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Individual attributes and self-organizational processes affect dominance network structure in pukeko

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Dominance relationships are an important type of social relationship that can influence group dynamics and individual fitness. However, most studies on dominance have been restricted to investigating the orderliness of dominance hierarchies and how individual traits influence dominance rank. Here, we used a social network approach to investigate the patterns and quality of dominance interactions in the pukeko, a cooperatively breeding bird that lives in stable, mixed-sex social groups. By using a combination of modern statistical techniques, including one of the first applications of exponential random graph models in behavioral ecology, we show that pukeko dominance networks emerge from both the attributes of individuals, as well as from endogenous, self-organization of dominance relationships (i.e., structural dependence). Pukeko dominance networks were influenced by sexual differences in dominance interactions, sexual homophily, characteristics of status signals, and a tendency to form transitive triad motifs. These factors have differential effects on submissive and aggressive behaviors but ultimately lead to the formation of orderly and highly asymmetrical dominance hierarchies that are temporally stable. This study demonstrates the utility of multivariate statistical tools for network analysis of animal societies and provides a rich understanding of the factors that influence dominance interactions in this interesting species.

Key words: **ERGM, linearity, self-organization, status, steepness, subordinate.**

INTRODUCTION

Dominance relationships are a ubiquitous type of social relationship observed among a taxonomically diverse set of animals. Because dominance relationships influence access to various resources (including mating opportunities, e.g., Ellis 1995), they can be a strong contributor to individual variation in fitness. As a result, understanding both the causes and consequences of dominance has been an intense research focus in behavioral ecology ever since Schjelderup-Ebbe (1922) first described "peck order" in domestic chickens (*Gallus gallus*). Dominance is fundamentally a relationship between a pair of individuals (Drews 1993), however many researchers have been interested in the structure of dominance interactions among groups of actors (hereafter termed dominance networks). In the vast majority of species studied to date, dominance networks are more orderly (i.e., transitive or linear; see below) than expected by random processes (e.g., see meta-analyses by Shizuka and McDonald 2012; McDonald and Shizuka 2013).

While orderly dominance networks can be due to differences in individual attributes alone (Piper 1997), there is good evidence that dominance networks are influenced by factors such as winner, loser, and bystander effects (Dugatkin and Earley 2003). These processes act independently of the attributes of individuals and can promote the self-organization of orderly hierarchies (Chase et al. 2002; Chase and Seitz 2011). Regardless of the mechanism, the consistency with which animals form orderly dominance networks suggests that patterns of dominance interactions are an important aspect of group living. Indeed stable, hierarchical dominance relationships could provide various benefits such as minimizing physical aggression (Meese and Ewbank 1973; Mock and Ploger 1987) and increasing the speed of collective decision making (Lampkin 1972).

Despite general agreement that dominance relationships have consequences for group dynamics and impact individual fitness (Ellis 1995; Barta and Giraldeau 1998), we know very little about variation in dominance network structure beyond measures of orderliness such as linearity (Landau 1951; de Vries 1995) or triangle transitivity (Shizuka and McDonald 2012). This focus on orderliness is a logical extension of studies that have investigated what factors cause certain individuals to become dominant or

subordinate. But while orderliness and rank are certainly important aspects of group living, they do not fully describe the variation in dominance interactions experienced by animals. For example, a dominant animal that is subject to frequent physical challenges from subordinates experiences a much different social environment than one who predominantly receives submissive gestures, despite occupying similar ranks. Likewise, within an orderly hierarchy, individuals may primarily interact with other individuals of similar rank or may interact equally with other group members regardless of rank. These types of variation in animal dominance networks have been largely unexplored, which may be partially because few dominance studies have considered replicate social groups of their focal species, and it is therefore difficult to test for general underlying factors that contribute to variation in dominance interactions. However, with proper study design and new statistical tools (see below), researchers should be able to explicitly study the causes and consequences of variation in dominance network structure, which will contribute to a much richer understanding of how dominance relationships affect the lives of social animals.

