i(t)Y_j(t), \quad \text{where } Y_i(t) = \frac{1}{1 + \exp(-F_i(t)/\theta)}. \tag{2}$$

- The dominance component is modeled by a sigmoid probability function that i dominates j,

$$Q_{ij}(t) = \frac{1}{1 + \exp(-\eta(F_i(t) - F_j(t)))}. \tag{3}$$

- Animal i's force variable is incremented according to the outcome of the interaction,

$$\begin{aligned} F_i(t) &\xrightarrow{i\text{-dominant}} F_i(t) + \delta^+, \\ F_i(t) &\xrightarrow{i\text{-submissive}} F_i(t) - \delta^-. \end{aligned} \tag{4}$$

- Under the assumption of no prior history for the agents involved,

$$F_i(0) = 0, \quad \forall i. \tag{5}$$

As presented in (2)–(5), this model contains four free parameters. Three, θ, δ^+, and δ^- have units of "force." The fourth, η, is introduced so that it has units of "inverse force"; η^{-1} determines the scale for which force differences, $F_i(t) - F_j(t)$, are significant in determining dominance. θ serves as a similar force scale for determining interaction. δ^+ and δ^- are winning and losing force increments. In the absence of theoretical considerations for assigning values to these parameters, we must extract values from fits to experimental data.

With the assumption that an increment in the value of the force attribute occurs with (*and only with*) *each peck interaction between two birds*, then (4) and (5) imply

$$F_i(t) = \delta^+ D_i(t) - \delta^- S_i(t). \tag{6}$$

If (6) is inserted in (2) and (3), the four effective independent parameters become $\varsigma^+ = \delta^+/\theta$, $\varsigma^- = \delta^-/\theta$, $\alpha^+ = \delta^+\eta$, and $\alpha^- = \delta^-\eta$, which are dimensionless ratios of force parameters. Equations (4) and (5) are then replaced by

$$\begin{aligned} D_i(t) &\xrightarrow{i\text{-dominant}} D_i(t) + 1, \qquad D_i(0) = 0, \\ S_i(t) &\xrightarrow{i\text{-submissive}} S_i(t) - 1, \qquad S_i(0) = 0. \end{aligned} \tag{7}$$

If we assume equal impact of winning and losing, that is, if we assume $\delta^+ = \delta^- = \delta$, the model reduces to having two independent dimensionless parameters, $\varsigma = \delta/\theta$ and $\alpha = \delta\eta$. Equations (2) and (3) then simplify to

$$P_{ij}(t) = Y_i(t)Y_j(t), \quad \text{where } Y_i(t) = \frac{1}{1 + \exp(-\varsigma(D_i(t) - S_i(t)))}, \tag{8}$$

and

$$Q_{ij}(t) = \frac{1}{1 + \exp(-\alpha[(D_i(t) - S_i(t)) - (D_j(t) - S_j(t))])}. \tag{9}$$

The force variable and its incrementing parameters are completely removed from the models (7)–(9), in favor of experimentally measured variables D_i, S_i, and dimensionless parameters α and ς. (Values for α and ς are to be inferred by fitting Eqs. (8) and (9) to experimental data.) Note that if we set $D_i(t) = 0$ in (8) and (9) we can remove winner effects completely from the model; similarly setting $S_i(t) = 0$ eliminates loser effects. Thus, (8) and (9) allows us to compare the hen data against the Bonabeau model at three critical points in its parameter space: no winner effects; equal winner and loser effects; no loser effects.

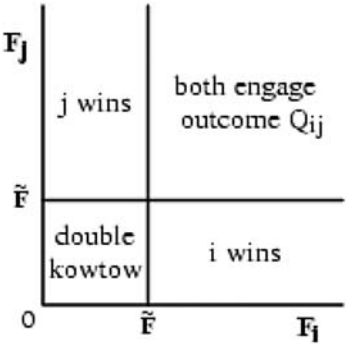

Fig. 1 The interaction component of the Dugatkin model.

The Dugatkin model (*Dugatkin,* 1997): This model assigns each animal a resource holding power F_i.

- As with the Bonabeau model, the pairing component of this model has both random and round-robin versions—i.e., is an equi-likelihood pairing component.
- The interaction component allows each animal to separately decide whether to engage in an interaction or not. If both engage, a probability decision determines the outcome. If only one animal engages, it is declared the winner. If neither animal engages (double kowtow) both animals emerge unchanged in resource holding power. The probability $P_i(t)$ that animal i will engage during an interaction is

  $$P_i(t) > \phi, \quad \text{where } P_i(t) = F_i(t)/\hat{F}. \tag{10}$$

  Here ϕ is a probability threshold (dimensionless) for an animal to engage in an interaction, and $\hat{F}$ is the maximum value for the resource holding power. While the engagement probability is written as a two-parameter model, (10) can be simplified to

  $$F_i(t) > \tilde{F}, \quad \tilde{F} \equiv \phi\hat{F}, \tag{10$'$}$$

  revealing that the resource holding power threshold $\tilde{F}$ is the single critical parameter governing whether an animal interacts. The interaction component is graphically summarized in Fig. 1. Since the experimental data on the hens is a record of only those instances in which "both engage," the data and model align provided we examine the equations of this model with $\tilde{F} = 0$.
- The probability that i dominates j in an interaction when both engage is

  $$Q_{ij}(t) = F_i(t)/\big(F_i(t) + F_j(t)\big). \tag{11}$$

- Animal i's dominance variable is incremented according to the outcome of the interaction,

  $$\begin{aligned} F_i(t) &\xrightarrow{i\text{-dominant}} (1+W)F_i(t), \\ F_i(t) &\xrightarrow{i\text{-submissive}} (1-L)F_i(t). \end{aligned} \tag{12}$$

- With the assumption of no prior history for the animals involved, the initial data are

$$F_i(0) = F_0, \quad \forall i. \tag{13}$$

As presented, (12) and (13) form a three-parameter (W, L, F_0) system of equations with $W \geq 0$ and $0 \leq L < 1$. With the assumption that an increment in the value of the resource holding power is coupled with (and only with) each peck interaction between two birds, then when the time variable t is discrete (for example, when t counts the accumulated number of interactions in the group), (12) and (13) form a system of recurrence relations having solution

$$F_i(t) = (1+W)^{D_i(t)}(1-L)^{S_i(t)} F_0, \tag{14}$$

where $D_i(t)$ and $S_i(t)$ are the win and loss counters defined previously. Equation (14) states that the resource power, $F_i(t)$, changes as a product of the exponential factors $(1+W)^{D_i(t)}$ and $(1-L)^{S_i(t)}$. By converting these factors to a common, natural logarithm base,

$$1 + W = e^{\alpha}, \qquad 1 - L = e^{\beta}, \quad \alpha, \beta > 0, \tag{15}$$

(14) simplifies to $F_i(t) = e^{[\alpha D_i(t) - \beta S_i(t)]} F_0$, and (11) simplifies to

$$Q_{ij}(t) = \frac{1}{1 + \exp\{-[\alpha(D_i(t) - D_j(t)) - \beta(S_i(t) - S_j(t))]\}}. \tag{16}$$

In (16), the theoretical force variable F_i has been eliminated in favor of the experimentally accessible variables D and S. Setting $\alpha = 0$ or $\beta = 0$, respectively, removes winner or loser effects from the model.

The Hemelrijk model (*Hemelrijk*, 2000): Hemelrijk presents a family of models. The models assign each animal a dominance variable, $F_i(t)$, that develops in time. The models are all variations of a core model, which she refers to as "direct obligatory," whose predictions we compare against our data.

- The pairing component is based upon an involved geometrical algorithm for moving animals spatially.
- When two animals, i and j are spatially close at time t, the probability of interaction is

$$P_{ij}(t) = 1. \tag{17}$$

- The probability that i dominates j in the interaction is

$$Q_{ij}(t) = \frac{F_i(t)}{F_i(t) + F_j(t)}. \tag{18}$$

- Animal i's dominance variable is incremented according to the outcome of the interaction,

$$\begin{aligned} F_i(t) &\xrightarrow{i\text{-dominant}} F_i(t) + \frac{F_j(t)}{F_i(t) + F_j(t)}\delta, \\ F_i(t) &\xrightarrow{i\text{-submissive}} F_i(t) - \frac{F_i(t)}{F_i(t) + F_j(t)}\delta. \end{aligned} \tag{19}$$

Note that (19) makes no allowance for separately removing winner or loser effects from the model.

- With the assumption of no prior history for the animals involved, the initial data are

$$F_i(0) = F_0, \quad \forall i. \tag{20}$$

As presented, Eqs. (18)–(20) form a two parameter (δ, F_0) system of equations, with δ as the parameter scale governing the increment of the dominance factor and F_0 being the initial value of dominance factor for each animal. When the time variable t is discrete, (18)–(20) is a stochastic system of recurrence relations. If the initial data is expressed as

$$F_o = \bar{F}_o \delta, \tag{21}$$

then, under the change of variable $\bar{F}_i(t) = F_i(t)/\delta$, the parameter δ drops from the system giving

$$Q_{ij}(t) = \frac{\bar{F}_i(t)}{\bar{F}_i(t) + \bar{F}_j(t)}, \tag{22}$$

$$\left.\begin{aligned} \bar{F}_i(t) &\xrightarrow{i\text{-dominant}} \bar{F}_i(t) + \frac{\bar{F}_j(t)}{\bar{F}_i(t) + \bar{F}_j(t)}, \\ \bar{F}_i(t) &\xrightarrow{i\text{-submissive}} \bar{F}_i(t) - \frac{\bar{F}_i(t)}{\bar{F}_i(t) + \bar{F}_j(t)}, \end{aligned}\right. \qquad \bar{F}_i(0) = \bar{F}_0, \tag{23}$$

which depends on the single parameter $\bar{F}_0$. System (22)–(23) has the property

$$\sum_{i=1}^{n} \bar{F}_i(t) = n\bar{F}_0, \tag{24}$$

where n is the number of animals in the group. Thus, the conserved quantity, $n\bar{F}_0$, is the “total amount of dominance” in the system, to be partitioned among the animals. The effect of increasing $\bar{F}_0$ is to increase the range of individual dominance values and to increase the number of interactions necessary to clearly differentiate the animals in the hierarchy.

