

## Reproductive correlates of social network variation in plurally breeding degus (*Octodon degus*)



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Studying the causes and reproductive consequences of social variation can provide insight into the evolutionary basis of sociality. Individuals are expected to behave adaptively to maximize reproductive success, but reproductive outcomes can also depend on group structure. Degus (*Octodon degus*) are plurally breeding rodents, in which females allonurse indiscriminately. However, communal rearing does not appear to enhance female reproductive success, and larger group sizes are correlated with decreasing per capita pup production. To further investigate mechanisms underlying these patterns, we asked how differences in sex, season and average group reproductive success are related to degu association networks. We hypothesized that if reproductive differences mirror social relationships, then females (core group members) should show stronger and more stable associations than males, and female association strength should be strongest during lactation. We also hypothesized that, at the group level, social cohesion would increase reproductive output, while social conflict would decrease it. Females did have higher association strength and more preferred partners than males, but only during lactation, when overall female associations increased. Females also had more stable preferred social partnerships between seasons. A measure of social cohesion (average association strength) was not related to per capita pup production of female group members, but potential social conflict (heterogeneity of association strengths) was negatively related to per capita pup production of female group members. Our results highlight temporal and multilevel patterns of social structure that may reflect reproductive costs and benefits to females.

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The nature and structure of social interactions can vary in space and time in response to ecological and social factors, and studying this variation can provide insights into the evolutionary basis of sociality (Hinde 1974; Wrangham 1987; Sterck et al. 1997; Kappeler & van Schaik 2002; Krause & Ruxton 2002; Whitehead 2008). In an adaptive framework, individuals are expected to maximize their fitness, and social behaviour should reflect relevant selective pressures. Within sexes, individuals typically compete for resources and mates, and differential selective pressures between females and males often result in different reproductive strategies (Emlen & Oring 1977; Andersson 1994). In social systems that exhibit cooperation, same-sex interactions can also have reproductive benefits. For example, in some systems, stronger female–female bonds enhance offspring survival (Silk et al. 2003, 2009; Cameron et al. 2009), and males of some species form coalitions to increase

mating opportunities (Harcourt 1992; Connor et al. 2001). Seasonal variation in resource availability can influence the timing of reproductive events such as breeding and subsequent investment in offspring. Thus, the potential costs and benefits of social interactions, such as cooperation and aggression, often vary within a year, and social structure is expected to change accordingly as individuals change their social tendencies (Terborgh & Janson 1986; Wittemyer et al. 2005; Aureli et al. 2008; Smith et al. 2008; Henzi et al. 2009; Maher & Burger 2011).

Even as individual behaviour determines emergent social structure, group structure can exert influence back on individual reproductive success. For example, in species that exhibit steep hierarchies or disparate outcomes by rank, dominant individuals can monopolize most, if not all, direct reproductive success (Dewsbury 1982; Keller & Reeve 1994; Ellis 1995; Johnstone 2000). Moreover, increased conflict can negatively impact the direct reproductive success of social group members due to fighting and chronic stress (de Waal 2000; Flack et al. 2006; Young et al. 2006) or through reduced mating activity (Sih & Watters 2005). While

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social cohesion and conflict are frequently discussed in socio-ecological theory, these concepts are rarely measured directly, and more commonly group size is used as a proxy. However, group size can have different implications in different mammalian systems (Silk 2007), and measuring between- and within-group variation in social connections (i.e. the social network) should increase our resolution on the causes and consequences of social cohesion or conflict (Wey et al. 2008; Sih et al. 2009). Furthermore, approaches that consider processes occurring at both the individual and group level can be especially informative if there are possible conflicts or feedbacks between individuals and groups (Couzin 2006; Hock et al. 2010; Royle et al. 2012).

A social network approach offers methods for quantifying the sources of social variation at different levels of interest, such as for individuals, dyads or groups (Wasserman & Faust 1994; Scott 2000), and thus offers novel ways to address existing questions about social variation in behavioural ecology (e.g. Vonhof et al. 2004; Cross et al. 2005; Flack et al. 2006; McCowan et al. 2008; Fischhoff et al. 2009; Madden et al. 2009; Kerth et al. 2011). A social network is a representation of the social relationships connecting individuals. Network structure can reflect important social features such as conflict, stability and cohesion. Moreover, a central idea in network theory is that individuals embedded within networks can both gain benefits and suffer constraints due to social structure (Wasserman & Faust 1994, page 4). For example, social cohesion resulting from strong internal connections may enhance group performance, while diversity of external connections may facilitate access to new opportunities (e.g. Gargiulo & Benassi 2000). Animal social network connections have been linked to individual reproductive outcomes in a range of taxa including some insects (Formica et al. 2012), lizards (Godfrey et al. 2012), birds (McDonald 2007; Ryder et al. 2008; Oh & Badyaev 2010) and mammals (Silk et al. 2009; Wey & Blumstein 2012). Group-level analyses that explicitly focus on fitness outcomes of cohesion and conflict are still rare, but offer important insights into the evolution of social structure. For example, variance in group association strength, but not individual centrality, is negatively correlated with adult longevity in plurally breeding rock hyrax, *Procapra capensis* (Barocas et al. 2011), and association network structure of nestling great tits, *Parus major*, predicts family fitness in a way that suggests kin-group selection for effective conflict resolution (Royle et al. 2012).