Social network analysis (SNA) is a promising tool for investigating dominance network structure because it provides a quantitative framework for analyzing patterns of interactions among groups of individuals (Croft et al. 2008). In a social network representation of dominance interactions, individual animals are depicted by nodes, whereas dominance interactions are represented by ties (also called edges) that link the nodes. In addition to this relational data, SNA can also integrate aspects of each individual's phenotype (e.g., sex) and the structural dependence between ties (e.g., "friend of a friend" effects) which allows researchers to analyze the relationships between individual, dyadic, local, and group-level phenomena (see Krause et al. 2007; Wey et al. 2008, Sih et al. 2009; Pinter-Wollman et al. 2013 for reviews of SNA in behavioral ecology). To date, the majority of SNA studies in behavioral ecology have used univariate statistical methods (Pinter-Wollman et al. 2013), which do not allow for strong inference on the factors that determine network structure because other potentially important factors have not been accounted for. However, the application of statistical tools that allow for simultaneous evaluation of the influence of multiple variables (e.g., exponential random graph models [ERGMs], Wasserman and Pattison 1996; Snijders et al. 2006) should allow for more rigorous hypothesis testing of the factors that determine network structure in animal groups (Pinter-Wollman et al. 2013). In this paper, we provide one of the first uses of these multivariate methods in the field of animal behavior.

The study of dominance relationships is especially pertinent for cooperatively breeding animals. In these species, the shared investment in offspring production could have an important influence on dominance network structure, and dominance networks in cooperative breeders may differ significantly from animals that congregate for other reasons (e.g., to exploit food resources). In this study, we explore patterns of dominance interactions in social groups of the cooperative breeding pukeko (*Porphyrio melanotus melanotus*). This ground-dwelling bird has a highly variable social system (Jamieson 1997) and on the North Island of New Zealand (where this study was conducted), most pukeko live in complex social groups that may contain multiple breeding males and females, as well as nonbreeding helpers of both sexes. Within these groups, pukeko are thought to form an orderly (i.e., linear) dominance hierarchy (Jamieson and Craig 1987), and socially dominant individuals gain priority access to food and have different social roles than do subordinate individuals (e.g., differences in parental care and territory defense; Craig

1980). Additionally, dominance determines the order of replacement for female breeders (Jamieson and Craig 1987), but whether there is a relationship between dominance and male reproduction is currently unclear due to limited molecular parentage data (Jamieson et al. 1994; Lambert et al. 1994).

While there is some information on the consequences of dominance rank for individual pukeko, we have almost no understanding of the patterns of dominance interactions among members of pukeko social groups. Because this species has a variable social system, it provides an excellent opportunity to test how individual attributes influence the quantity and quality of dominance interactions among group members. In addition to sex, dominance interactions in this species are likely influenced by the frontal shield ornaments of interacting individuals (Craig 1977). These fleshy ornaments extend up from the bill onto the crown, and function as a signal of social status, with larger frontal shields indicating more socially dominant individuals (Dey et al. 2014). In this study, we explored how these individual attributes (sex and shield size) influence the quality and quantity of dominance interactions in replicate social groups of wild, free-living pukeko. Additionally, we asked whether pukeko dominance networks show evidence of self-organization, after controlling for the effects of the individual attributes discussed above.

We considered 3 particular aspects of network structure in this study: 1) the orderliness of dominance interactions, 2) how individual attributes and structural dependence influence dominance interactions, and 3) the temporal stability of dominance interactions.

First, we investigated 2 aspects of dominance network orderliness, which collectively describe the degree to which animals form ordered and strong (i.e., directionally consistent) dominance relationships. To measure whether pukeko dominance networks show an ordered structure, we used the triangle transitivity method (Shizuka and McDonald 2012). To measure the strength of dominance relationships, we examined the degree to which dominant pukeko are likely to win a contest over subordinates (i.e., "hierarchy asymmetry," Dey et al. 2013). Since pukeko are thought to form strong and hierarchical dominance relationships (Jamieson and Craig 1987), we predicted that dominance interactions would be highly transitive and asymmetrical.