In order to keep the probability (22) (equivalently (18)) positive, the dominance variable must be prevented from going negative, hence $\bar{F}_i$ is restricted to the range $[0, \infty)$. In practice, Hemelrijk suggests restricting $\bar{F}_i$ to the range $[\varepsilon, \infty)$, where $\varepsilon > 0$ is a small value, in order to retain some small probability for any animal to win an interaction. Restricting $\bar{F}_i$ means that (24) will not hold once t is sufficiently large. Thus, for sufficiently large time, the value of the left-hand side of (24) will exceed that of the right-hand side. As we are interested in the pure makeup of the model, we ignore the introduction of this modifying parameter. In order to compare Hemelrijk’s model with our data, we will again make the assumption that increments (Eq. (23)) in the dominance force occur when (and only when) peck interactions occur between hens.

2.4. *Qualitative comparison of sample data records*

The music notation technique provides a way to visualize interaction records in small groups of individuals (Chase, 2006). We use it here to give an immediate, qualitative comparison between model and experimental data records. We employ two minor modifications of the original technique. First, rather than using clock time, we measure time by interaction count (the cumulative number of interactions starting from when the group members were introduced) on the abscissa. Second, rather than using the rank index (1, 2, 3, 4) of individuals on the ordinate axis, we represent each individual by the value of its dominance index, $X_i(t)$. Each aggressive act between individuals is indicated by a vertical arrow from the line that represents the dominance index of the initiator of the act to the receiver of it.

The music notation in Fig. 2 compares the data record for group Q14 with the records of an equal number of interactions simulated by the models. For clarity of presentation, only the records of interactions 1–100 and 200–300 are shown. *For this comparison only*, we selected parameter values for running the models. Choice of parameter values (given in the figure caption) was guided by a combination of suggested values from the models' authors and our own examination of the parameter spaces in order to select values that favorably reflected each model's performance as compared to the data. To make the comparison additionally favorable for the models, we used the hen data to determine the pairing schedule for the models. (That is, rather than use the specific pairing component prescribed by each model, e.g., random, round robin, or geometric, we adjusted the models so that they would use the same sequence of pairwise interactions as occurred in the real data. If we had not done so, the discrepancy between the hen data and the models would have been greater.) Again, in comparing model predictions with our experimental data, we assume the only times that dominance force changes is when there is an experimental peck interaction.

As individual bird identity is not considered in winner-loser models, the identity of each bird is arbitrary, and the fact that the birds were not ranked in the same order by the models as in the experimental data is not relevant. However, there are some immediate differences apparent between the models and the data. First, and most noticeable, the repetitious pecking behavior (long sequences of repeated pecks by an individual against another) that is seen in the data is not captured by any of the models. We refer to this feature as "bursting," and we discuss it further in part three. Second, the number and timing of the pair inversions (a submissive hen pecking a dominant hen) that were seen in the Hemelrijk and Dugatkin models are different from those in the experimental data. In the two models, the pair inversions resulted in very slow dominance differentiation between the top two birds. In fact, in the Dugatkin model, the eventual dominant individual achieved its dominance only *after* 300 interactions. The high pair inversion rate is also responsible for the lack of differentiation after many interactions between dominance index values achieved by the two most- and the two least-dominant birds in the Hemelrijk model as compared to the corresponding pairs in Q14. Finally, we note that the individuals in the Bonabeau model achieved dominance differentiation much more rapidly than did individuals in the data. By interaction 5, the relative ranking of all individuals in the Bonabeau model is locked in. In contrast, in the experimental group, note the relatively slower emergence of the top-ranked individual as well as the late-time differentiation between the two lowest ranked individuals.

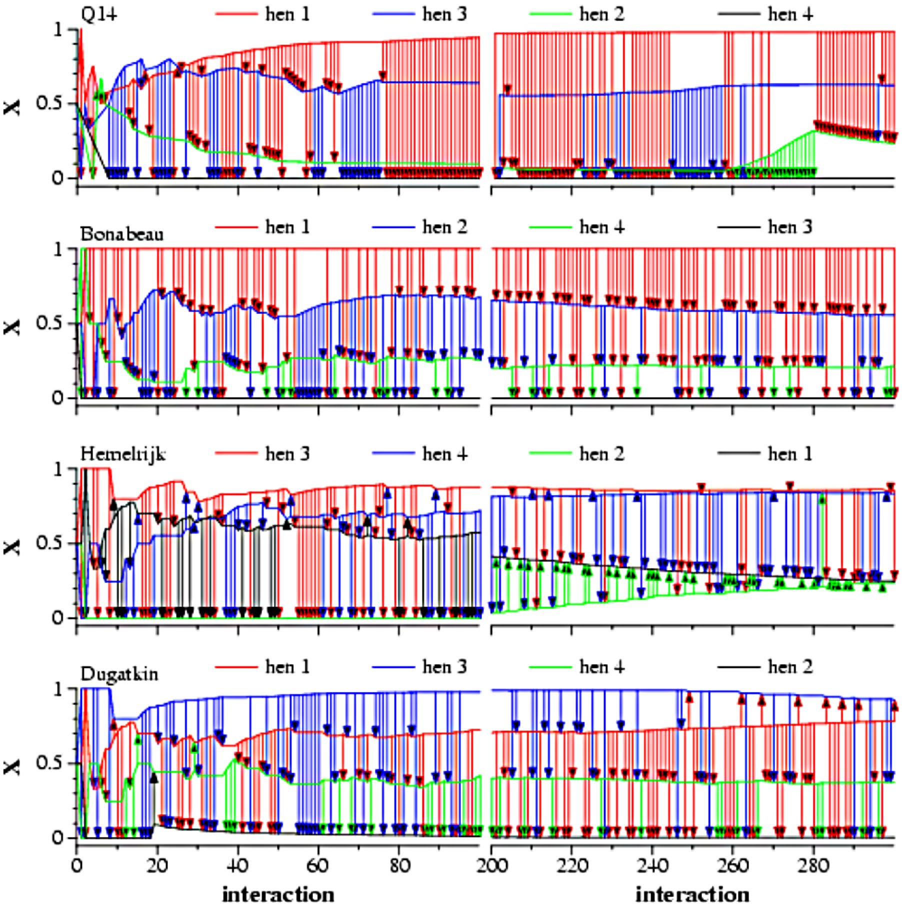

Fig. 2 Music notation of two, time-separated, 100 interaction periods for one data set (Q14) compared with model simulations. Line types (colors) indicate the final rank of the bird (ordered heavy solid (red), dashed (blue), dotted (green), light solid (black)—with heavy solid (red) most dominant). Arrows going from the X_i value of the initiator to that of the receiver indicate aggressive acts. Parameter values used in the model simulations: Bonabeau—$\eta = 1$, $\theta = 100$, $\delta^+ = \delta^- = 1$; Hemelrijk—direct obligate, $\delta = 5$, $F_0 = 15$; Dugatkin—$W = 0.4$, $L = 0.0$, $F_0 = 10$, $\phi = 1$. (Color figure online.)

2.5. Quantitative evaluation of the pairing-interaction component of the models

We addressed the pairing-interaction components of the winner-loser models by comparison with actual pair interactions ("pecks") in the hen data. Since nonaggressive meetings of the hens were not recorded, the experimental data presented only the combined result of the pairing-interaction component—that is, the pairing and interaction components of the data could not be separated (nor separately compared with the models). Fortunately, as we show below, the assumptions made in the Bonabeau and Dugatkin models are such that either the pairing or interaction component dominates and can be tested against the data. (We emphasize that the analysis in this section, and the next, did not require choos-

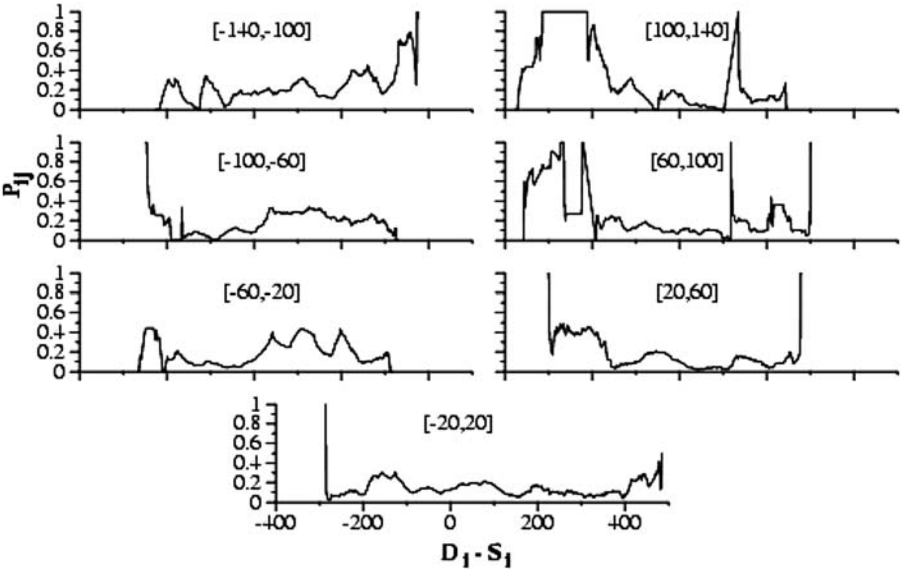

Fig. 3 Experimental determination of P_{ij} as a function of $D_i - S_i$ for fixed values of $D_j - S_j$. To overcome data sparsity, the data is accumulated over fixed ranges (each covering 40 units) of values of $D_j - S_j$. Thus, in the top right plot for each value of $D_i - S_i$, the plotted results are accumulated for values of $D_j - S_j$ in the range [100, 140].

ing model parameters—rather, if the model prediction agrees well with the data, values for the model parameters can be extracted.)

