

RÉSEAUX SOCIAUX CHEZ LE MOUFLON D'AMÉRIQUE (*OVIS CANADENSIS*)

par

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SOMMAIRE

Les réseaux sociaux sont de plus en plus utilisés en écologie pour représenter et analyser la structure sociale. Modéliser la structure sociale permet de mieux comprendre les processus de transmission des maladies et de l'information entre les individus, ainsi que les bénéfices de la socialité sur la valeur adaptative des individus. Jusqu'à maintenant peu d'études ont identifié les déterminants et les conséquences des associations sociales. De surcroît, on connaît peu sur l'influence du type de données comportementales et du choix de l'indice d'association sur la structure des réseaux sociaux. Ma maîtrise explore les déterminants et conséquences de la socialité de même que l'impact du type de données pour la construction de réseaux sociaux grâce à la disponibilité de différents types de données comportementales et au suivi à long terme de la population de mouflons d'Amérique (*Ovis canadensis*) à Ram Mountain en Alberta.

J'ai comparé trois réseaux sociaux construits avec trois types de données comportementales: co-occurrence dans un groupe, fréquence de proximité à $\leq 1,5$ mètre et interactions agonistiques pour quantifier dans quelle mesure ces trois réseaux représentant la structure sociale des brebis adultes étaient similaires. Pour ce faire, j'ai contrasté des mesures individuelles et de réseaux. L'approche fréquemment utilisée d'utiliser les groupes pour inférer les associations sociales se révèle imparfaite: à l'intérieur d'un groupe, les associations sociales ne sont pas égales entre tous les membres. Ce travail souligne l'importance de choisir le type de données qui permet de répondre aux questions biologiques d'intérêt. Or, il semble que pour la population étudiée, les réseaux construits avec la composition de groupe et avec les événements de proximité soient pertinents dans des contextes différents.

Par conséquent, j'ai utilisé les événements de proximité qui font appel à une association à fine échelle pour identifier les déterminants des associations entre les dyades. Pour une dyade, il y a un effet positif de la similarité du statut reproducteur sur la fréquence des associations pour les années 2011 et 2012. L'apparement, la similarité en âge ou en rang de dominance n'influence pas la fréquence d'association d'une dyade. Quant au niveau de sociabilité à l'échelle individuelle, les brebis plus jeunes sont les plus centrales dans les réseaux sociaux et donc les plus sociables.

Mes travaux de maîtrise amènent un nouveau regard sur l'étude de la socialité chez les animaux grâce à l'utilisation de réseaux sociaux pour explorer les déterminants et conséquences des associations sociales.

Mots-clés : Réseaux sociaux, socialité, colliers de proximité, structure sociale, indices d'association.

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LISTE DES ABREVIATIONS

<i>AIC</i>	Critère d'information d'Akaike
<i>AIC_w</i>	Poids du critère d'information d'Akaike
$\hat{\beta}$	Estimé
ID	Identification individuelle
CI	Intervalle de confiance
95CI	Intervalle de confiance à 95%
CV	Coefficient de variation
GoG	<i>Gambit of the group</i>
HWI	Half-weight-index
HWIG	Half-weight-index corrigé pour la grégarité tel que proposé par Godde et al. (2013)
<i>P</i>	Valeur de <i>P</i> avec un seuil de significativité à 0,95
<i>r</i>	Coefficient de corrélation
R^2	Coefficient de détermination
SD	Écart-type
SE	Erreur standard
\bar{x}	Moyenne arithmétique
Σ	Sommation

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CHAPITRE 1: INTRODUCTION GENERALE

