Kin in space: social viscosity in a spatially and genetically substructured network

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Population substructuring is a fundamental aspect of animal societies. A growing number of theoretical studies recognize that who-meets-whom is not random, but rather determined by spatial relationships or illustrated by social networks. Structural properties of large highly dynamic social systems are notoriously difficult to unravel. Network approaches provide powerful ways to analyse the intricate relationships between social behaviour, dispersal strategies and genetic structure. Applying network analytical tools to a colony of the highly gregarious Galápagos sea lion (*Zalophus wolfebaeki*), we find several genetic clusters that correspond to spatially determined ‘network communities’. Overall relatedness was low, and genetic structure in the network can be interpreted as an emergent property of philopatry and seems not to be primarily driven by targeted interactions among highly related individuals in family groups. Nevertheless, social relationships between directly adjacent individuals in the network were stronger among genetically more similar individuals. Taken together, these results suggest that even small differences in the degree of relatedness can influence behavioural decisions. This raises the fascinating prospect that kin selection may also apply to low levels of relatedness within densely packed animal groups where less obvious co-operative interactions such as increased tolerance and stress reduction are important.

Keywords: altruism; co-operation; cross-fostering; *Zalophus wolfebaeki*; kin selection; social network

1. INTRODUCTION

Population substructuring is a key component in animal social systems. A growing number of theoretical studies recognize that who-meets-whom is not random, but determined by spatial relationships or other forms of assortment (Lion & van Baalen 2008). Social interactions on local and global population levels delimit the boundaries in which fitness-relevant behaviours are displayed, thus controlling patterns of gene flow (Sugg *et al.* 1996). Owing to philopatry and strategies of delayed dispersal (social viscosity), individuals are often physically assorted into kin clusters where animals share the same alleles by descent with an increased probability (Dobson 1982; Fowler 2005). For communally breeding species, where the average relatedness within these clusters is high and close relatives recognize each other, genetic structure is often dictated by the placement of related individuals and usually co-varies with social structure (Faulkes *et al.* 1997; Dobson 1998). For such systems, kin selection theory provides an appealing solution to understand how even costly social behaviours such as cooperation and altruism evolve as a direct evolutionary consequence of inclusive fitness benefits (Hamilton 1964; Griffin & West 2003). In large, colonially organized animal groups much less is known about the potential role of kin

and the interplay between dispersal strategies, genetic structure and social behaviour. In such groupings, interactions between kin are diluted by the presence of numerous neighbours and average relatedness quickly drops with increasing group size (Lukas *et al.* 2005). Particularly in fission–fusion groups, where structural features are not intuitive, it is a major challenge to understand the assortative forces behind the structural properties of the system.

A promising approach is offered by the application of recent network theory to animal societies (e.g. Lusseau *et al.* 2005; Croft *et al.* 2006). This approach has the potential to explore apparently complex societies with seemingly ambiguous structure (Krause *et al.* 2007; Wey *et al.* 2008). Rooted in mathematical graph theory, network analysis can model the evolution of social behaviour (e.g. Ohtsuki *et al.* 2006; Taylor *et al.* 2007) and illustrate social tendencies with spatially explicit graphs. Parallel to the idea of social viscosity in kinship theory, most of the models expose population substructuring as the key element promoting the evolution of social behaviour (Lion & van Baalen 2008). Graph theoretical approaches and the traditional framework of inclusive fitness obey the same mathematical formalism and have other central elements in common (Lehmann *et al.* 2007; Taylor *et al.* 2007). Network approaches are thus appropriate for studying the relative role of kin selection in structured animal populations. While the theoretical literature on the subject is thriving, empirical studies only gradually appear to recognize the potential of social networks in addressing questions related to the evolution of social behaviour.

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Figure 1. Hierarchical structure in a social network of the Galápagos sea lion (modified after Wolf *et al.* 2007a). (a) Community structure in the overall social network. Nodes symbolize individual animals; lines stand for social ties. In the network, social entities can be identified, where members are more densely connected among themselves than with the rest of the network. They are called ‘communities’ and indicated by different colours. It is important to note that network structure is solely derived from social interaction data. (b) A map of the study island (approx. 250 m in width) shows that communities can largely be defined by patterns of space use. The coloured patches correspond to the home ranges of individuals from a given community showing that community members have common areas to which they are all faithful. (c) Communities further split into social cliques indicated by different symbols. Cliques represent an individual’s most intimate social neighbourhood. In contrast to communities, the existence of cliques cannot be explained by patterns of space use. Home ranges of all clique members fully overlap regardless to which clique they belong.