Bonabeau model: As the Bonabeau pairing component involves particular implementations of equi-likelihood pairing, in the limit of a large number of observed interactions the pairing-interaction component will be dominated solely by the interaction probability, Eq. (8). As we have hundreds (the average is 518) of recorded interactions for each group, we can, therefore, with some confidence, estimate the accuracy of (8) from an examination of the data.

Equation (8) models the probability of interaction as a product of two sigmoid functions. Functionally, the probability can be denoted $P_{ij}(D_i - S_i, D_j - S_j; \zeta)$—that is, it is a function of two arguments and one parameter. If the first argument, $D_i - S_i$, is held constant, then P_{ij} is just a scaled sigmoid function of its second argument, and vice versa. It is therefore instructive to plot the experimental data results for P_{ij} using constant values of one of the first two arguments. As P_{ij} is symmetric in its first two arguments, without loss of generality, we may hold the second argument constant. As the experimental data is relatively sparse when plotted against pairs of $(D_i - S_i, D_j - S_j)$ values, Fig. 3 plots the experimentally determined results that accumulated over fixed ranges of values for the second argument. It is clear that none of the plots in Fig. 3 are sigmoidal in form, as is required by Eq. (8), and that the assumptions of this equation are not supported by the experimental data.

Dugatkin model: The pairing component of this model is again modeled by particular instances of an equi-likelihood process. Equation (10′) models the interaction component. With $\tilde{F} = 0$, the interaction component is forced. (Any animal having a nonzero resource

Table 1 Fraction of interactions involving ranked pairs. "dij" indicates interactions between birds of rank i and rank j

Ranked pair	$d12$	$d13$	$d14$	$d23$	$d24$	$d34$
Fraction of interactions	0.163	0.161	0.179	0.207	0.180	0.110

holding value must interact. Note that the multiplicative method for changing resource holding value (Eq. (12)) guarantees that no resource holding value can go to zero.) Thus, the combined pairing-interaction component is governed solely by the pairing component which dictates that over time each possible pair of animals will interact the same percent of the time.

Table 1 presents the frequencies of observed interactions between ranked individuals aggregated over all 14 groups. A Pearson's X^2 test ($X^2 = 0.188$, $\mathrm{df} = 5$) indicates that there is no significant difference from a uniform distribution. Thus, it does appear that an equi-likelihood model is appropriate for describing the pairing component over many interactions. Note, however, (Section 4.1) that the observed phenomenon of "bursting" imposes an important short-timescale interaction modulation on the longer-time uniform pairing behavior.

Hemelrijk model: The interaction component of this model is determined by (17); having this probability set to unity means that the pairing-interaction component is determined solely by the pairing component. However, the pairing component involves a complicated geometrical model. Analyzing this model would have required data observations that were not taken—we are therefore unable to comment on the accuracy of this pairing-interaction component.

Of the two models whose pairing-interaction components we could test with our data, the form (8) proposed by the Bonabeau model is clearly not supported by the data. An equi-likelihood model for the long-term behavior of the pairing component is consistent with the data.

2.6. *Quantitative evaluation of the dominance component*

We evaluated the accuracy of the dominance component of each model by comparing how well the Q_{ij} formulation of each model fit the hen data. (Again, doing so did not require choosing model parameters—parameter values can be extracted from satisfactory fits to the data.)

Bonabeau model: Defining the time variable as interaction time, we used the experimental data to test the validity of the dominance component of this model, Eq. (9). The observed probability, Q_{ij}, of winning an interaction as a function of the observed win-loss differences, $DS_i - DS_j \equiv (D_i - S_i) - (D_j - S_j)$, for the 14 groups of hens is plotted in Fig. 4. A least-squares fit of the data in Fig. 4 to the model form (9) gave a value for $\alpha = 0.091 \pm 0.004$. (Note that the fit is highly influenced by the rise around the abscissa value of 0.) While the sigmoid form of the model (9) captured part of the functional form of the data in Fig. 4, the model missed a significant randomized component of the data. The data suggest that a more appropriate model for Q_{ij} would be

$$Q_{ij} = \Sigma\big((DS_i - DS_j); \alpha\big) - \mathrm{sgn}(DS_i - DS_j)\chi, \tag{25}$$

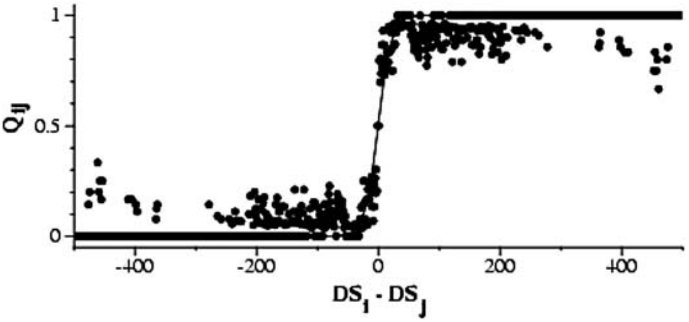

Fig. 4 Experimental determination of Q_{ij} as a function of the win-loss difference, $DS_i - DS_j \equiv (D_i - S_i) - (D_j - S_j)$, between two agents i and j (solid points). The solid line represents the least-squares best fit to Eq. (9) of the Bonabeau model.

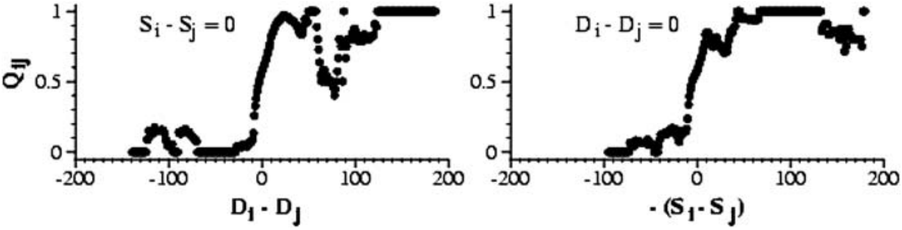

Fig. 5 Experimental determination of Q_{ij} as functions of: (*left*) $D_i - D_j$ when $S_i - S_j = 0$ and (*right*) $S_i - S_j$ when $D_i - D_j = 0$.

where $\Sigma(\cdot;\cdot)$ is the sigmoid function, $\mathrm{sgn}(\cdot)$ is the sign function, and χ is a random variable of mean value roughly 0.1 and standard deviation roughly 0.03. The Bonabeau model does not provide for this significant random aspect of the data.

Dugatkin model: Note (by comparing (16) and (9)) that the Dugatkin dominance component (16) reduces to the Bonabeau dominance probability (9) when $\beta = \alpha$. Given that the random aspect of the experimental data could not be captured (Fig. 4) by the Bonabeau dominance model (9), making β independent of α in the Dugatkin model (16) cannot provide a better fit (since the β term in (16) does not add any random component). Confirming this, in Fig. 5, we plot $Q(D_i - D_j, S_i - S_j)$ separately along the contours $S_i - S_j = 0$ and $D_i - D_j = 0$. Equation (16) predicts that the resulting curves should be sigmoidal, with the rise of the sigmoid governed, respectively, by α and β. As expected, the plots in Fig. 5 make it apparent that the random component in the real data provided a strong modulation to the sigmoidal form which can not be captured by either the Dugatkin or Bonabeau models.

Hemelrijk model: Regarding (22) as the function $Q_{ij}(\bar{F}_i, \bar{F}_j)$, we see that (22) predicts that along the contours $\bar{F}_i + \bar{F}_j = c$, Q_{ij} will vary linearly with $\bar{F}_i$ with slope c^{-1}. Figure 6 shows the Q_{ij} vs. $\bar{F}_i$ relationship exhibited by the experimental data for values of $\bar{F}_0 = 120$, and $c = 120$, 180 and 240. (These multiples, 1×, 1.5×, and 2×, of $\overline{F_0}$ are arbitrary, but reasonable choices to explore: with 4 birds, c can never exceed $4\overline{F_0}$, and since c is the sum of $\bar{F}_i + \bar{F}_j, c$ is not going to exceed $2\overline{F_0}$ on average.) Superimposed on each

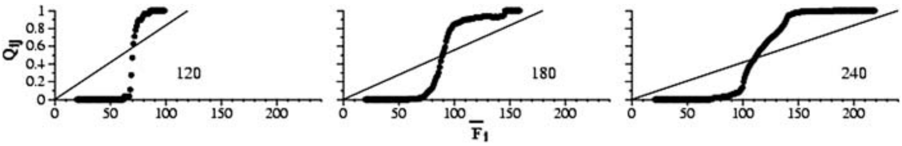

Fig. 6 Experimental determination (solid points) of Q_{ij} plotted as a function of $\bar{F}_i$ for three constant values of the sum $\bar{F}_i + \bar{F}_j$ compared to the Hemelrijk model Eq. (22) (straight lines).

plot is the linear relationship predicted by (22). The data plots are sigmoidal in shape and have only a very rough resemblance to the model's linear relationship. Equation (22) is therefore not supported by the data.

The experimental data clearly disagree with the dominance component in Hemelrijk's model. However, the data in Figs. 4–6 do suggest an underlying sigmoidal form for any model of the dominance component. However, the data also suggest a strong randomizing component must also be part of such a model.

3. Part two: support for the assumptions of the dominance components of the models in the experimental literature

As indicated in the Introduction, the dominance components of the models rest upon four common assumptions A1 through A4. Having addressed assumptions A1 and A2 in part one; in this section, we evaluate assumptions A3 and A4. We also return briefly to assumption A2.