Here we investigate the reproductive correlates of social network variation in a wild population of degus (*Octodon degus*), social rodents endemic to Chile. Degus are plural breeders with communal care; that is, nearly all (>95%) of the adult females in a group reproduce (Hayes et al. 2009; Ebensperger et al. 2011a; Burger et al. 2012) and multiple group members share parenting (Brown 1978; Hayes 2000; Silk 2007). In the laboratory, female degus provide milk to their own and nondescendent offspring (Ebensperger et al. 2006; Jesseau et al. 2009). Communal rearing by females (Ebensperger et al. 2007) and males (Ebensperger et al. 2010) does not appear to enhance the reproductive success of females. In fact, at our study site, per capita direct pup production is negatively correlated with the number of adult females per group (Hayes et al. 2009; Ebensperger et al. 2011a). These results are surprising for a number of reasons. First, degus at our site typically breed and reproduce only once in a lifetime (Ebensperger et al. 2009); therefore, females that do not reproduce during their first opportunity may not experience any direct fitness. Second, behavioural observations and molecular data suggest that social groups lack strong kin structure, providing little opportunity for indirect fitness gains (Quirici et al. 2011; but see Ebensperger et al. 2004). Thus, we studied patterns of social associations to also clarify the mechanisms that influence individual and group social variation, and how group structure is related to female reproduction.

We hypothesized that female degus would modify their social behaviour in response to reproductive pressures associated with seasonal variation, which should lead to sex and seasonal differences in the structure of association networks. Females are core members of social groups (Ebensperger et al. 2004, 2009; Hayes et al. 2009), so we predicted that females would show stronger and more stable associations than males overall. Because female degus communally nurse and care for young (Ebensperger et al. 2006; Jesseau et al. 2009), we predicted that females would have stronger associations with other females during lactation than during the mating season or gestation. Previous studies have documented negative relationships between group size measures and per capita pup production in degus (Hayes et al. 2009; Ebensperger et al. 2011a) and other rodents (Hoogland 1995; Lacey 2004; Solomon & Crist 2008), but did not investigate how fine-scale social differences, such as strength or heterogeneity of associations among adults in a group, are related to reproductive output. We hypothesized that stronger associations among females should indicate greater social cohesion or cooperation, which would be related to greater group reproductive output. On the other hand, greater within-group variation in association strength represents the presence of relatively strong and weak relationships in the same group. This would suggest lower overall social cohesion and greater potential social conflict, which would be expected to lower reproductive output. Thus, we predicted that per capita pup production would increase with greater strength of within-group associations and decrease with increasing within-group heterogeneity in association strengths.

## METHODS

### Data Collection

We trapped and collected data from a free-living population of degus in Estación Experimental Rinconada de Maipú (33°23'S, 70°31'W, altitude 495 m), a field station of the Universidad de Chile. This population is part of ongoing research, and most individuals within the study area are captured and marked regularly. Habitat and seasonal variation in precipitation and temperature at this site are characteristic of Mediterranean climates (warm, dry summers and cold, wet winters), and degu life history events coincide with seasonal patterns. Breeding usually occurs once per year, and coincides with winter rains and associated primary productivity (Ebensperger & Hurtado 2005; Ebensperger et al. 2009). In this area, mating typically takes place during the austral autumn (May–June), gestation occurs during the winter (June–August), and birth and lactation occur during the austral spring (September–October). As part of the ongoing work during 2007–2009, all trap events across every season (autumn, winter and spring) resulted in a total of 240 unique adults (148 females, 92 males): 34 females and 10 males in 2007; 79 females and 35 males in 2008; 52 females and 51 males in 2009. After restricting data to standardized time periods (May and June for autumn, September and October for spring) and excluding individuals trapped less than five times in a year, this resulted in 30 females and 9 males in 2007, 30 females and 5 males in 2008, and 33 females and 13 males in 2009.