Second, we determined how differences in individual attributes (Piper 1997), and structural dependence between ties (i.e., network self-organization, Chase et al. 2002; Chase and Seitz 2011), influence pukeko dominance networks. We performed separate network analyses on subordinate displays and on physical aggression, as the factors we were interested in could have differential effects on these 2 types of dominance interactions. In particular, we considered how the individual attributes of sex and frontal shield size influence dominance interactions. Same-sex dyads may be more likely to have dominance interactions than opposite-sex dyads because only same-sex individuals compete for reproductive opportunities; therefore we tested whether our networks exhibit sexual homophily (i.e., tendency to interact with others of the same type). Frontal shield size is also likely to influence dominance interactions because it communicates information about fighting ability and social rank. In general, more dominant (i.e., larger shielded) individuals are expected to receive more subordinate displays and are less likely to receive physical aggression, although this need not be the case (Francis 1988). Additionally, the difference in frontal shield size between individuals could influence the likelihood of an interaction. We predicted that subordinate displays would occur more often when dyads had large difference in shield size, as this type

of interaction can be used by weaker animals to avoid physical confrontations with much stronger individuals. Conversely, we predicted that physical aggression would occur more often when individuals have similar shield sizes, because when the difference in fighting ability is small, subordinates have more motivation to challenge dominants, and dominants should also physically suppress subordinates to maintain their rank. Finally, we analyzed how structural dependence between ties influenced pukeko dominance networks. Specifically, we tested whether pukeko dominance networks show an effect of reciprocity, where interactions from one individual to another influence the likelihood of the reciprocal interaction. We also tested whether these networks exhibit a tendency to form transitive triad motifs, which form the basis of orderly dominance hierarchies (Shizuka and McDonald 2012). Since our analysis controlled for differences in individual attributes, a significant effect of transitive triad closure would suggest that the networks have self-organizational features.

In our final analysis, we evaluated whether pukeko dominance interactions are stable over time. While a previous study showed that dominance rank is stable between years in pukeko (Jamieson and Craig 1987), we do not know if the patterns of dominance interactions are consistent. If dominance interactions are driven by factors that are relatively stable (e.g., individual attributes such as sex or rank), then dyads should have similar patterns of dominance interactions between years. Alternatively, if dominance network structure is primarily influenced by more variable factors (e.g., exogenous ecological conditions), then patterns of dominance interactions may not be consistent between years. Here, we explored this stability by testing whether the frequency of dominance interactions between a dyad is consistent between 2 successive years.

METHODS

Field methods

This study was conducted at Tawharanui Regional Park (36° 22′ S, 174° 49′ E) on the North Island of New Zealand. At this site, pukeko social groups defend an all-purpose territory throughout the year, and long-term research has resulted in regions with a high percentage of banded individuals (trapping and banding procedures are published in Quinn et al. 2012; Dey et al. 2012). For this study, we selected social groups in which all adult individuals were uniquely banded, which allowed us to record all dominance interactions among members of each group. At the time of trapping, a suite of morphological measurements were taken including measurements of frontal shield size (shield width). When multiple sets of measurements were taken (i.e., an individual was caught multiple times), we used the set of measurements with the greatest temporal proximity to when the behavioral observations (see below) were performed. Sex was determined by measurement as described in Craig et al. (1980).