3.1. Winner and loser effects in groups

Considerable experimental evidence indicates that animals across a wide variety of species show loser effects (Bakker et al., 1989; Bakker and Sevenster, 1983; Beacham, 1988; Beacham and Newman, 1987; Burke, 1979; Drummond and Canales, 1998; Drummond and Osorno, 1992; Francis, 1983, 1987; Frey and Miller, 1972; Hsu and Wolf, 1999; Zucker and Murray, 1996). These effects are often pronounced, and may last for a day or two after an initial loss. The evidence for winner effects is more mixed, with only some species showing them and others not (Bakker et al., 1989; Bakker and Sevenster, 1983; Burke, 1979; Chase et al., 1994; Drummond and Canales, 1998; Frey and Miller, 1972; Hsu and Wolf, 1999). Where winner effects do occur, they appear to operate briefly, perhaps for an hour or less after an initial win. *All* this evidence is derived from experiments in *isolated pairs* of animals: experiments in which either a winner or a loser and a single new opponent meet by themselves separated from any other individuals. As far as we are aware, only one study has ever investigated whether or not these effects actually do occur for pairs of animals interacting as part of a larger group (Chase et al., 2003). This study found that winner, loser, and other effects exhibited in isolated pairs of cichlid fish either did not occur at all or occurred at significantly lower rates in socially embedded pairs. While further research is certainly called for, the present experimental results suggest that the assumption that winner and loser effects are significant in groups forming hierarchies may not be justified.

3.2. Lack of individual identification and absence of memory of previous encounters; determination of encounters by differences in dominance scores

While the dominance score is a compendium of an individual's past record of wins and losses, it does not retain (and hence the probability of winning an encounter is not influenced by) the memory of the outcome of any single past encounter—reflecting the models' assumption that animals are not able to identify one another as individuals. These assumptions (dominance score difference, no memory of past encounters, and no individual identification) are therefore linked in the models, and we discuss them together. In particular, if animals do identify one another as individuals and if their memories of past encounters with one another do influence the outcomes of subsequent encounters, the assumption that outcomes are only determined by differences in dominance scores cannot be supported.

Experiments have demonstrated individual recognition in a broad range of species including mammals, birds, crustaceans, fish, and even certain insects (wasps, ants, and fruit flies) that do form dominance relationships (Brown and Colgan, 1986; Cheney and Seyfarth, 1990; D'Eath and Keeling, 2003; D'Ettorre and Heinze, 2005; Gherardi and Atema, 2005; Karavanich and Atema, 1998; Lai et al., 2005; McLeman et al., 2005; Tibbetts, 2002; Todd et al., 1967; Yurkovic et al., 2006). Animals often recognized others in subsequent contests even after only brief prior exposure and these memories lasted for considerable periods of time. To take some very impressive examples in invertebrates, hermit crabs remembered one another for up to 4 days after only 30 minutes of interaction (Gherardi and Atema, 2005), while fruit flies recognized each other as individuals after 30 minutes of separation (Yurkovic et al., 2006).

A strict interpretation of these experiments might be that the findings only show that animals can identify each other as either "familiar" or "unfamiliar," and not as specific individuals (see more discussion of this point in Gherardi and Atema, 2005). However, this interpretation is enough to invalidate these winner-loser model assumptions since these experiments show that familiar individuals meeting again tend to resume their original relationships while unfamiliar individuals establish new relationships not influenced by their (individual) previous dominance encounters. More conclusively, in a number of cases in which researchers have used more elaborate experimental designs (e.g., in studies of wasps, hamsters, and hermit crabs) results strongly suggest that animals are indeed capable of specific individual recognition (Gherardi and Atema, 2005; Lai et al., 2005; Tibbetts, 2002).

4. Part three: empirical dynamics of hierarchy development

In this section, we identify several prominent behavioral features of the hierarchy formation process in the data records for the hens that have previously received little or no attention. We suggest that these features are likely to be common dynamics of hierarchy formation across many other species. If so, they will need to be captured by future models of hierarchy formation.

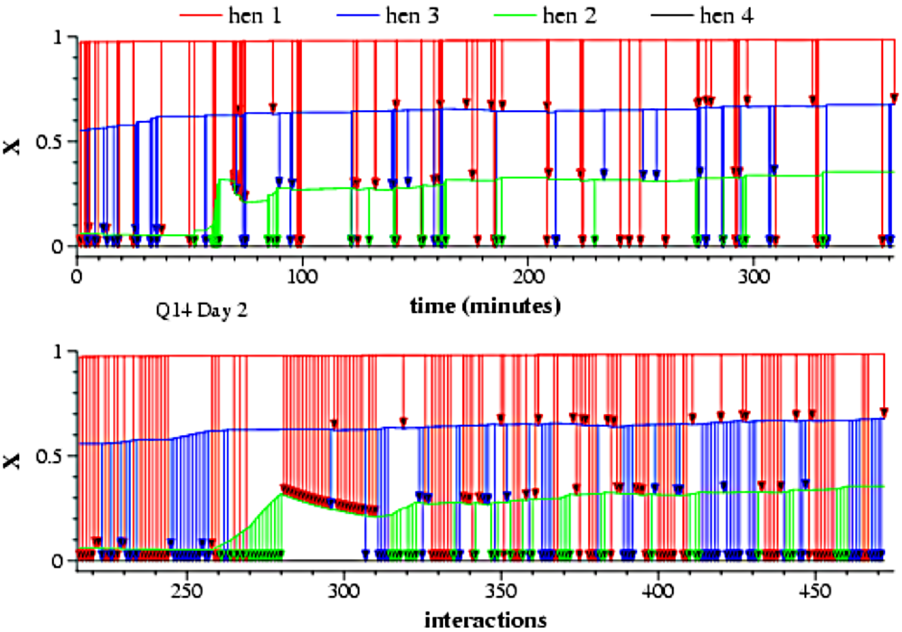

Fig. 7 *Top*: Music notation summary of pair-wise interactions and evolving dominance index values for group Q14 during the second day of observation using time elapsed from beginning of second day. *Bottom*: Replot of the top figure using interaction count for the time variable. Use of interaction count helps reveal the bursting behavior of individual birds. (Color figure online.)

4.1. Bursting

The top plot in Fig. 7 uses music notation to summarize the aggressive acts among the 4 hens in group Q14 during their second day of meeting. The graph shows periods of nonaggressive activity interrupted by interactions between pairs. However, the use of clock-time for the abscissa (coupled with the compression of 6 hours of interaction into the width of a page) suppresses details of the interaction. Particularly obscured are aggressive "bursts" (repeated pecks in quick succession) by one hen against another group member. The individual attacks in these bursts can be shown more clearly by replacing elapsed time (in minutes) on the abscissa by the successive interaction count for the group (lower graph in Fig. 7). (By using interaction count as the "time variable", individual interactions show clearly while periods of time when no interactions occurred are suppressed.) An examination of the lower graph clearly indicates that the top-3 ranked hens usually pecked in bursts directed almost exclusively at lower-ranked hens. The bottom-ranked hen, of course, had no one to burst against except perhaps during the initial periods of hierarchy formation (not shown) when it might be contesting for rank.

Figure 8 summarizes the observed bursting behavior, categorized by final rank of the hens, for all 14 experimental groups combined. There is a marked similarity in the plots for the top 3 individuals. We suspect the behavior for the bottom-ranked individual would be similar; unfortunately, occupying the bottom position in the hierarchy limits the total number of pecks it can mete out. We conclude that, except when precluded from doing so

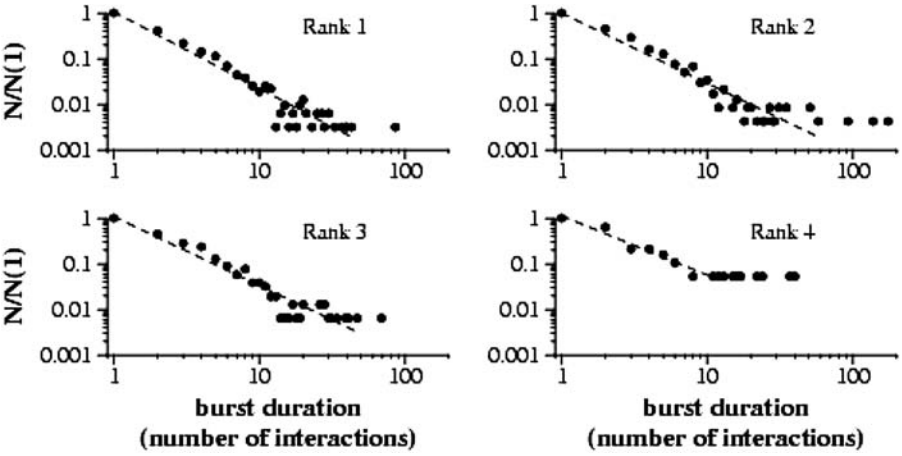

Fig. 8 Measured distributions of burst duration (number of consecutive attacks) summarized over all groups organized according to the final ranking of the bird doing the bursting. Each dashed line represents a least-squares fit to the power law form (26).

by being the bottom-ranked individual, each hen pecked in bursts with duration (number of pecks) generally given by the power-law distribution function

$$N(d) = N(1)d^{-p}. \tag{26}$$

Based on least-squares fits to the data for the three top-ranked birds, we find $p = 1.6 \pm 0.1$. *We postulate that expressing aggression to other group members in bursts, perhaps following a similar power-law distribution, is shown by animals of many species during hierarchy formation.*