We conducted telemetry at night to locate burrows that degus used (Ebensperger et al. 2004) and live-trapping in the morning to determine burrow systems from which adults and offspring emerge (Hayes et al. 2007, 2009). Trapping took place when female degus were lactating in 2007–2009 (32, 45 and 44 days, respectively) and when degus were mating in 2008 and 2009 (25 and 36 days, respectively). During each trapping session, 8–10 Tomahawk live traps (model no. 201 Tomahawk Live Trap, LLC, Hazelhurst, WI, U.S.A.) and Sherman traps (H.B. Sherman Traps, Inc., Tallahassee, FL,

U.S.A.) were placed around burrows in the early morning (0700–0800 hours) prior to adult emergence as in previous studies (Burger et al. 2009; Hayes et al. 2009). After traps were open for 1–1.5 h, the identity and location of all captures were determined and traps were closed until the next trapping event. We marked each individual with a unique set of eartags the first time it was caught, and every time we caught an animal, its ID (eartag numbers), sex, body mass, burrow location and reproductive condition (if it was female) were recorded. We measured degus at the field site and released them immediately after the trapping session at the burrow system at which they were caught, to minimize interference with their daily activities. Night telemetry took place during both seasons, with ca. 15–20 telemetry locations per individual. During trapping in late August, adult females that weighed more than 170 g ( $N = 30$ – $35$  females per year) were fitted with radiocollars (ca. 8 g) with unique pulse frequencies (Holohil Systems, Ltd, Carp, ON, Canada, and AVM Instrument Company, Ltd, Colfax, CA, U.S.A.). Approximately 1 h after sunset, females were radiotracked to their burrows (once per evening), following methods detailed in previous studies (Ebensperger et al. 2004, 2011a; Hayes et al. 2009; Burger et al. 2012).

Each year, degu offspring were assigned to a burrow system based on their location of first capture in the spring (September–November). Per capita pup production of females was determined by dividing the number of offspring captured at a burrow system by the number of female group members assigned to that burrow system (Hayes et al. 2009; Ebensperger et al. 2011a; Burger et al. 2012). Preliminary pup assignment using microsatellite primers (Ebensperger et al. 2004; Quan et al. 2009) confirmed results from previous studies using burrow trapping and telemetry data (Hayes et al. 2009), indicating that the latter provide effective estimates of per capita pup production.

All procedures that involved handling of live animals were approved by the University of Louisiana at Monroe Institutional Animal Care and Use Committee and by the Faculty of Biological Sciences at Pontificia Universidad Católica de Chile (DFCB-021-2008), under appropriate Chilean permits issued by the Servicio Agrícola y Ganadero (1-109/2008 (3542), 1-31/2009 (1956) and 1-49/2010 (2332)). We attempted to minimize handling time and disturbance to the animals whenever possible, and radiocollars weighed less than 5% of the mass of tagged animals.

### Social Measures

We calculated associations in the program SOCPROG 2.4 (Whitehead 2009) using trapping data. We calculated the 'simple ratio' index (Ginsberg & Young 1992) for each pair of individuals, in each season within a year. The simple ratio index is defined as the number of times that two individuals were caught together at the same burrow (not necessarily in the same trap), divided by the total number of times each was caught, at the same or different burrows. Thus the association index indicates the proportion of burrow usage overlap between any two individuals in the population in that season (ranging from 0 to 1, 'never caught together' to 'always caught together'). We constructed 'association networks' from the matrices of associations for the population in each season in each year (Fig. 1). We also constructed 'preferred partner networks' from dyads that had association strengths that were significantly higher than expected, compared to the null hypothesis that individuals associate with the same probability with all other individuals, given their availability. These were determined using the SOCPROG procedure for testing for dyadic significance (Manly 1995; Bejder et al. 1998; Whitehead 1999), which performs a series of permutations within sampling periods (in our study, within the same day) on 1:0 group-individual matrices. At each step, the procedure randomly

selects a row and column pair and inverts ('flips') the association values between rows, keeping the row and column totals the same, and then recalculates association indices and test statistics. A large number of permutations generates a distribution against which the association indices and test statistics of the observed association matrix is compared. Significantly high (or low) associations between pairs are identified as those that are greater (or lower) than a certain percentage of their random association indices. We used 20 000 permutations (at which significance levels were stable) and significance level set to 0.05. Both association and preferred partner networks were symmetric, but association networks were weighted by association strength, whereas preferred partner networks were binary. Only individuals trapped at least five times were included in network and subsequent analysis to exclude poorly sampled individuals and wanderers.