We have recently studied the structural properties of a highly dynamic fission–fusion social network that integrates proximity relationships of several hundred individuals (Wolf *et al.* 2007a). The network described in this study refers to a colony of sea lions (*Zalophus wollebaeki*; Wolf *et al.* 2007b) that dwell on a tiny islet (approx. 250 m wide) in the Galápagos archipelago. Approximately, 1000 individuals maintain social interactions year round (Wolf & Trillmich 2007). Newly developed algorithms screening the network’s topology unveiled hierarchical elements of social structure consisting of intermediate tiers that would have otherwise gone undetected. Figure 1 shows a schematic of the network’s essential structural properties: the overall social network is partitioned into large ‘communities’ and smaller ‘cliques’ nested therein. Community membership describes an individual’s general social neighbourhood and can be explained by home range overlap (i.e. static interaction). Clique membership, however, represents an individual’s closer social neighbourhood and cannot be explained spatially (i.e. dynamic interaction). The immediate social relationships of an individual are represented by the direct connections (ties) to other individuals in the network.

As a high degree of fine-scale site fidelity and possibly female biased home range inheritance have been

documented in this species (Wolf & Trillmich 2007) exploring this network holds the potential to work out the relationship between spatial, social and genetic structure. Specifically, genetic structure within a social group can emerge in two non-mutually exclusive ways which natural selection could act to favour: either as a by-product of philopatric behaviour *per se* or by selection on targeted kin interactions among small groups of highly related animals. The network approach allows us to make predictions on the relative role of the two processes.

- (i) If genetic relatedness emerges primarily as a by-product of cross-generational site fidelity, then average relatedness among individuals across the colony as a whole should be generally low and genetic structure should be governed by the spatially defined communities within the network. Owing to philopatry, individuals of the same community would be expected to be more related to each other than to the global population background. Relatedness within cliques (the socially defined tier) should not be higher than in communities.
- (ii) However, if social ties are strongest among close kin that benefit from shared alleles via inclusive fitness, then there will be a higher degree of relatedness within the cliques than within the spatially defined communities. We may then expect to see cooperative or altruistic behaviour within cliques. One of the most conspicuous altruistic behaviours is cross fostering, which is widespread in some pinniped species despite its costs (e.g. Riedman & Le Boeuf 1982; Boness *et al.* 1998; Childerhouse & Gales 2001). Thus, we expect such behaviour to occur preferentially among highly related individuals from the same clique in the network.

2. MATERIAL AND METHODS

This study is part of a long-term project conducted on a small Galápagos islet (Ecuador), which is used as a breeding and resting site by approximately 1000 sea lions (for details of the study area, study population, capture and tagging procedure, see Wolf *et al.* 2005 and Wolf & Trillmich 2007).

(a) Genetic and network analyses

The network part of this work is based on a study by Wolf *et al.* (2007a) on sea lion social behaviour witnessed during 10 September 2004–20 November 2004. For all 380 individuals forming part of the network, genomic DNA was amplified in a multiplex PCR approach (Qiagen multiplex PCR Kit). Samples were genotyped on an ABI 3730 capillary sequencer at 22 fluorescently marked dinucleotide microsatellite loci, most of which have been specifically designed for the Galápagos sea lion (Wolf *et al.* 2006; Hoffman *et al.* 2007). Individuals were only included in subsequent analyses if a minimum of 20 loci were successfully scored (Wolf *et al.* 2007b, 2008). Maximum-likelihood estimates of pairwise relatedness coefficients and genealogical relationships were then calculated from the multilocus genotypes with the software package ML-RELATE (Kalinowski *et al.* 2006). These estimates were used to infer whether kinship clusters would mirror the social structure revealed by network visualization here described as communities and cliques (figure 1).