4.2. Pair-flips

We define the occurrence BpA ("B pecks A") to be a *pair-flip* (counter-attack) if the previous aggressive act between A and B was ApB. When isolated pairs of animals set up a dominance relationship they often exchange counter-attacks for an extended period of time before they establish a stable relationship in which one individual initiates all, or nearly all, of the aggressive activity. In contrast to behaviors in isolated pairs, we find a very low incidence of pair-flips in the hen data. Of the 7,257 recorded interactions between the 84 (6 pairs × 14 groups) pairs, only 138 interactions (1.9%) involved a pair-flip, and two groups by themselves contributed 60 of these pair-flips. Of the 138 total pair-flips, one-half (70) occurred within the first 60 interactions after group members were introduced on the first day of observation. In addition, most pair-flips occurred in sequences of two—a counter attack followed by a reverse counter attack. (For example, the pattern *ApB, ApB, ApB, BpA, ApB* involves two sequential pair-flips, where the first pair-flip (*BpA*) is immediately followed by a countering pair-flip (*ApB*)). Accounting for this observation, that pair-flips are often coupled, we note that effectively only 1% of all interaction sequences involved pair-flip behavior. The pair-flip data thus show that immediate retaliation to aggression, while occurring, is very infrequent. Furthermore, half of all pair-flip

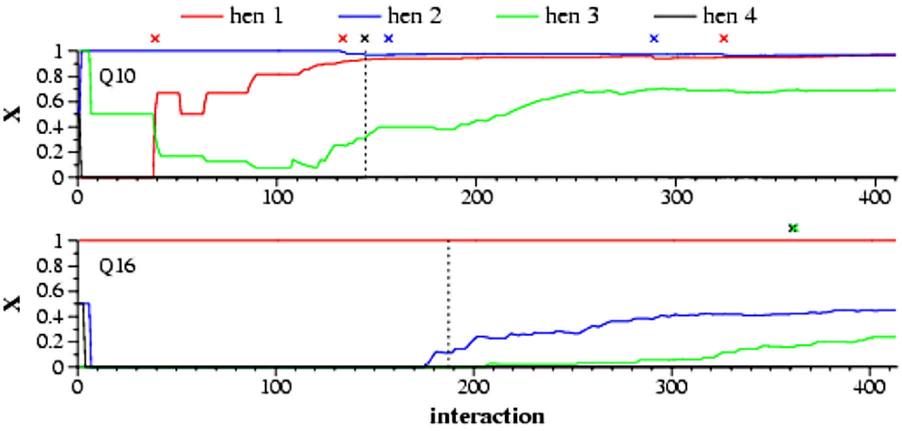

Fig. 9 Individual dominance index value as a function of time (in interaction counts) for groups Q10 and Q16. The traces show "rank emergence" behavior (for hens 1 and 3 in Q10, hens 2 and 3 in Q16), suggesting that the birds appear to be reinforcing their rank status. The dotted vertical line indicates the day 1/day 2 observation delimiter. Positions marked by an '×' along the top of a plot indicate times at which pair-flips occur. (Color figure online.)

challenges occurred in the early-stage of hierarchy formation. These two observations imply that rank-position is determined rapidly in groups of hens, in a manner that might be termed "efficient." *We suggest that efficiency, namely the lack of pair-flips, may be a general characteristic of hierarchy formation across species and that it stands in contrast to relationship formation in isolated pairs, which are characterized by higher numbers of pair-flips.*

4.3. *Rank emergence*

Figure 9 shows the time-development of the dominance index, $X_i(t)$, for the individual birds in two example groups Q10 and Q16. In each group, an initially dominant hen emerges early (hen 2 in Q10, hen 1 in Q16). However, both sets of traces show subsequent, time separated, "rank emergence" behavior by other hens (birds 1 and 3 in Q10, birds 2 and 3 in Q16). In fact, for hen 1 in Q10, the emergence is sufficiently strong that it vies for, and eventually surpasses, hen 2 as the dominant individual. This behavior of time separated, relatively rapid, rise in individual X-values suggests that the hens may be trying to declare and cement their rank. (The graphs also show that although rank emergence of some hens occurred only after a considerable number of interactions, it was not triggered by the reintroduction of group members on day 2, after their overnight separation. The emergence of bird 1 in Q10 and the beginning of the emergences of bird 3 in Q10 and bird 2 in Q16 all occurred during day 1.) Rank emergence can only occur when a bird pecks either birds of lower or higher rank. The "×" symbols at the top of each graph in Fig. 9 indicate times at which pair-flips occurred. From these, we see that there is no correlation between rank emergence and pair-flips; rank emergence is therefore overwhelmingly attained by pecking birds of lower rank (as is evident from Fig. 7) and, of course, correlates with bursting. *It is tempting to speculate that rank emergence appears to be the result of a concentrated and perhaps purposeful series of actions.*

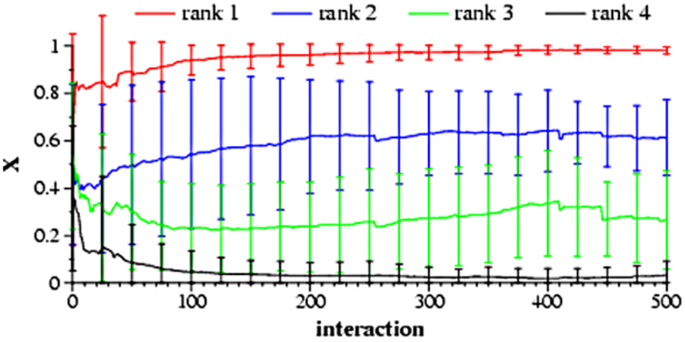

Fig. 10 Mean and standard deviation (over the 14 groups) of the dominance index according to the final ranking achieved by the individual. (Color figure online.)

Figure 10 shows the time development (measured in interaction count) of the average and standard deviation (determined over the 14 groups) of $X(t)$ according to the final ranking achieved by the individual over the 2 days of observation. Except for the highest ranked individual, the coefficient of variation (standard deviation/mean) of $X(t)$ remained sizable, even after many interactions. *The behavior of the coefficient of variation indicates that, on average, the dominant individual emerges early, but the emergence of the remaining ranks occurs on a more variable time scale.*

4.4. State occurrence and stability

To investigate how dominance relationships evolve, we have developed a new methodology—tracing each group's development through intermediate configurations of dominance relationships. We call each possible configuration of relationships among members of the group a "state"; the set of all configurations is the "state space"; the route that a group takes through state space is a "path." (See Doreian (2006) and the literature reviewed therein for related ideas.)

Using directed-graph representation, Fig. 11 displays the 41 distinct states documenting all dominance relationship structures (except for the trivial state showing no dominance relationships) possible among 4 individuals. The organization concentrates only on the structural form of the relationships in a group and not the identity of the particular animals—two states are the same if their graphs differ only by vertex relabeling. Use of relabeling symmetry reduces to a manageable number the combinatorially large number of states required if the identities of the animals were preserved. The states are grouped into classes by structure. Pair-flips can convert any state within a class into any other state in the same class but cannot take a state from one class to another.

We refer to subgroups of three individuals within a larger group as triads. In D_T (state 10, Fig. 11), the dominance relationships expressed are said to form a transitive triad, in D_I (state 11) the dominance relationships form an intransitive triad (Chase and Rohwer, 1987). (A state comprised of more than 3 animals is a linear hierarchy if and only if all possible pairwise relationships are established and the state contains only transitive triads.) In recognition of the distinction between transitive and intransitive relationships, we further divide each of classes H, F, and S into a subclass containing configurations

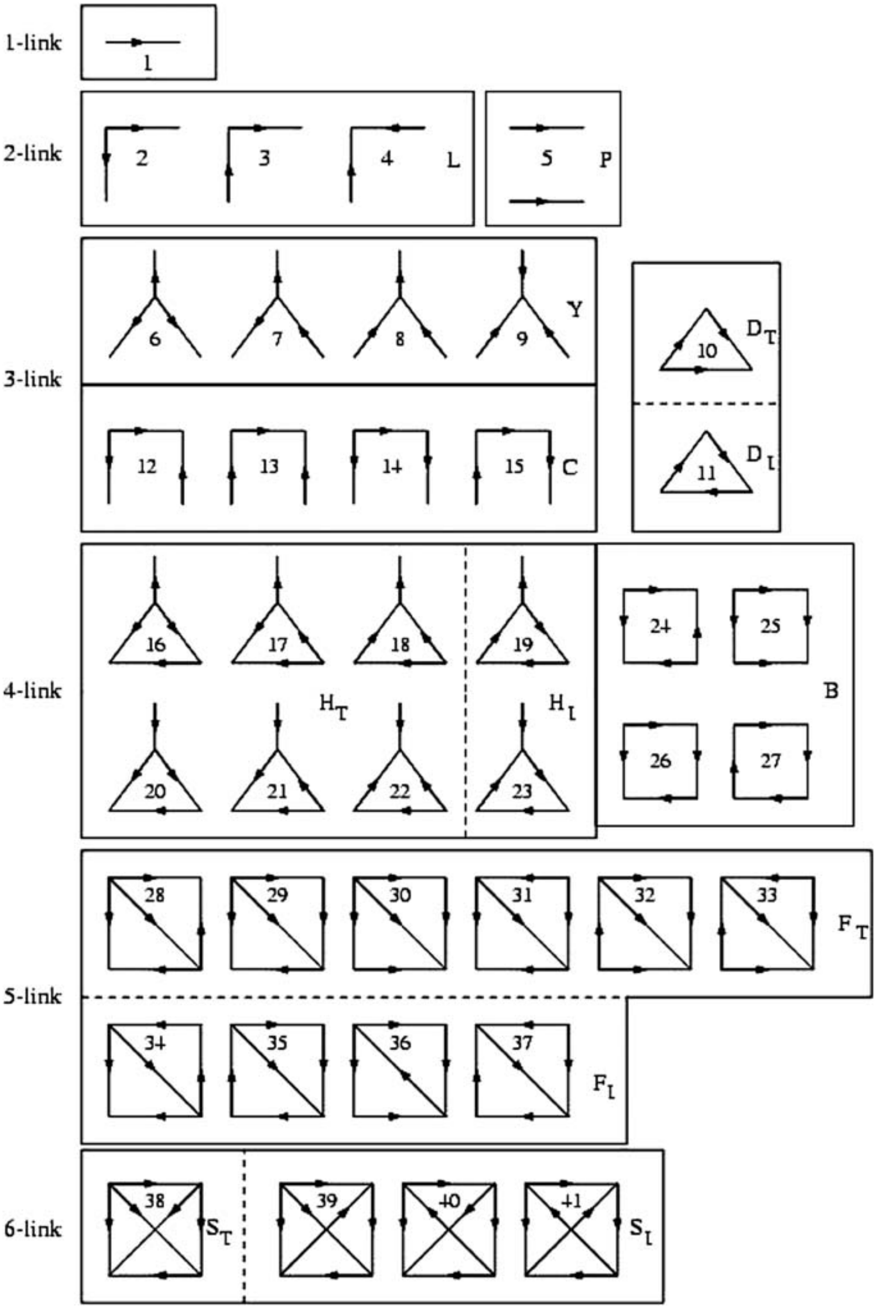

Fig. 11 Directed graphs representing the 41 distinct states for a group of 4 animals. The states are labeled 1 to 41 and arranged according to number of established relationships (links), classes, and transitive-intransitive subclasses. Vertices are animals, directed links indicate dominance. Missing vertices indicate animals that have not (yet) participated in any dominance relationship.

with only transitive triads and a subclass containing configurations with at least one intransitive triad. Note in particular that state 38 represents the only 6-link (6-relationship) state in which the hierarchical structure is linear.