For each individual, we calculated three measures of social variation.

(1) Strength: the sum of associations (Whitehead 2008), calculated from weighted association networks. High strength indicates a high total amount of overlap with other individuals, which could result from strong associations, many associations, or a combination of both. During lactation, stronger associations could reflect communal nursing or other behaviours resulting in greater overlap.

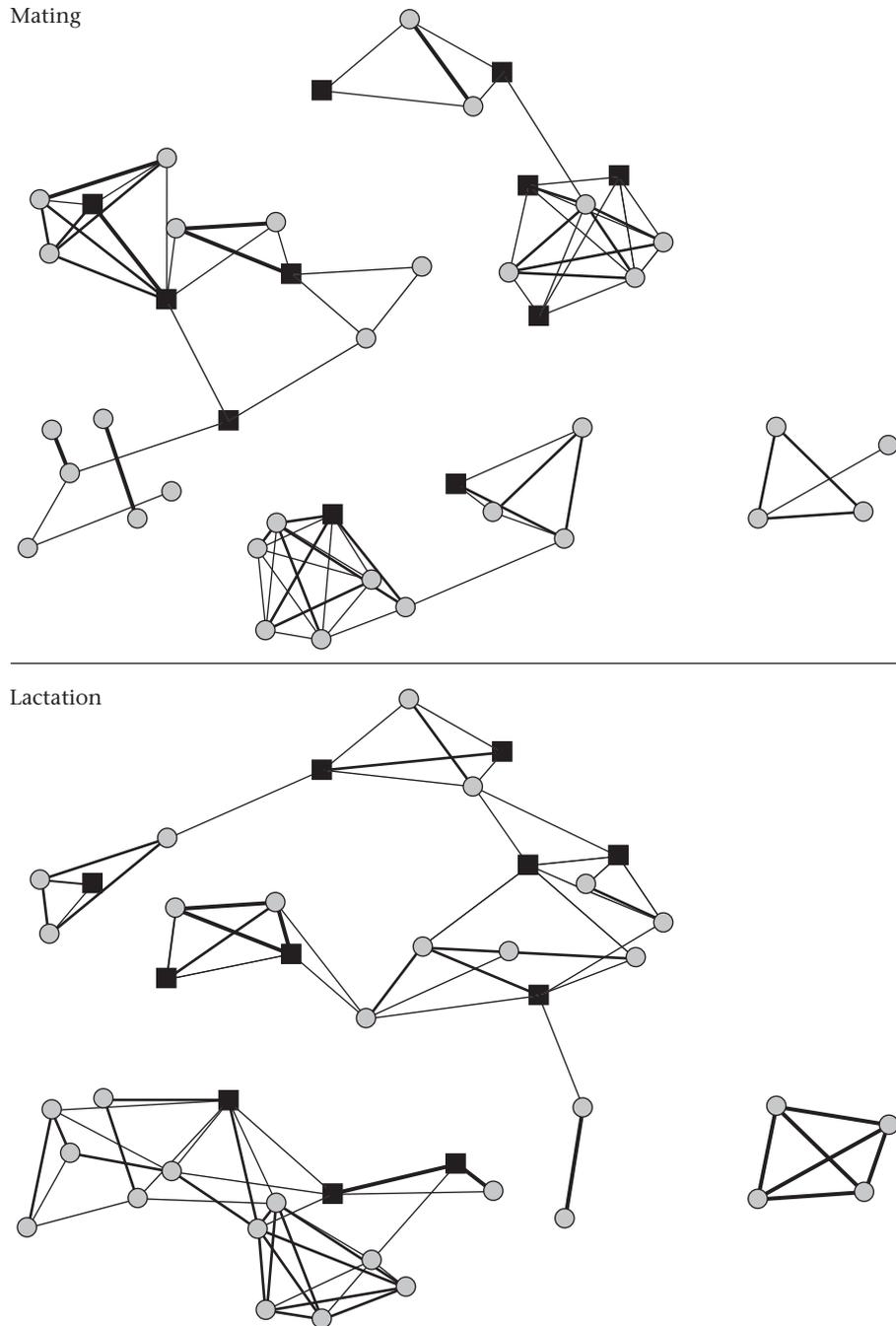
(2) Coefficient of variation (CV) of association: the ratio of the standard deviation to the mean association strength, used here as a standardized measure of the heterogeneity of an individual's associations. Individuals with a high CV of association would have greater combinations of stronger and weaker associations, while individuals with a low CV of association would have relatively even associations. Higher CV of association might be caused by more movement between burrows or strong preference for some social partners over others.