As it was not our aim to detect the most trivial kinship structure given by mother–offspring dyads, all known mother–offspring pairs where the offspring was still nursed were excluded. Mother–offspring pairs were known with high confidence (see Trillmich & Wolf 2008, see also cross fostering below). To further rule out that kinship structure was determined by offspring that had been weaned only recently, all analyses were carried out on a subset of the network restricted to adult females. All statistical inference on kinship structure was based on randomization techniques that were programed in R (R Development Core Team 2006). We deliberately applied three different approaches to validate the robustness of the results. In the following, we outline the general logic behind each approach (for further details, see electronic supplementary material).

(i) *Matrix correlation between social tie strength and relatedness coefficient*

The network in figure 1 is a binary visualization of a symmetric matrix that summarizes social association of individuals in local social groups over 141 behavioural surveys. Pairs of individuals that have been sighted at least twice together in a local group during all surveys are inter-connected (for details on how social association based on shared group membership is defined, see Wolf *et al.* 2007a). Contrary to the impression of the binary network (figure 1), the total number of times that a pair was found together in a local group (tie strength) varies considerably and ranges from 0 to 25. Tie strength thus provides a quantitative measure for social affinity and can be used to test whether social bonds between related individuals are stronger than between less related individuals. This is achieved by comparing the tie strength matrix to the matrix containing the estimates of pairwise relatedness using a partial Mantel test (ECODIST package in R, 10 000 permutations). To prevent the influence of spurious observations, pairs that were seen together less than twice were excluded.

(ii) *Relatedness coefficients and simulated Wilcoxon test statistic*

The general idea behind this approach is to compare the degree of average pairwise relatedness between the different hierarchical components of the network: cliques; communities; and the global population background. To this end, all possible relationships between individuals in the network were divided into two groups: pairs of individuals that share membership of a given unit and those that come from different units (e.g. same community versus different communities). Groups were then statistically compared using a randomized Wilcoxon rank sum test with 10 000 Monte Carlo resamplings. Relative frequencies of simulated values that are equal to or larger than the empirical value can be interpreted as the *p*-value, the probability of committing a type I error (Manly 1997).

(iii) *Pedigrees, simulated contingency tables and χ^2 -test statistic*

Along the lines of the aforementioned procedure, this approach compares relatedness coefficients via an estimated relationship category between individuals. Relationship categories include parent–offspring (PO), full sibling (FS), half sibling (HS) and unrelated (U), as estimated on the basis of shared alleles. Analysis was restricted to individual pairs where the relationship was attributed with at least 95% confidence based on 5000 iterations (Kalinowski *et al.* 2006); ambiguous categories such as HSorFS, FSorPO, etc. were excluded. All pairs where specific estimates were available

were again divided into two groups. Frequency information of each relationship category was then summarized in a contingency table for both groups and a randomized χ^2 -statistic with 10 000 Monte Carlo resamplings was used to test for statistical independence between groups. Simulated χ^2 residuals were used to infer which of the categories significantly contributed to the overall effect.

(b) *Cross fostering*

Galápagos sea lions give birth to only one pup every year or every second year (Trillmich & Wolf 2008). Cross-fostering events can therefore be determined easily by a combination of behavioural monitoring of suckling bouts and genetic relatedness analyses. From 2003 to 2005, we recorded suckling bouts between individually tagged female–young pairs during a total of 510 behavioural surveys (Wolf & Trillmich 2007). To eliminate misidentifications by tag reading errors, we restricted the analyses to suckling pairs that had been sighted at least three times or had been explicitly confirmed by the observer. Altogether, a total of 2304 suckling bouts were observed in 176 pairs of individually identified female–young pairs. These pairs included 123 females that were seen with different offspring over the years and 174 young, two of which were seen suckling multiple females. After genotyping all pairs we used CERVUS v. 3.0 (Marshall *et al.* 1998; Kalinowski *et al.* 2007) to determine whether the observed suckling pairs were biological mother–offspring units. The most likely mother was estimated for each offspring from the entire candidate set of females with a 99% confidence threshold. Pairs with no significant match or where the inferred genetic mother–offspring combinations differed from the suckling pairs observed in the field were scored as cross-foster pairs. The degree of genetic relatedness between these pairs was estimated with ML-RELATE (Kalinowski *et al.* 2006).