La vie en groupe est caractéristique de plusieurs espèces animales. Par exemple, dans le Serengeti, on retrouve des groupes de gnous bleus (*Connochaetes taurinus*; Estes 1966), de buffles d'Afrique (*Syncerus caffer*; Jolles 2007) et de zèbres (*Equus burchelli*; Fischhoff et al. 2007) regroupant plusieurs centaines, voire milliers, d'individus. Une des hypothèses proposée pour expliquer ce phénomène est la diminution du risque de prédation (Elgar, 1989). Les avantages inhérents à la vie en groupe auraient favorisé l'émergence des comportements sociaux et de la socialité (Silk et al., 2010). La socialité est le fait d'avoir et de maintenir des interactions avec d'autres individus (Whitehead, 2008). Il existe toutefois une grande diversité dans les degrés de socialité entre les espèces et celle-ci se répartit sur un continuum : certaines espèces ont des liens sociaux presque exclusivement durant la période de reproduction et d'élevage des jeunes, alors qu'à l'autre extrémité du gradient se trouvent les espèces eusociales avec une division sociale des tâches (Nowak et al., 2010). Comprendre pourquoi les animaux forment ou non des groupes sociaux malgré les coûts potentiels de la compétition (West-Eberhard, 1979) et de l'augmentation de la probabilité d'infection par des pathogènes (Freeland, 1976; Loehle, 1995) a fasciné les écologistes depuis plusieurs décennies (Alexander, 1974; Vehrencamp, 1983; Whitehouse & Lubin, 2005). Étudier les causes proximales et ultimes de même que les conséquences évolutives de la socialité est donc fondamental pour comprendre l'évolution des comportements sociaux.

La grande diversité des tactiques sociales observée chez les animaux génère également une grande diversité de structures sociales. Une structure sociale est définie comme étant l'ensemble des liens complexes qui existent entre les individus d'un groupe donné. La structure sociale d'un groupe ou d'une population est le résultat des interactions sociales entre toutes les paires d'individus (ci-après dyades) et prend différentes formes. Par exemple, chez le loup gris (*Canis lupus*), la structure sociale est marquée par une forte hiérarchie (Mech,

1999) alors que chez les mangoustes rayées (*Mungos mungo*), la structure sociale est plutôt égalitaire (de Luca & Ginsberg, 2001). Établir le type de structure sociale nous informe sur la position qu'occupent les individus dans leur groupe et les répercussions que cette position peut avoir sur leur valeur adaptative

Représenter l'organisation sociale au-delà d'un simple cadre descriptif n'est toutefois pas aisé. Les premiers scientifiques à s'être intéressés au comportement animal ont posé les bases de l'éthologie qui consistait en l'observation des comportements et en leur interprétation d'un point de vue évolutif (Lorenz & Kickert, 1981). On tentait alors de dégager de ces observations et descriptions des hypothèses qui permettraient d'identifier les pressions de sélection ayant mené à l'expression des comportements sociaux. Hinde (1976) a proposé un cadre conceptuel davantage quantitatif (Figure 1.1), mais la structure sociale était difficile à analyser formellement. Plus récemment, le cadre analytique des réseaux sociaux a permis des analyses plus détaillées dans l'optique de décrire, mais aussi d'analyser les structures sociales et leurs conséquences. Cette méthode prometteuse et innovatrice permet de modéliser les relations directes et indirectes entre les individus (Krause et al., 2007; Sih et al., 2009; Wey et al., 2008) à l'échelle du groupe ou de la population. Ces analyses ont donc une portée plus grande parce qu'elles ne se limitent pas à la dyade. Ma maîtrise traite de l'importance du type de données pour construire des réseaux sociaux de même que les déterminants et les conséquences sur la valeur adaptative des associations sociales en prenant comme modèle d'étude la population de mouflon d'Amérique (*Ovis canadensis*) à Ram Mountain en Alberta.

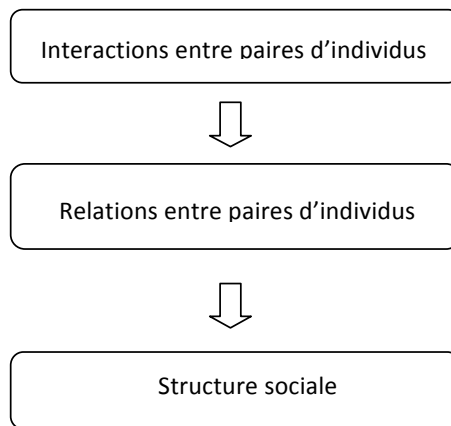


Figure 1.1 : Cadre conceptuel décrivant la structure sociale, adapté de Hinde (1976). Chaque paire d'individus a un certain nombre d'interactions desquelles émerge la relation qui les unit. Cette relation, par exemple de dominant et dominé ou de partenaire préférentiel, de même que les relations de toutes les autres dyades forment la structure sociale du groupe.