(3) Degree: the number of preferred associates, calculated from binary preferred partner networks; that is, it included only those relationships that had association strengths that were higher than expected (from random). Individuals with high degree of association have many significant relationships. This measure should help distinguish between relationships resulting from active preference versus those that are a by-product of proximity or other passive mechanisms. Preferred partner network measures were calculated in UCINET 6 (Borgatti et al. 2006). We calculated the same indices for networks including only females to test specific predictions about female–female relationships.

To assign group membership during lactation, we used both trapping and telemetry data to determine the simple ratio index between all individuals (Hayes et al. 2009). We then ran hierarchical cluster analysis (Whitehead 2008) in SOCPROG and confirmed the fit of data with the cophenetic correlation coefficient, which reflects the correlation between the actual association indices and the levels of clustering in the diagram. All clusters had values above 0.8, indicating that hierarchical cluster analysis provided an effective representation of the data (Bridge 1993). We used maximum modularity criteria (Newman 2004) to determine the appropriate cutoff in the resulting dendrogram to define social groups. Group size was defined as the number of individuals included in each cluster.

### Statistical Analysis

We tested for sex differences in association strength, CV of association and association degree using each as the dependent variable in a multiple regression with sex and year as dummy-coded independent variables. Dependent variables were square-root transformed to meet assumptions of residual normality and homoscedasticity. The regressions were performed in UCINET, and significance of the overall



**Figure 1.** Degu association networks from 2009 mating and lactation periods, illustrating seasonal changes in social connections. Grey circles: females; black squares: males. The thickness of lines reflects the strength of association between two individuals. Only nodes (individuals) that were present in both seasons are included in this diagram, and nodes are presented in the same positions to facilitate comparison. Better connected individuals are placed nearer to each other in the diagram, and thus the layout of nodes does not directly reflect spatial distribution.

model and parameter coefficients were determined using 10 000 random permutations of the dependent vector, recomputing the regression and determining the proportion of random permutations that resulted in coefficients as extreme as the observed value. For these analyses, we fitted separate models for the mating and lactation seasons. We used permutation tests to determine significance to account for nonindependence of data points when dependent variables were network measures (Croft et al. 2011), for all analyses in which individual was the unit of analysis.

For individuals present in both mating and lactation periods of a given year, we also tested for interseasonal changes in sociality. First, we used a nonparametric Wilcoxon signed-ranks test to

examine differences in individual association strength, CV of association and association degree. We split this analysis by sex, and significance was determined from Monte Carlo permutations with 10 000 permutations. Next, we tested for sex differences in the number of preferred partners lost and gained from mating to lactation, controlling for year, using two-way ANOVAs. Finally, we used quadratic assignment procedure (QAP) models in UCINET, which use matrix permutations to test for correlations between two networks. In our case, this was done by testing the preferred partner network during lactation against the preferred partner network during mating to determine the effect of prior association from the autumn on likelihood of spring association.

To test for female reproductive benefits and costs of network structure, we conducted analyses for both males and females and for females only. For each social group during lactation, we calculated the mean and CV of association strength and degree. Mean values are intended to reflect social cohesion (i.e. higher association strength and degree indicate greater association among group members), while CV values reflect social conflict (i.e. higher CV of association indicates greater inequality in association strengths among group members). Group values were then used as independent covariates in ANCOVAs with year as a fixed effect and pups per female as the dependent variable. We fitted two separate models: one with mean association strength and its CV, and another with mean association degree and its CV. CV of strength and CV of degree were square-root transformed to meet assumptions of residual homoscedasticity. We did not include group size as a covariate in these models because it was strongly correlated with CV (Spearman rank correlation:  $r_s = 0.801$ ,  $N = 31$ ,  $P < 0.001$ ). All analysis not performed with UCINET were performed with SPSS 20.0 (IBM Corporation, Armonk, NY, U.S.A.). We used an alpha level of  $P < 0.05$  for all tests and omitted nonsignificant interaction terms from final models.