3. RESULTS

(a) *Social network analyses*

(i) *Kinship structure is tightly linked to spatial behaviour*

Overall relatedness was low in both cliques and communities (table 1). Degree of relatedness was higher among individuals within than among communities. Average within-community relatedness was twice as high as among communities (Wilcoxon statistic: $p < 0.001$, χ^2 -statistic: $p = 0.007$; table 1). This pattern held if only adult females were considered (115 females instead of 379 individuals of the overall network). Adult females sharing community membership were on average 1.82 times more related than females of different communities (Wilcoxon statistic: $p = 0.051$, χ^2 -statistic: $p = 0.011$; table 1). In both cases (overall network and females only), χ^2 residuals showed that the number of full siblings, half siblings and former mother–offspring pairs was higher within communities than between them. Unrelated individuals were found significantly more often across different communities (figure 2).

(ii) *Targeted kin selection between highly related individuals does not create kin clusters*

If social relationships in the colony were mainly driven by targeted kin selection, we would expect social cliques to be the core units of relatedness. Under this prediction, the median degree of pairwise relatedness within a clique

Table 1. Average relatedness between individuals in the sea lion social network (figure 1). We report average relatedness between individuals that share membership of a given tier (within) or that are associated with different tiers (between). The ratio (within/between) indicates, if within tier relatedness is higher (more than 1) or lower (less than 1) than between tiers. Statistical significance is symbolized by asterisks according to common standards; n.s., not significant.

			mean relatedness	median relatedness
all individuals	cliques	within	0.0505	0.0065
		between	0.0499	0.008
		within/between ^{n.s.}	1.0	0.80
	communities	within	0.0500	0.0075
		between	0.0469	0.0037
		within/between ^{***}	1.07	2.02
adult females	cliques	within	0.0554	0.00951
		between	0.0522	0.0073
		within/between ^{n.s.}	1.06	1.30
	communities	within	0.053	0.008
		between	0.047	0.004
		within/between [*]	1.12	1.82

Figure 2. Relative contribution of different pairwise relationship categories to kinship structure in social communities of the Galapagos sea lion (figure 1a). Individuals from the same community (white bars) are compared with those from different communities (grey bars). Depicted are simulated residual values that show how strong a given category deviates from the random expectation of no difference between the two groups (i.e. no kinship structure). Positive values indicate that a category is relatively overrepresented, negative values that it is underrepresented. Asterisks indicate how well the deviation is statistically supported. (a) Comparison including all 379 individuals of the entire network. (b) Comparison restricted to 115 adult females. Category abbreviations: HS, half sibling; FS, full sibling; PO, parent-offspring.

should be significantly higher than between cliques of the same community. However, the degree of relatedness within cliques was not distinguishable from the community background (simulated Wilcoxon statistic: $p=0.581$, simulated χ^2 -statistic: $p=0.410$). Nonetheless, when observed mother-offspring pairs were included in the analysis, median relationship within cliques exceeded that of the community background (Wilcoxon statistic: $p=0.002$, χ^2 -statistic: $p<0.001$). Even so, animals within cliques were only 1.06 times more closely related than between cliques. From this, we conclude that in the social core unit of the network (cliques) kin selection only acts in its most trivial form of direct parental care.

(iii) *Social tie strength and genetic relatedness are correlated*
Strength of social relationships was approximated by the number of times that a pair of individuals was sighted together (tie strength; see §2). Thus, we can ask whether behavioural decisions at the level of interaction were influenced by the degree of relatedness. Indeed, we found that the tie strength and the degree of relatedness between connected pairs of individuals were correlated (Mantel test: $r=0.16$, $p<0.001$; figure 3).

(b) Cross fostering

During three years of observation, we recorded a cross-foster frequency of 0.006% (14 non-filial/2304 total suckling events). Parentage was genetically inferred for 97% (171 out of 176) of suckling female-pup pairs. Of the five pairs where pup and female did not fit genetically, only one case could be scored as true non-filial nursing (less than 0.01% of all pairs). The remaining four pairs included one adult male (greater than female size) that was seen suckling once, and three young that usually suckled their biological mother and were only observed to steal milk occasionally. Non-filial nursing, therefore, did not represent stable cross-fostering relationships. Overall relatedness of cross-suckling pairs was very similar to the overall relatedness background of random pairs in the immediate social neighbourhood ($r_{\text{mean}}=0.086$, $r_{\text{median}}=0.06$, compare with table 1).