In tracing the pathway of a group through state space, we track the occurrence of each successive aggressive act in the group and consider that a relationship is formed whenever an aggressive act *first occurs* between each distinct pair of animals.

Once a group has reached a particular state, the pairwise interactions may simply repeat previously formed relationships before the group evolves to a new state. We consider the length of time during which interactions maintain a given state as an indication of its *class-stability*. We compute the class-stability of a state as the ratio of the number of interactions during which all groups remain in that particular state to the total number of interactions during which all groups remained in all states of the same link-number class. For example, of all interactions during which groups remained in 4-link states, 88.5% of these involved groups remaining in state 16 of class H. Thus, the class-stability factor (CSF) for state 16 is 0.885.

We differentiate class-stability of a state from its frequency of occurrence. We calculate class occurrence frequency (COF) as the fraction all groups that went through a particular state during the development of their hierarchies. For example, state 29 showed up in 9/14 (COF = 0.643) of the groups. Note that path history can serve to preclude certain states from a group. For example, once in state 5 (class P), a group can never evolve to states in classes Y or D.

The top graph in Fig. 12 summarizes the observed COF of each state in the experimental groups; the bottom graph summarizes the CSF of each state. We make several observations about the data in Fig. 12 and state space pathway.

The first observation is general. Although all of the groups eventually reached state 38, the linear hierarchy, there was considerable variation among the specific paths that individual groups took (path data not shown, but available on request). In spite of this variation, some states were frequently visited and some were rarely visited, i.e., there were states that were highly class-stable and some that were relatively class-unstable.

Second, the states that occurred most frequently (in at least 50% of the groups) were 14, 16, 29, 38, and 39. It is not clear whether there is a common reason for these frequently occurring states. We note that states 16, 38, and 39 are the only 4- and 6-link states that contain one individual that dominates all the others (a "DAO"). This is also true for the, respectively, 3- and 5-link states, 14 and 29, but there are also other, infrequently-occurring states in their link classes that share this trait. Surprisingly, and in some contrast, one of the 3-link states, state 6, which contains a DAO, occurred in only one experimental group. Thus, in many of the group state space pathways, a DAO emerged early in the development of a hierarchy.

Third, except for state 39, which occurred in 50% of the groups, states that contain triads with intransitive relationships rarely occurred. All of these intransitive states are highly class-unstable; they account for: 0% of the time that groups spent in 3-link states; 3.9% in 4-link states; 1.2% in 5-link states; and 1.8% in 6-link states.

Fourth, in each link class, one state was considerably more class-stable than the others—2-link: state 4 (CSF = 0.52); 3-link: state 6 (CSF = 0.64); 4-link: state 16 (CSF = 0.88); 5-link: state 28 (CSF = 0.53); and 6-link: state 38 (CSF = 0.98). *Class-stability is highly correlated with the presence of a DAO*: in the 3- and 4-link classes, the most stable state is the only one having a DAO; in the 5-link class, the aggregate CSF

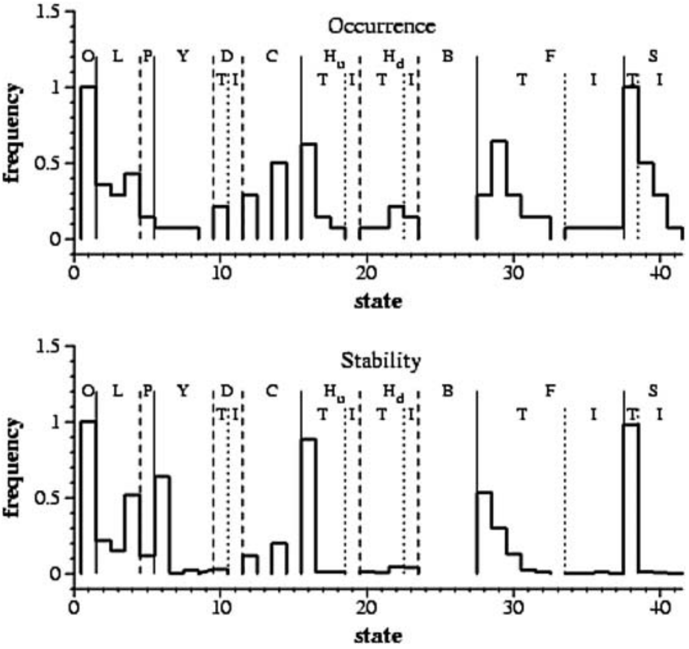

Fig. 12 *Top*: Observed class occurrence frequencies (top) and class-stability factors (bottom) for each state. In both plots, vertical solid lines divide states having differing number of links, vertical dashed lines indicate subclasses and vertical dotted lines, demark transitive/intransitive state subgroupings.

for the three DAO states (28, 29, and 30) is 0.96; state 38 is the linear hierarchy, and is the only 6-link state that has both a DAO and no intransitive relationships. In the 2-link class, the class-stability of state 4 is somewhat surprising in that state 2 would be most consistent with having a future DAO.

Fifth, some states were completely absent (COF = 0). These are state 9 in the Y class; states 13 and 15 in the C class, all of the B states, and state 33 in the F_T class. Several of these absences are striking in the sense that possible precursor states to the missing states are reasonable common. (State N is a precursor state to state M if M can be created from N by the addition of a single link.) We have been unable to identify a commonality among these states that would explain their absence—certainly sample-size statistics might account for some absences.

5. Discussion

While winner-loser models have been an important first step, our investigations suggest that they cannot adequately account for linear hierarchy formation in real animals and that a new generation of models reflecting the considerable abilities that animals use in forming hierarchies is needed. Our assessment in part one of the paper finds a lack of empirical verification for the mathematical formulations of the models, and our examination of the current empirical literature (part two) does not show support for the core assumptions of the models.

However, there are several points that should be considered in our evaluation of these models. First, we compared the mathematical formulations of the models only to one data set of real animals forming hierarchies. As far as we are aware, no other data set continuously following the aggressive activity in groups of animals from introduction through the establishment of stable dominance hierarchies is presently available. Bonabeau et al. (1999) indicate that their model was motivated by experiments with *Polistes* wasps and that it may not be appropriate for other types of animals. Hemelrijk (2000), on the other hand, was particularly interested in modeling the development of hierarchies in primate species. Dugatkin's (1997) model is of a more general nature and not directed toward a particular variety of species. Perhaps if data sets comparable to the one from the hens had been available for other animals, we might have found a different level of support for the mathematical formulations of the models.

Second, in comparing the mathematical formulations of the models against data from hierarchy formation in the hens, we assumed that changes in the dominance value ("force," "resource holding power (RHP)") of the hens occurred with interactions involving physical contact (pecks, jump ons, and claws). This is certainly the idea in the Bonabeau and Hemelrijk models, but the Dugatkin model is more inclusive and assumed that RHP may be updated in interactions beyond those involving physical contact e.g., ones consisting of chases of one animal by another. This raises the possibility that had our dataset also included dominance interactions not involving physical contact, we might have found a different level of fit—either better or worse—between the mathematical formulations of that model and the empirical data. In defense of our analysis, we argue that aggressive physical contact interactions are certainly very good indicators of relative dominance status between hens and should correlate strongly with dominance change.

We have also assumed the most natural relationship between the experimental measures $D_i(t)$, $S_i(t)$ and each model's force parameter (Eqs. (6) and (14)) or, in the case of the Hemelrijk model, between the experimental measures and the increment indicator (Eq. (23)). It can be argued that more complex relationships should be used to relate the experimental measures to the force parameter. We concede the point, but have no theoretical or data-driven basis on what other choice should be made.

Third, as we have stated, as far as we are aware, only one study has investigated the presence of winner and loser effects in groups of animals. While this study found neither of these effects in groups of a species of cichlid fish (Chase et al., 2003), it is possible that they could be found in other species.

Any possible limitations of our evaluation of the models aside, recent research shows that animals across many species bring a rich array of abilities of social cognition to the formation of dominance relationships. This literature itself argues for a new generation of models of hierarchy formation. We now know that animals eavesdrop on the encounters of other individuals and that they are capable of making quite sophisticated inferences about what they have seen and to alter their behavior when they meet those that they have earlier observed (Beecher and Campbell, 2005; Cheney and Seyfarth, 1990; Earley and Dugatkin, 2002; Hogue et al., 1996; Johnstone, 2001; McGregor, 2005; Oliveira et al., 2001; Oliveira et al., 1998; Paz-y-Mino et al., 2004). This literature demonstrates that animals of various species react differently to those they have seen lose or win previous contests and use escalated or de-escalated levels of aggressive behaviors, respectively, when they later meet the individuals observed. We also know that animals of various species can infer transitivity in dominance relationships; the list includes several species of nonhuman primates, rodents, birds, and fish (Bond et al., 2003; Davis, 1992; Gillian, 1981; Grosenick et al., 2007; Paz-y-Mino et al., 2004; Roberts and Phelps, 1994; Steirn et al., 1995; von Fersen et al., 1991). We suggest that inferences about networks of relationships, such as those about transitivity, will prove particularly important to understanding the development of linear hierarchy structures.