Dominance observations

Detailed behavioral observations were made in January and February 2012 on 11 social groups (mean group size = 7.5, range = 4–13). This time period is outside the typical breeding season for pukeko at this site (most reproduction occurs from August–October; Dey and Jamieson 2013), and no copulations or courtship behavior was observed during this study. For each group, we performed one 30-min observation per day for a period of 10 days, resulting in a total of 5h of observation (following the methods in Jamieson and Craig 1987; Dey et al. 2014). Immediately prior to each period, the observer placed approximately 50 g of dried corn on the territory of the group to increase the frequency of dominance interactions. Pukeko are accustomed to human presence at this site and quickly resumed normal behaviors after this disturbance. The observer then recorded occurrences of 2 classes of dominance behaviors, subordinate displays (i.e., subordinate postures and displacements; Craig 1977) and aggressive interactions (i.e., pecks, kicks, or charges; Craig 1977), that occurred among members of the focal group (average number of interactions over 5 h of observation = 85.2, range = 5 – 241). Interactions between members of the focal group and members of other social groups occurred very infrequently. These typically consisted of a member of the focal group chasing away an intruder, and they were not recorded or considered in our analysis. The observer was concealed in a camouflaged blind and observed the social group using a spotting scope or binoculars. All observations were conducted between 06.30 and 10.00 h.

To determine whether pukeko dominance hierarchies were temporally stable, we performed an additional set of dominance observations on 6 of the same social groups, during March and April 2013 (about 1 year after the initial observations). At our study site, group membership is highly stable among years (similar to data in Craig and Jamieson 1988). Prior to our observations in 2013, any new adult group members were caught and banded (most of these individuals were offspring from 2012). The group was then subject to behavioral observations on 10 days, identical to those described above.

Statistical analysis

Network analysis was performed in R version 3.0.1 (R Core Team 2013) using the statnet (Handcock et al. 2008; Hunter et al. 2008; Handcock et al. 2014a,b) suite of packages and the ergm.count package (Krivitsky 2013). Our analysis of network orderliness and network structure was conducted on the 11 social groups observed in 2012. There were a total of 102 individuals in these social groups; however, 19 individuals were never captured as adults (i.e., they were banded as juveniles) and thus, their sexes and adult shield sizes were unknown. These individuals were removed from all analyses, leaving 83 individuals in our analysis of orderliness and structure. Our analysis of network stability required that known individuals were observed across 2 years. In the 6 social groups observed in 2012 and 2013, 32 individuals met these criteria, and these individuals were considered for this analysis.

Dominance network orderliness

While one previous study has examined the linearity of pukeko dominance hierarchies (Jamieson and Craig 1987), the authors used methods that become biased when pairs of individuals do not interact or when group size varies (Klass and Cords 2011; Shizuka and McDonald 2012). Accordingly, we tested whether pukeko dominance hierarchies are orderly, using Shizuka and McDonald's (2012) triangle transitivity method. This measure is equivalent to linearity if the relationship among all dyads are known but does not become biased when dyads do not interact. To perform this test, we first built a weighted, directed network for each of the 11 social groups observed in 2012. These networks were based on all the observed dominance interactions pooled across all 10 observation periods (ties were drawn from the dominant to subordinate in each interaction and tie weight was determined by the total number of dominance interactions). Then, we used these networks to

calculate the triangle transitivity, t_{tri} (Shizuka and McDonald 2012), and dominance hierarchy asymmetry (Dey et al. 2013) for each group. Triangle transitivity measures the tendency of groups to form transitive triad substructures as opposed to cyclical triads (see Figure 1), and dominance asymmetry represents the global proportion of interactions in which dominant individual acts as such (i.e., they give aggression or receive submission). To calculate t_{tri}, we converted our weighted network to a binary "dominant-subordinate" network (i.e., each member of each dyad was designated as the "dominant or subordinate" based on who acted dominant in more than 50% of the interactions). Dyads in which each individual acted as dominant in exactly 50% of the interactions were considered unresolved and were given no tie. Next, we calculated the proportion of transitive triads out of the total number of triads (in null models this proportion is 0.75) and used this value as a test statistic in a permutation test, as described in the supplementary material and corrigendum of Shizuka and McDonald (2012). For dominance asymmetry, we calculated the empirical value for each group by dividing the number of interactions in which the dominant individual in each dyad (as defined in the dominant-subordinate network above) acted dominant (i.e., was the aggressor in an interaction or received a subordinate display), by the total number of interactions across the group. This value ranges from 0.5 (each individual in a dyad was equally likely to act dominant) to 1 (in each dyad, one individual always acted dominant). Then, for each social group, we permuted tie weight in the weighted network of dominance interactions, while holding the total number of dominance interactions constant and preventing self-loops (i.e., the diagonal in all permuted matrices was set to 0). In both analyses, we conducted 2000 permutations per social group and calculated P values based on 2-tailed tests. P values were then combined using Fisher's omnibus test (see also Croft et al. 2006; Dey et al. 2013 for a similar approach).