## RESULTS

### Sex Differences and Seasonal Patterns

During lactation, females had greater association strength ( $\beta = 0.187$ ,  $P = 0.046$ ; Fig. 2a) and association degree ( $\beta = 0.205$ ,  $P = 0.026$ ; Fig. 2b) than did males, indicating that females had stronger associations and a larger number of preferred partners than did males ( $N = 93$  females, 27 males). There were no sex differences in association strength ( $\beta = 0.140$ ,  $P = 0.252$ ; Fig. 2a) or degree ( $\beta = 0.146$ ,  $P = 0.245$ ; Fig. 2b) during mating ( $N = 58$  females, 15 males). There were no sex differences in the CV of associations during mating ( $\beta = -0.096$ ,  $P = 0.439$ ) or lactation ( $\beta = 0.014$ ,  $P = 0.881$ ), indicating that females and males had similar heterogeneity of associations.

Among females that were present in both seasons in a year ( $N = 59$ ), association strength ( $Z = -2.476$ ,  $P = 0.012$ ) and degree ( $Z = -3.568$ ,  $P < 0.001$ ) were both higher during lactation than during mating. There were no seasonal differences in males ( $N = 14$ ) for association strength ( $Z = -0.596$ ,  $P = 0.584$ ) or degree ( $Z = -0.705$ ,  $P = 0.549$ ). In both 2008 and 2009, prior preferred association during mating significantly predicted preferred

association during lactation, when controlling for sex. In both years, the overall model (2008:  $R^2_{\text{adj}} = 0.144$ ,  $P < 0.001$ ; 2009:  $R^2_{\text{adj}} = 0.167$ ,  $P < 0.001$ ) and the individual effect of prior association (2008:  $\beta = 0.381$ ,  $P < 0.001$ ; 2009:  $\beta = 0.410$ ,  $P < 0.001$ ) were statistically significant. The test of individual changes between mating and lactation showed that males gained ( $F_{1,69} = 11.103$ ,  $P = 0.001$ ) and lost ( $F_{1,69} = 5.344$ ,  $P = 0.024$ ) more preferred associations than females did, indicating that males had higher turnover in preferred associates than females (Fig. 3).

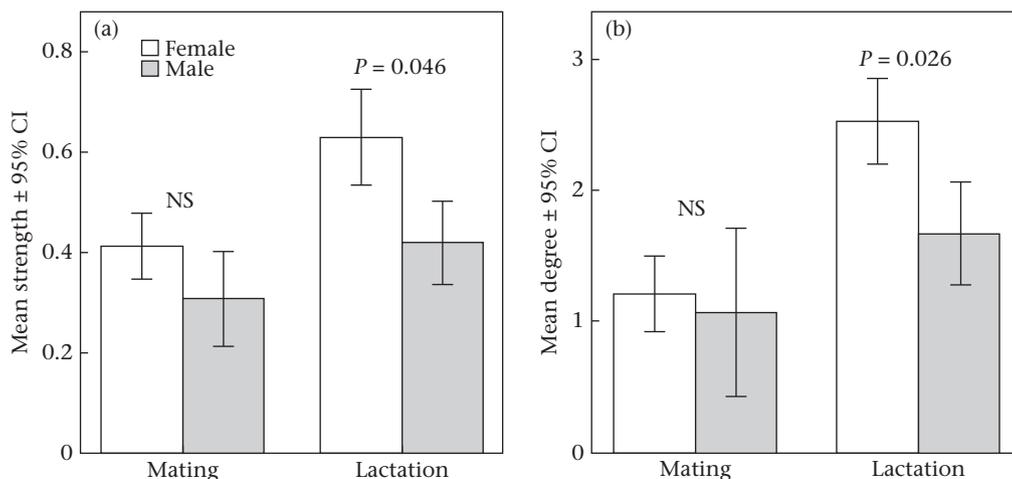
### Female Reproductive Outcomes

There was no relationship between mean within-group strength of female associations and per capita pup production ( $F_{2,24} = 2.122$ ,  $P = 0.157$ ), but there was a significant negative relationship between CV of association strength and per capita pup production ( $F_{2,24} = 8.422$ ,  $P = 0.007$ ; Fig. 4). Neither the mean within-group female–female degree ( $F_{2,24} = 0.797$ ,  $P = 0.381$ ) nor the CV of within-group female–female degree ( $F_{2,24} = 0.907$ ,  $P = 0.351$ ) of association was significantly associated with per capita pup production. Results were similar when all associations, including males as well as females, were considered.