Some researchers have expanded winner-loser models to incorporate individual recognition and third party ("bystander") observation (Beacham, 2003; Dugatkin, 2001; Dugatkin and Earley, 2003, 2004). Indeed the "indirect" variations of the direct, obligatory model of Hemelrijk (2000) critiqued in this paper incorporate "indirect perception" effects. These models assume some level of individual recognition (though not transitive inference) but retain the fundamental formulation of winner-loser models in that the dominance score of the bystander is updated according to its observations on other interacting pairs. It is beyond the scope of the current paper to subject such bystander models to the data-based scrutiny performed here. However, such models simply provide an additional level of manipulation for the winning-losing probabilities of individuals in pair-wise contests and do not incorporate the more sophisticated levels of social cognition that animals use during hierarchy formation. Given this, it is not clear that the addition of bystander effects could duplicate real data on interactions during hierarchy formation.

While our intention in this paper was to consider only the best known winner-loser models, we acknowledge the existence of other models that depart from the winner-loser tenets. An example of these are the multiplayer game models of Broom, Cannings, and Vickers. (See references in Broom and Cannings, 2002). The model in Broom and Cannings (2002) combines n-round Swiss tournaments to organize pair-wise interactions with game-theoretic Hawk–Dove models for each interaction outcome. While this model is not strictly winner-loser and, therefore, not explicitly evaluated in this work, our data brings two points of caution in regards to this model. The first is the Broom–Canings model's prediction that once "basic" competition is over, "one would expect to see (after basic competition) primarily interactions between individuals of similar rank." This is not born out by our hen data; see, e.g., Fig. 7. The second is the prediction that "the chance of a triad involving the top player being cyclic (i.e., being intransitive) is zero." In the hen data, the top player is involved in 63% of all intransitive triads. Observations of this sort emphasize the need for more data, over more species, on group hierarchy formation.

Directly interacting with all members of a group can be time consuming, divert attention from more useful activities, and can lead to greater possibilities of injury or death (Cheney and Seyfarth, 2007; Seitz, 2003). Consequently, researchers have speculated that animals could be selected for the capacity to infer transitivity as a way to avoid these potential costs (Bond et al., 2003; Grosenick et al., 2007; Nakamaru and Sasaki, 2003). More broadly, as has been noted, the evolution of behavior in dominance hierarchy formation must be seen as occurring within networks of individuals rather than in independent pairs (Cheney and Seyfarth, 2007; McGregor, 2005; Mesterton-Gibbons and Sherratt, 2007; Oliveira et al., 1998). Although no investigative work has yet been done, our stability data suggests that, in addition to inferring transitivity, chickens may also be able to infer intransitivity in dominance relationships and to take actions to convert intransitive relationships to transitive ones. An earlier study of the formation of dominance relationship in relatively large groups of Harris sparrows (Chase and Rohwer, 1987) similarly found that intransitive relationships were less stable than transitive relationships and that, over time, the intransitive relationships converted to transitive ones. Taken together, our findings, plus experimental studies in the literature, suggest that hierarchy formation pathways may "favor" states with only transitive relationships because animals can infer transitivity and tend to fill in configurations of relationships that preserve this quality. However, our data show that the hens do not follow rigid state pathways (i.e., pathways that follow transitive-only states), but may use other mechanisms, very possibly cognitive ones, that allow them to register intransitive relationships and convert them to transitive ones.

In our analysis of hierarchy formation, we found a number of features that fit with this new research on social cognition and similarly suggest that the hens were intensely aware of the outcomes of their own interactions and those of their fellow group members. We propose that these features may be common across many species forming linear hierarchies, and we propose that they be considered in future models of hierarchy formation.

In conclusion, this paper makes three contributions to the understanding of hierarchy formation:

1. It combines empirical data on animals forming dominance hierarchies and the recent experimental evidence on social cognition to suggest that winner-loser models are not adequate accounts of the formation of linear dominance hierarchies in animals.
2. Combining the results reported here with those from the earlier work reviewed in the Introduction concerning prior differences in individuals and explanation of linear hierarchies, this paper suggests that neither models based upon intrinsic differences in individuals nor extrinsic ones—those that they develop through interaction—can explain the development of linear hierarchies. Thus, this earlier work and our findings here argue against both "state" and "trait" explanations, as they are sometimes called in the psychology literature (e.g., see the discussion in Magnusson and Endler, 1977). While this evidence is not proof that no model relying upon differences among individuals can adequately account for these linear social structures, it strongly suggests the possibility that a different type of approach may be needed.
3. It suggests new directions for experimental studies of the dynamic behavioral processes occurring during hierarchy formation and the incorporation of these processes in new models of hierarchy formation.

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References

Addison, W.E., Simmel, E.C., 1970. The relationship between dominance and leadership in a flock of ewes. Bull. Psychon. Soc. 15, 303–305.

Bakker, T.C.M., Sevenster, P., 1983. Determinants of dominance in male sticklebacks (*Gasterosteus aculeatus L*). Behaviour 86, 55–71.

Bakker, T.C.M., Feuthdebruijn, E., Sevenster, P., 1989. Asymmetrical effects of prior winning and losing on dominance in sticklebacks (*Gasterosteus aculeatus*). Ethology 82, 224–229.

Barkan, C.P.L., Craig, J.L., Strahl, S.D., Stewart, A.M., Brown, J.L., 1986. Social-dominance in communal Mexican Jays *Aphelocoma ultramarina*. Anim. Behav. 34, 175–187.

Beacham, J.L., 1988. The relative importance of body size and aggressive experience as determinants of dominance in pumpkinseed sunfish *Lepomis gibbosus*. Anim. Behav. 36, 621–623.

Beacham, J.L., 2003. Models of dominance hierarchy formation: Effects of prior experience and intrinsic traits. Behaviour 140, 1275–1303.

Beacham, J.L., Newman, J.A., 1987. Social experience and the formation of dominance relationships in the pumpkinseed sunfish, *Lepomis gibbosus*. Anim. Behav. 35, 1560–1563.

Beaugrand, J.P., Cotnoir, P.A., 1996. The role of individual differences in the formation of triadic dominance orders of male green swordtail fish (*Xiphophorus helleri*). Behav. Process. 38, 287–296.

Beecher, M.D., Campbell, S.E., 2005. The role of unshared songs in singing interactions between neighbouring song sparrows. Anim. Behav. 70, 1297–1304.

Bonabeau, E., Theraulaz, G., Deneubourg, J.-L., 1996. Mathematical model of self-organizing hierarchies in animal societies. Bull. Math. Biol. 58, 661–717.

Bonabeau, E., Theraulaz, G., Deneubourg, J.-L., 1999. Dominance orders in animal societies: the self-organization hypothesis revisited. Bull. Math. Biol. 61, 727–757.

Bond, A.B., Kamil, A.C., Balda, R.P., 2003. Social complexity and transitive inference in corvids. Anim. Behav. 65, 479–487.

Broom, M., Cannings, C., 2002. Modelling dominance hierarchy formation as a multi-player game. J. Theor. Biol. 219, 397–413.

Brown, J.A., Colgan, P.W., 1986. Individual and species recognition in centrarchid fishes: evidence and hypotheses. Behav. Ecol. Sociobiol. 19, 373–379.

Burke, T.E., 1979. An Analysis of Social Behaviour in Crickets. University of Oxford, Oxford.

Chase, I.D., 1974. Models of hierarchy formation in animal societies. Behav. Sci. 19, 374–382.

Chase, I.D., 1982. Behavioral sequences during dominance hierarchy formation in chickens. Science 216, 439–440.

Chase, I.D., 1985. The sequential analysis of aggressive acts during hierarchy formation—an application of the jigsaw puzzle approach. Anim. Behav. 33, 86–100.

Chase, I.D., 2006. Music notation: a new method for visualizing social interaction in animals and humans. Front. Zool. 3, 18.

Chase, I.D., Rohwer, S., 1987. Two methods for quantifying the development of dominance hierarchies in large groups with applications to Harris' sparrows. Anim. Behav. 35, 1113–1128.

Chase, I.D., Bartolomeo, C., Dugatkin, L.A., 1994. Aggressive interactions and inter-contest interval: how long do winners keep winning. Anim. Behav. 48, 393–400.

Chase, I.D., Tovey, C., Spangler-Martin, D., Manfredonia, M., 2002. Individual differences versus social dynamics in the formation of animal dominance hierarchies. Proc. Natl. Acad. Sci. U.S.A. 99, 5744–5749.

Chase, I.D., Tovey, C., Murch, P., 2003. Two's company, three's a crowd: differences in dominance relationships in isolated versus socially embedded pairs of fish. Behaviour 140, 1193–1217.

Cheney, D.L., Seyfarth, R.M., 1990. How Monkeys See the World: Inside the Mind of Another Species. University of Chicago Press, Chicago.

Cheney, D.L., Seyfarth, R.M., 2007. Baboon Metaphysics: The Evolution of a Social Mind. University of Chicago Press, Chicago.

Cloutier, S., Beaugrand, J.P., Lague, P.C., 1996. The role of individual differences and patterns of resolution in the formation of dominance orders in domestic hen triads. Behav. Process. 38, 227–239.

Clutton-Brock, T.H., Albon, S.D., Guinness, F.E., 1984. Maternal dominance, breeding success and birth sex-ratios in red deer. Nature 308, 358–360.

D'Eath, R.B., Keeling, L.J., 2003. Social discrimination and aggression by laying hens in large groups: from peck orders to social tolerance. Appl. Anim. Behav. Sci. 84, 197–212.