4. DISCUSSION

Using network analyses, we investigated the relationship between social and genetic structures and revisited the potential role of kin selection for the occurrence of

Figure 3. Correlation of minimum tie strength and relatedness between pairs of individuals that are connected in the social network (figure 1a). A non-parametric lowess smoothing line is shown for illustration. Total number of connections between individuals in the network with a given minimum tie strength is shown at the bottom.

altruistic behaviour in a colonial mammal. Genetic structure—inferred by both genetic relatedness coefficients and pedigree relationships—coincided with ‘social communities’, an intermediate tier of the social network that closely corresponds to spatial relationships among individuals. This finding supports the idea that kin structure can arise as an emergent property of limited dispersal alone and need not imply any targeted, beneficial interactions among kin. These results are consistent with many studies showing that philopatry is a powerful mechanism by which genetic structure can accumulate as a by-product (Pomeroy *et al.* 2000; Fowler 2005; Fabiani *et al.* 2006; Campbell *et al.* 2008). This makes intuitive sense in the Galápagos sea lion, a species where female offspring are prone to inherit their mother’s home range (Wolf & Trillmich 2007) and where male site fidelity might be related to long-term dominance hierarchies.

While spatial assortment bore on genetic structure, genetic relatedness among the lower level tiers in the network (cliques), which are defined by social preference, was not elevated. Likewise, altruistic cross-fostering behaviour was virtually absent and the exceptional female–young dyads that displayed cross-fostering showed no extreme degree of relatedness. Cross-fostering events appear to be best explained as occasional cases of misdirected parental care as has been suggested for other species (reviewed by Roulin 2002). Similarly, all previous studies that looked into the degree of relatedness between offspring and their foster mothers did not find any evidence for kin selection (Perry *et al.* 1998; McCulloch *et al.* 1999; Schaeff *et al.* 1999; Hoffman & Amos 2005). These results highlight how difficult it can be to interpret kinship structure in animal societies. Although it is often tempting to infer inclusive fitness benefits from correlational relationships between kinship structure and social behaviour, our findings point to the fact that co-operative behaviour need not evolve despite kinship structure, or may well be rooted in other non-genetic mechanisms (Clutton-Brock 2002).

This result notwithstanding, even a slightly elevated background of relatedness holds the potential for weakly selected co-operative behaviours to evolve. Compared with dynasties of communally breeding species, the average degree of relatedness in large animal groups should be low. Nonetheless, preferential associations among genetically more similar individuals may still be advantageous. This idea becomes particularly plausible if interactions are iterated many times between individuals with long-term memory (for sea lions, see Kastak & Schusterman 2002). If costs to the donor are small compared with the benefits gained by the receiver, low levels of average relatedness can suffice to induce co-operative behaviour.

Our finding that individuals maintained stronger social ties with genetically more similar interaction partners indeed suggests that the degree of relatedness, though comparatively low overall, influences behavioural decisions. Taking into account that a considerable amount of noise is artificially introduced by estimating low levels of relatedness with only 22 microsatellite markers (Blouin *et al.* 1996), we can assume that the correlation is stronger than it appears. Technically, this result is important insofar as it suggests that networks weighted by some additional criterion may outperform strictly binary networks (Whitehead 2008). More essentially, it raises the fascinating prospect that low levels of relatedness and even small differences in relatedness can be relevant for natural selection to act on certain types of social behaviour other than the sensational text book examples of cross fostering or ‘suicidal sacrifice in the name of others’ (Alcock 2005). We know that kin recognition works even with intriguingly low differences in relatedness (Jehle *et al.* 2007) and honest olfactory cues signalling an individual’s immunogenetic composition probably exist (Boehm & Zufall 2006). We further know that animals are able to adjust their degree of aggressiveness to the degree of relatedness of their opponent (Hanggi & Schusterman 1990; Piertney *et al.* 1999) and that this can pay in terms of fitness. Stress induced by aggressive behaviour not only towards non-filial young but also towards adult females is known to negatively impact on survival and fitness (Le Boeuf & Briggs 1977; Vilá & Cassini 1990; Ceacero *et al.* 2007). This predicts a role of less obvious co-operative behaviours such as social tolerance for the successful formation and stability of animal aggregations (Hare *et al.* 2007).

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