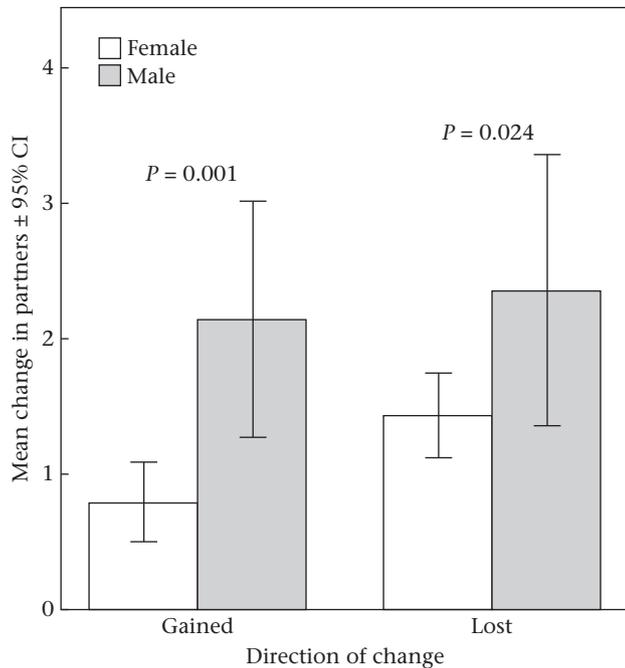
## DISCUSSION

### Sex Differences and Seasonal Patterns

Female degus had stronger associations and a larger number of preferred social partners than males during lactation, but not during the mating season. Additionally, degree and strength of associations in females were both higher during lactation than during mating. Sex differences in patterns of social interaction are common (e.g. Lusseau 2003; Manno 2008; Wey & Blumstein 2010; Holekamp et al. 2012), and our results suggest that social relationships are particularly important for female degus during lactation. The mechanisms driving specific social partner preference are less clear. Many social networks are structured by partner preference based on characteristics, such as sex, body size or kinship (McPherson et al. 2001; Lusseau & Newman 2004; Croft et al. 2005; Wolf et al. 2007; Patriquin et al. 2010). We found no evidence for preferred associations by sex or body mass in degus in either season (T. W. Wey, J. R. Burger, L. A. Ebensperger & L. D. Hayes, unpublished data), but the role of kinship in structuring associations remains to be tested. One hypothesis is that kinship plays a



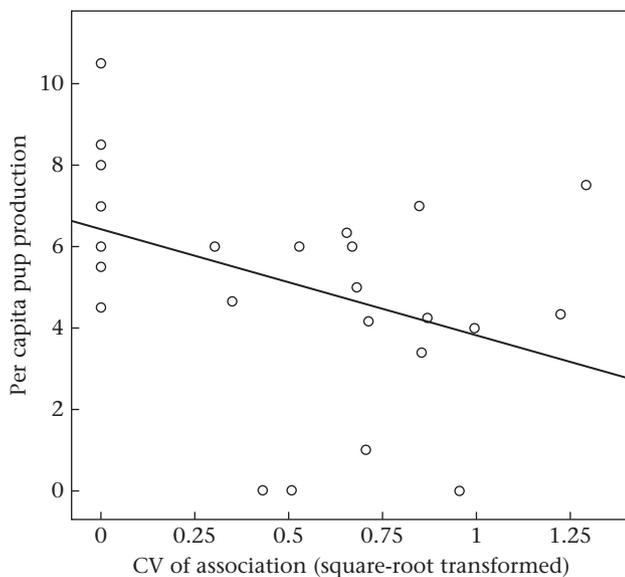
**Figure 2.** Sex differences in (a) association strength and (b) preferred partner degree in degus during mating ( $N = 58$  females, 15 males) and lactation ( $N = 93$  females, 27 males). Strength was calculated as the sum of an individual's associations, and degree was the number of preferred partners that an individual had. CI: confidence intervals.



**Figure 3.** Turnover in preferred partner associations between mating and lactation in degus ( $N = 59$  females, 14 males). CI: confidence intervals.

role in maintaining cohesion among related females during communal nursing, but there is conflict among nonkin. While female kinship may play a role in degu group formation (Ebensperger et al. 2004, 2009), the benefits of kinship in this system are not clear-cut (Hayes et al. 2009; Ebensperger et al. 2011b; Burger et al. 2012). Additional genetic work is needed to determine patterns of kinship and social structure under natural conditions.

Preferred associations among female degus were more stable than those of males. This suggests that females better maintain longer-term associations, and also that males have more social partners over multiple seasons than would be indicated by considering either season alone. This also indicates greater stability,



**Figure 4.** Relationship between per capita female fitness (pup production) and heterogeneity of association strength (coefficient of variation (CV) of association strength) among female degus (Pearson correlation:  $r_{29} = -0.428$ ).

at least at the dyadic level, than might otherwise be suggested by the high turnover in social group membership by both sexes (Ebensperger et al. 2009). Social systems often contain multiple levels of organization exhibiting different temporal patterns (Hinde 1974; Couzin 2006; Ryder et al. 2008; Whitehead 2008). In fission–fusion societies, for example, groups may form and disband flexibly, and some higher-level groupings are temporary, while other smaller units remain stable over longer terms (Connor et al. 2001; Wittemyer et al. 2005; Aureli et al. 2008; Croft et al. 2011; Kerth et al. 2011). Longitudinal studies on marked individuals over multiple seasons are especially important for studying longer-term temporal variation or stability (Whitehead 2008).