D'Ettorre, P., Heinze, J., 2005. Individual recognition in ant queens. Curr. Biol. 15, 2170–2174.

Davis, H., 1992. Transitive inference in rats (*Rattus norvegicus*). J. Comp. Psychol. 106, 342–349.

Doreian, P., 2006. Actor network utilities and network evolution. Soc. Netw. 28, 137–164.

Drews, C., 1993. The concept and definition of dominance in animal behavior. Behaviour 125, 283–313.

Drummond, H., 2006. Dominance in vertebrate broods and litters. Q. Rev. Biol. 81, 3–32.

Drummond, H., Canales, C., 1998. Dominance between booby nestlings involves winner and loser effects. Anim. Behav. 55, 1669–1676.

Drummond, H., Osorno, J.L., 1992. Training siblings to be submissive losers: dominance between booby nestlings. Anim. Behav. 44, 881–893.

Dugatkin, L.A., 1997. Winner and loser effects and the structure of dominance hierarchies. Behav. Ecol. 8, 583–587.

Dugatkin, L.A., 2001. Bystander effects and the structure of dominance hierarchies. Behav. Ecol. 12, 348–352.

Dugatkin, L.A., Earley, R.L., 2003. Group fusion: the impact of winner, loser, and bystander effects on hierarchy formation in large groups. Behav. Ecol. 14, 367–373.

Dugatkin, L.A., Earley, R.L., 2004. Individual recognition, dominance hierarchies and winner and loser effects. Proc. R. Soc. Lond. Ser. B Biol. Sci. 271, 1537–1540.

Earley, R.L., Dugatkin, L.A., 2002. Eavesdropping on visual cues in green swordtail (*Xiphophorus helleri*) fights: a case for networking. Proc. R. Soc. Lond. Ser. B Biol. Sci. 269, 943–952.

Ellis, L., 1995. Dominance and reproductive success among nonhuman animals: a cross-species comparison. Ethol. Sociobiol. 16, 257–333.

Francis, R.C., 1983. Experiential effects of agonistic behavior in the paradise fish, *Macropodus opercularis*. Behaviour 85, 292–313.

Francis, R.C., 1987. The interaction of genotype and experience in the dominance success of paradise fish (*Macropodus opercularis*). Biol. Behav. 12, 1–11.

Frey, D.F., Miller, R.J., 1972. The establishment of dominance relationships in blue gourami, *Trichogaster trichopterus* (Pallas). Behaviour 42, 8–62.

Gherardi, F., Atema, J., 2005. Memory of social partners in hermit crab dominance. Ethology 111, 271–285.

Gillian, D.J., 1981. Reasoning in the chimpanzee: II. Transitive inference. J. Exp. Psychol. Anim. Behav. Process. 7, 87–108.

Goessmann, C., Hemelrijk, C., Huber, R., 2000. The formation and maintenance of crayfish hierarchies: behavioral and self-structuring properties. Behav. Ecol. Sociobiol. 48, 418–428.

Grosenick, L., Clement, T.S., Fernald, R.D., 2007. Fish can infer social rank by observation alone. Nature 445, 429–432.

Hausfater, G., Altmann, J., Altmann, S., 1982. Long-term consistency of dominance relations among female baboons (*Papio cynocephalus*). Science 217, 752–755.

Heinze, J., 1990. Dominance behavior among ant females. Naturwissenschaften 77, 41–43.

Hemelrijk, C.K., 1999. An individual orientated model of the emergence of despotic and egalitarian societies. Proc. R. Soc. Lond. Ser. B: Biol. Sci. 266, 361–369.

Hemelrijk, C.K., 2000. Towards the integration of social dominance and spatial structure. Anim. Behav. 59, 1035–1048.

Hogue, M.E., Beaugrand, J.P., Lague, P.C., 1996. Coherent use of information by hens observing their former dominant defeating or being defeated by a stranger. Behav. Process. 38, 241–252.

Holekamp, K.E., Smale, L., 1993. Ontogeny of dominance in free-living spotted hyenas: juvenile rank relations with other immature individuals. Anim. Behav. 46, 451–466.

Hsu, Y.Y., Wolf, L.L., 1999. The winner and loser effect: integrating multiple experiences. Anim. Behav. 57, 903–910.

Jackson, W.M., 1988. Can individual differences in history of dominance explain the development of linear dominance hierarchies. Ethology 79, 71–77.

Jackson, W.M., Winnegrad, R.L., 1988. Linearity in dominance hierarchies: a second look at the individual attributes model. Anim. Behav. 36, 1237–1240.

Johnstone, R.A., 2001. Eavesdropping and animal conflict. Proc. Nat. Acad. Sci. U.S.A. 98, 9177–9180.

Karavanich, C., Atema, J., 1998. Individual recognition and memory in lobster dominance. Anim. Behav. 56, 1553–1560.

Lai, W.-S., Ramiro, L.-L.R., Yu, H.A., Johnston, R.E., 2005. Recognition of familiar individuals in golden hamsters: a new method and functional neuroanatomy. J. Neurosci. 25, 11239–11247.

Landau, H.G., 1951. On dominance relations and structures of animal societies. Bull. Math. Biophys. 13, 1–19.

Lazareva, O.F., 2004. Transitive responding in hooded crow requires linearly ordered stimuli. J. Exp. Anal. Behav. 82, 1–19.

Magnusson, D., Endler, N.S., 1977. Personality at the Crossroads, p. 464. Lawrence Erlbaum Associates, Hillsdale.

McGregor, P.K., 2005. Animal Communication Networks, Cambridge University Press, Cambridge.

McLeman, M.A., Mendl, M., Jones, R.B., White, R., Wathes, C.M., 2005. Discrimination of conspecifics by juvenile domestic pigs, *Sus scrofa*. Anim. Behav. 70, 451–461.

Mesterton-Gibbons, M., Sherratt, T.N., 2007. Social eavesdropping: A game-theoretic analysis. Bull. Math. Biol. 69, 1255–1276.

Nakamaru, M., Sasaki, A., 2003. Can transitive inference evolve in animals playing the hawk-dove game? J. Theor. Biol. 222, 461–470.

Nelissen, M.H.J., 1985. Structure of the dominance hierarchy and dominance determining group factors in *Melanochromic auratus* (Pices, Cichlidae). Behaviour 94, 85–107.

Oliveira, R.F., McGregor, P.K., Latruffe, C., 1998. Know thine enemy: fighting fish gather information from observing conspecific interactions. Proc. R. Soc. Lond. Ser. B Biol. Sci. 265, 1045–1049.

Oliveira, R.F., Lopes, M., Carneiro, L.A., Canario, A.V.M., 2001. Watching fights raises fish hormone levels—Cichlid fish wrestling for dominance induce an androgen surge in male spectators. Nature 409, 475–475.

Paz-y-Mino, G., Bond, A.B., Kamil, A.C., Balda, R.P., 2004. Pinyon jays use transitive inference to predict social dominance. Nature 430, 778–781.

Post, W., 1992. Dominance and mating success in male boat-tailed grackles. Anim. Behav. 44, 917–929.

Raleigh, M.J., McGuire, M.T., Brammer, G.L., Pollack, D.B., Yuwiler, A., 1991. Serotonergic mechanisms promote dominance acquisition in adult male Vervet monkeys. Brain Res. 559, 181–190.

Roberts, W.A., Phelps, M.T., 1994. Transitive inference in rats—a test of the spatial coding hypothesis. Psychol. Sci. 5, 368–374.

Sapolsky, R.M., Share, L.J., 1994. Rank-related differences in cardiovascular function among wild baboons: role of sensitivity to glucocorticoids. Am. J. Primatol. 32, 261–275.

Savin-Williams, R.C., 1980. Dominance hierarchies in groups of middle to late adolescent males. J. Youth Adolesc. 9, 75–85.

Seitz, K., 2003. The dominance hierarchy as a supraindividual trait: historical perspectives and future directions. Master's thesis, Binghamton University.

Skiena, S., 1990. Implementing Discrete Mathematics: Combinatorics and Graph Theory with Mathematica. Addison–Wesley, Reading.

Skvoretz, J., Faust, K., Fararo, T.J., 1996. Social, structure, networks, and E-state structuralism models. J. Math. Soc. 21, 57–76.

Slater, P.J.B., 1986. Individual-differences and dominance hierarchies. Anim. Behav. 34, 1264–1265.

Steirn, J.N., Weaver, J.E., Zentall, T.R., 1995. Transitive inference in pigeons: Simplified procedures and a test of value transfer theory. Anim. Learn. Behav. 23, 76–82.

Tibbetts, E.A., 2002. Visual signals of individual identity in the wasp *Polistes fuscatus*. Proc. R. Soc. Lond. Ser. B Biol. Sci. 269, 1423–1428.

Todd, J.H., Attema, J., Bardach, J.E., 1967. Chemical communication in social behavior of a fish, the yellow bullhead (*Ictalurus natalis*). Science 158, 672–673.

Vannini, M., Sardini, A., 1971. Aggressivity and dominance in river crab *Potomon fluviantile* (Herbst). Monit. Zool. Ital. 5, 173–213.

von Fersen, L., Wynne, C.D., Delius, J.D., Staddon, J.E., 1991. Transitive inference formation in pigeons. J. Exp. Psychol. Anim. Behav. Process. 17, 334–341.

Wilson, E.O., 1975. Sociobiology. Harvard University Press, Cambridge.

Yurkovic, A., Wang, O., Basu, A.C., Kravitz, E.A., 2006. Learning and memory associated with aggression in *Drosophila melanogaster*. Proc. Natl. Acad. Sci. U.S.A. 103, 17519–127524.

Zucker, N., Murray, L., 1996. Determinants of dominance in the tree lizard *Urosaurus ornatus*: The relative importance of mass, previous experience and coloration. Ethology 102, 812–825.