Dominance network structure

We explored how individual attributes influence dominance network structure using 2 ERGMs (also called p* models, Wasserman and Pattison 1996). These statistical models, which are somewhat analogous to logistic regression, model the presence or absence of ties in an empirical network given various predictor variables (Lusher et al. 2012). Importantly, ERGMs assume that network ties depend on one another and that global network structure is the result of local processes influencing tie formation. Through stochastic model fitting, ERGMs allow researchers to determine whether each predictor variable influences tie formation, while controlling for the other predictor variables in the model. As a result, ERGMs provide a statistically robust method for testing which factors contribute to the complex networks observed in animal

societies and should be a useful tool for SNA studies in behavioral ecology (Pinter-Wollman et al. 2013).

In our analysis, we considered 2 separate ERGMs using the observed subordinate displays and physical aggressive interactions as our empirical networks. In each network, we included the 11 social groups observed in 2012 and considered only the behavioral data collected in 2012. The individual attributes included in the models were sex, sexual homophily, frontal shield size, and the dyadic difference in frontal shield size. Additionally, we investigated structural dependence between ties by considering whether there was a tendency for reciprocity, and transitive triad closure, in each of the networks. Further details on implementation of ERGMs is provided in the Supplementary Material.

Dominance network stability

To analyze temporal stability of dominance networks, we tested if the number of dominance interactions between a dyad in 2012 was correlated with the number of dominance interactions between that same dyad in 2013. For this analysis, we considered 2 graphs (one from 2012, and one from 2013) composed of individuals that were observed in both years (32 individuals from 6 social groups). These graphs were weighted and undirected, and the tie weight was number of dominance interactions pooled across the 10 observation periods from each year. Dyads that could not possibly interact (i.e., individuals from different social groups) were given "NA" (i.e., not available) values in the corresponding cell. We tested for a correlation using a Mantel test based on Spearman's rank correlation (Mantel and Valand 1970; Legendre and Legendre 2012) implemented in the "vegan" package in R (Oksanen et al. 2013). We used 2000 permutations and specified the "strata" argument such that permutations were only done within social groups.

RESULTS

Dominance network orderliness

Dominance networks in pukeko social group were found to be significantly more transitive (permutation test: mean $t_{tri} = 0.86$, $f_{24} = 75.92$, $P < 0.001$) and asymmetrical (mean dominance asymmetry = 0.94, $f_{24} = 94.53$, $P < 0.001$), than expected by null models.