#### *Social Networks and Female Reproductive Outcomes*

We found no support for the hypothesis that stronger female–female group cohesion during lactation is associated with increased reproductive success of females. However, greater heterogeneity in the strength of associations between females was tied to lower per capita pup production. Thus, on average, female degus did not appear to gain a direct benefit of increasing association with other females, but could suffer costs associated with certain social structures, which is consistent with expectations for a plural breeder (Ebensperger et al. 2012). Barocas et al. (2011) found no effect of individual association strength but found negative effects of group variance in association strength on adult longevity in rock hyrax, a plural breeder with female-biased social groups and communal care, suggesting costs to individual health in less egalitarian social structures. In contrast, Royle et al. (2012) found that strength of within-nest associations predicted fitness in families of great tits, but CV of association strength had no effect; notably, these results suggested selection at the family level for conflict reduction, despite selection at the level of individual nestlings for better competitive ability. Groups form and function in diverse ways, and the fitness correlates of strength and heterogeneity of within-group interactions may be expected to vary widely depending on the context. It should be especially important to consider different levels of organization if there are conflicting pressures between individual position and higher-level dynamics (Hock et al. 2010).

In a laboratory setting, communally nesting female degus experience reduced per capita pup production, and the costs are shared unevenly (Ebensperger et al. 2007). Genetic analysis to assign maternity will be key to testing this idea in degus in the field, and indeed, preliminary results from a small number of individuals suggest there is greater female reproductive skew in groups with more females (Quan 2010). This still leaves questions about why females that suffer disproportionate costs choose to nest communally, given that females do not appear to be burrow limited in this system (Ebensperger et al. 2011a). Communal nursing could influence aspects of pup quality and survival, such as immune function (Roulin & Heeb 1999), or it may be more costly to avoid communal care (Packer et al. 1992). Within-group heterogeneity in associations likely reflects dynamic ongoing social processes that occur in conjunction with female reproductive decisions.

Measuring social group heterogeneity in this way has potential relevance for understanding reproductive skew, particularly in plurally breeding mammals where the prospects of skew have been given less attention. Much theory has focused on the partitioning of reproduction among cooperatively breeding females to understand the evolution of high-skew societies (i.e. social species in which one or a few females in a group dominate direct reproduction; Vehrencamp 1983; Keller & Reeve 1994; Solomon & French 1997; Johnstone 2000; Silk 2007; Nonacs & Hager 2011). In mammalian cooperative breeders, care provided by philopatric individuals

generally improves the direct reproductive output of breeders (Ebensperger et al. 2012) and can contribute to skew. Theory predicts that nonbreeders offset the lack of direct fitness with increased indirect fitness gained by helping closely related kin rear offspring (Hamilton 1964; Maynard Smith 1964) or gain benefits that enhance their future reproduction (Solomon & Hayes 2009). In contrast, in plurally breeding mammals, females tend to have lower reproductive output than breeding females in singularly breeding species (Ebensperger et al. 2012). There is also evidence that plural breeding results in lower direct reproductive output than singular breeding in species that use both strategies (Solomon & Crist 2008). Although theory for the causes of skew in plural breeders is emerging (Rubenstein & Shen 2009), we know very little about the underlying causes of differences in reproductive success of females in the same plurally breeding groups. We suggest the utility of quantifying variation in social associations in order to identify novel, within-group influences on reproductive variation.

The consequences of group heterogeneity for individual outcomes are still relatively understudied compared to the effects of group size, and measuring within-group variation in association strength offers a useful way to capture potential social conflict in animal groups. The heterogeneity of relationship strengths appears to influence conflict in human organizations (e.g. Nelson 1989), but has received less attention in other animal groups. Recent studies have focused on patterns of the network substructures that suggest animal groups are more 'orderly' and thus exhibit less structural conflict than expected by chance (Shizuka & McDonald 2012; McDonald & Shizuka 2013). Examining multiple structural properties, at both the individual and group level, should inform us about mechanisms of social conflict generation and resolution, and to what extent these may vary by system and context.

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