Dominance network structure

Sex and frontal shield size influenced the structure of dominance interactions in pukeko social groups (Figure 2). Male pukeko were less likely to use subordinate displays (Table 1; actor effect of sex) and more likely to use physical aggression (Table 2; actor effect of sex) than were female pukeko. However, after controlling for these effects, we found that males were more likely to produce subordinate displays to other males (Table 1; male sexual homophily), and that females were more likely to be physically aggressive with other females (Table 2; female sexual homophily). As predicted, individuals with larger frontal shields were more likely to receive subordinate displays (Table 1; receiver effect of shield size) and were more likely to give physical aggression (Table 2; actor effect of shield size), than were individuals with smaller frontal shields. However, we found no significant effect of the difference in shield size on the occurrence of subordinate displays or physical aggression (Tables 1 and 2; difference in shield size). After controlling for the individual attributes above, there was still a positive and significant effect of transitive triad closure in both the network of submissive displays and physical aggression (Tables 1 and 2, effect transitivity). Additionally, there
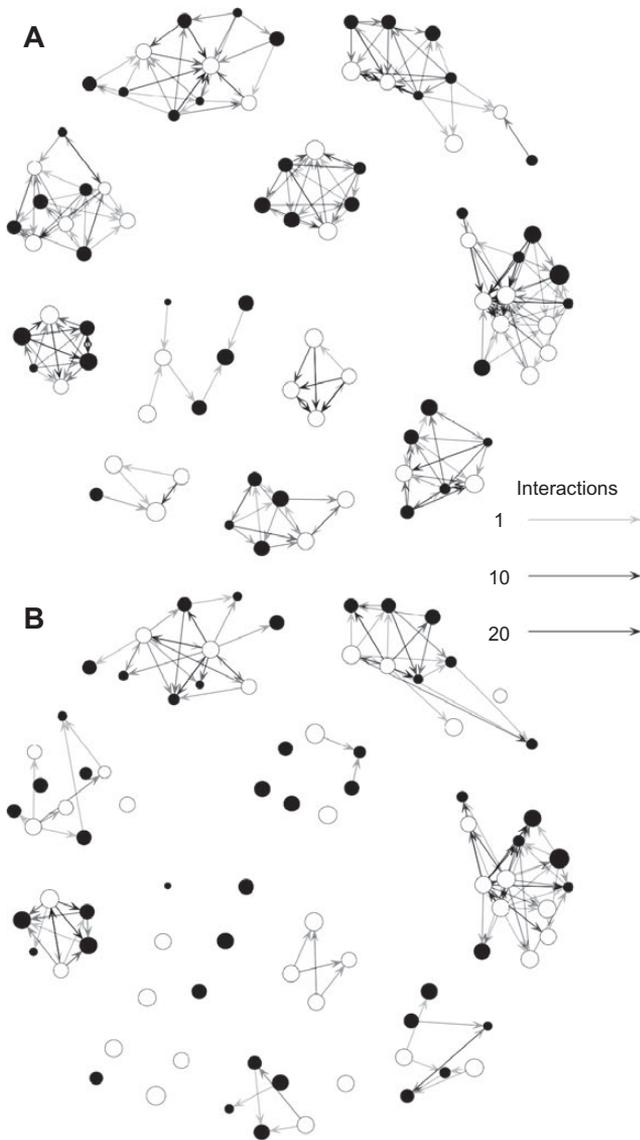
Transitive triad   Cyclical triad

Figure 1

Transitive and cyclic triad motifs. Transitive triads can be reordered into a linear hierarchy (here i > j > k) and are therefore thought of as "orderly." Cyclical triads do not have this property.

Figure 2
Networks of submissive displays (A) and physical aggression (B) in pukeko social groups. Nodal orientation was determined using the Fruchterman–Reingold algorithm and shows individuals clustering into 11 subgraphs representing the 11 social groups. Node size was scaled to frontal shield size, and node color is used to indicate sex, with white and black filled circles representing males and females, respectively. Tie color indicates the number of interactions, with darker lines indicating more interactions (see legend). Figure created in statnet (Handcock et al. 2008; 2014a).

Table 1
ERGM fit for a network of pukeko subordinate displays

Model term	Estimate	SE	P value
Sum	−0.73	0.42	0.08
Nonzero	−2.85	0.19	**<0.0001**
Actor effect of sex (male)	−1.04	0.22	**<0.0001**
Sexual homophily			
Male–male	1.08	0.22	**<0.0001**
Female–female	−0.10	0.08	0.21
Actor effect of shield size	−0.02	0.01	0.14
Receiver effect of shield size	0.07	0.01	**<0.0001**
Difference in shield size	−0.01	0.01	0.71
Transitivity	0.23	0.07	**0.001**
Reciprocity	−0.24	0.09	**0.007**

Significant *P* values are shown in bold. SE, standard error.

Table 2
ERGM fit for a network of physical aggression between pukeko

Model term	Estimate	SE	P value
Sum	−1.64	0.66	**0.01**
Nonzero	−3.57	0.20	**<0.0001**
Actor effect of sex (male)	1.48	0.43	**0.0006**
Sexual homophily			
Male–male	−0.09	0.10	0.34
Female–female	1.18	0.44	**0.007**
Actor effect of shield size	0.04	0.02	**0.02**
Receiver effect of shield size	−0.01	0.01	0.62
Difference in shield size	0.00	0.02	0.77
Transitivity	0.37	0.07	**<0.0001**
Reciprocity	−0.15	0.12	0.23

Significant *P* values are shown in bold. SE, standard error.

was a significant, negative effect of reciprocity on the network of subordinate displays (Table 1, effect of reciprocity).

Dominance network stability

The number of dominance interactions between a dyad was highly correlated between years (Mantel test: Spearman's ρ = 0.57, *P* = 0.005; Figure 3).

DISCUSSION

Patterns of dominance interactions in cooperatively breeding animals will often have an important influence on group dynamics and individual fitness. In this study, we show that pukeko form highly transitive (i.e., orderly) and strongly directional dominance relationships. Additionally, we show that individual attributes have important influences on patterns of dominance interactions. Specifically, submissive and aggressive interactions were influenced by the sex and shield size of both the actor and the receiver, although these traits may have different effects on different types of dominance interactions. Furthermore, our models show that pukeko tend to form closed transitive triads, which suggests that pukeko dominance networks are not simply due to differences in individual attributes, but are at least partially dependent on structural dependence between ties (i.e., self-organization; Chase and Seitz 2011). Finally, we show that patterns of dominance interactions were stable over a 1-year period, as would be expected if dominance interactions are strongly determined by individual attributes and those attributes are relatively stable.

This study is one of the first in the field of behavioral ecology to use ERGMs to analyze animal social networks. ERGMs have been widely used in the social sciences to analyze relationships among humans (e.g., Goodreau et al. 2009) and their utility in animal studies is readily apparent (Pinter-Wollman et al. 2013). One of the benefits of using ERGMs is that these models can consider how network ties self-organize through local substructures. These local substructures are commonly found in human social networks (Lusher et al. 2012) and are likely to be important factors in the organization of animal networks as well. In this study, we show that pukeko have a tendency to form transitive triad motifs, even after controlling for differences in individual attributes. Additionally,
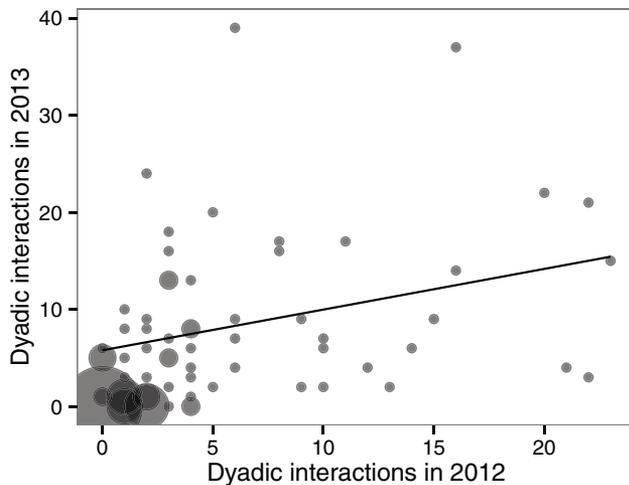
Figure 3
Temporal stability of dominance relationships. The total number of dominance interactions (both subordinate displays and physical aggression) is plotted for each dyad observed in both 2012 and 2013 (32 individuals from 6 social groups). Point size is scaled to the number of dyads that share the same coordinates in the plot. Figure created in ggplot2 (Wickham 2009).

there was a negative effect of reciprocity on the network of subordinate displays, suggesting that pukeko are less likely to produce submissive behaviors toward individuals that have previously submitted to them. These effects could be due to winner, loser, or bystander effects (e.g., Dugatkin and Earley 2003) and the models used in this study cannot distinguish among these mechanisms. However, careful combinations of certain structural motifs (e.g., in-stars, out-stars, 2-paths and triads) could probably be used to investigate the relative importance of winner, loser, and bystander effects at the group level. Unfortunately, the use of structural motifs in weighted ERGMs is not as developed as their use in binary ERGMs, and we were unable to perform this type of analysis here.

The influence of individual attributes on dominance networks was largely consistent with our predictions based on expected patterns of conflict in cooperative breeding animals. Network structure was influenced by sexual homophily, which is expected if same sex individuals are competing for breeding positions (Dey et al. 2013). Interestingly, female homophily was more prevalent in the network of physical aggression, which is consistent with data suggesting that females have intense intrasexual competition for breeding positions in this species (Dey et al. 2012). Individual frontal shield size was also related to network structure, being positively correlated with the likelihood of giving aggression and receiving submissive displays. However, contrary to predictions, we found no significant effect of the difference in frontal shield size on these interactions. It is possible that the difference in frontal shield size influences the intensity of dominance interactions, rather than the frequency. For example, aggressive interactions between dyads that have large differences in shield size may be relatively low cost (i.e., pecks), while aggressive interactions that occur between individuals with similar sized shields may be more likely to escalate to more intense interactions (i.e., kicking and biting). Indeed, fights (reciprocal kicking and/or biting in short-time periods) are more likely to occur between individuals who are close in dominance rank than those who have large rank differences (C. J. Dey, unpublished data), which is consistent with this hypothesis. Further examination of the importance of difference in shield size on interaction intensity, as

well as the inclusion of other individual attributes not considered in this study (e.g., age), may yet reveal other important influences on the structure of dominance networks in pukeko.

Collecting interaction or association data for network analyses on animals can be challenging and warrants careful consideration (Whitehead 2008). In most cases, researchers are restricted to collecting data in specific contexts (e.g., during daylight hours or when animals are in a particular habitat type) or taking proxy measures of social relationships (e.g., "gambit of the group"), which could result in differences between the data collected and the true social relationships among groups of animals (James et al. 2009). In this study, we used an artificial patch of food to increase the rate of dominance interactions in our focal groups, which is a common approach used to study dominance in both wild and captive animals (e.g., Tarvin and Woolfenden 1997; Val-Laillett et al. 2008). While pukeko do frequently compete over natural food resources (Craig 1977; C. J. Dey, personal observation), these resources are more dispersed than the food piles used in this study and it is possible that the networks produced in this study do not perfectly reflect natural networks of dominance interactions. However, pukeko dominance rank as determined through artificial feeding is correlated with frontal shield size (Dey et al. 2014), with differences in copulations (Jamieson and Craig 1987) and with differences in parental investment (Craig 1980), which together suggest that this method of measuring dominance encompasses at least part of the true dominance relationships among individuals. Nonetheless, it is important to consider the data collection methods when interpreting the findings of social network studies in behavioral ecology, and the results of the current study should be interpreted with an understanding of this caveat.

Dominance is a rich type of social relationship that has important links to individual fitness. While most previous studies have focused on dominance hierarchies and social rank, there is a large scope for SNA to greatly improve our understanding of dominance interactions. In this study, we used network analyses to perform a comprehensive exploration of dominance interactions in the cooperatively breeding pukeko. In addition to demonstrating that pukeko dominance relationships are transitive, asymmetrical, and temporally stable, we also show that the structure of dominance networks is influenced by both individual attributes and structural dependence between ties. This network-based approach provides a more detailed understanding of the causes and consequences of dominance in this species, and the methods used here should be widely applicable to other studies on dominance in animal societies.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

data analysis. Additionally, we thank the Tawharanui Open Sanctuary Society and the Tawharanui Regional Park staff, especially M. Maitland, M. Puckett, C. Wards, and A. Stanes, for logistical assistance.

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