Évolution de la socialité chez les animaux

Les relations entre les individus d'une espèce s'établissent à la suite d'interactions répétées et l'ensemble de celles-ci façonne la structure sociale (Hinde, 1976; Wey et al., 2008; Whitehead, 2008). La socialité peut représenter à la fois des coûts et des bénéfices et l'importance des compromis varie grandement en fonction des circonstances écologiques. Parmi les coûts, il peut y avoir une augmentation de la compétition intraspécifique (Whitehead, 1997) et une propagation accrue des pathogènes (Loehle, 1995). Une meilleure transmission de l'information, une thermorégulation facilitée, des déplacements moins exigeants ou une diminution des risques de prédation comptent parmi les bénéfices à s'établir en sociétés (Croft et al., 2009; Krause et al., 2007). Ces compromis de la socialité influencent la structure sociale, de sorte que les coûts sont minimisés et les bénéfices sont maximisés (Silk et al., 2010). Conséquemment, le degré de cohésion de la structure sociale peut varier en

fonction de l'écologie d'une espèce pour maximiser la valeur adaptative (Formica et al., 2012; Silk et al., 2003; Stanton & Mann, 2012). Par exemple, Silk et al. (2009, 2010) ont mis en évidence une structure sociale complexe, stable et cohésive chez des babouins de la Savane (*Papio hamadryas ursinus*). Cette organisation sociale serait favorisée par les nombreux avantages individuels inhérents à l'entretien de liens sociaux étroits, à savoir un meilleur succès reproducteur, une meilleure survie de la progéniture et un accroissement de la longévité (Silk et al., 2009, 2010). Par contre, la cohésion sociale n'est pas toujours favorisée. Les marmottes à ventre jaune femelles (*Marmota flaviventris*) ont très peu d'interactions entre elles. Ces résultats suggèrent que, pour ce système, la cohésion sociale n'est pas positivement liée à la valeur adaptative. Toutefois, les coûts sociaux peuvent différer en fonction des caractéristiques intrinsèques des individus tel que le sexe (Wey & Blumstein, 2012). En effet, chez les marmottes, les mâles exhibant davantage de comportements agonistiques ont un meilleur succès reproducteur (Wey & Blumstein, 2012).

Les réseaux sociaux

L'organisation sociale d'une population peut être traduite par des réseaux sociaux où les individus sont représentés par des nœuds et leurs liens par des lignes les reliant. Les patrons que forment ces nœuds et ces liens peuvent être analysés grâce à des mesures de réseaux (Tableau 2.1). Les réseaux peuvent être plus ou moins complexes selon les informations qu'ils incluent : interactions directionnelles, caractéristiques des individus et force des affiliations (Krause et al., 2007; Wey et al., 2008).

Un des avantages de la méthode des réseaux sociaux, c'est que l'on peut considérer le degré de socialité de chaque individu au sein d'un groupe ou d'une population (Wey et al., 2008). Au même titre que certains individus se reproduisent mieux que d'autres de façon générale,

chaque individu occupe une position unique dans un réseau social parce que les liens avec ses congénères sont eux aussi uniques (Hock et al., 2010). La méthode des réseaux sociaux permet de traduire cette unicité grâce à des mesures individuelles de centralité faisant référence à la position d'un individu dans le réseau. La position d'un individu dans un réseau peut être mesurée de différentes façons qui incluent ou non les liens indirects (Tableau 2.1; Costenbader & Valente 2003)

La centralité d'un individu dans un réseau social est une mesure de son importance structurale basée sur sa position dans le réseau. La centralité individuelle est un paramètre des réseaux sociaux largement utilisé (Faust, 1997). Des individus sont considérés centraux lorsqu'ils ont de fréquentes interactions et lorsqu'ils interagissent avec des individus eux aussi centraux (Faust, 1997). Par opposition, les individus périphériques ont peu de liens sociaux et avec peu d'individus. La centralité a une signification biologique importante puisqu'elle mesure l'importance relative d'un individu comme point de liaison avec les autres individus (Costenbader & Valente, 2003). Ainsi, pour l'étude de la transmission de pathogènes, les individus centraux doivent être identifiés puisqu'ils ont le potentiel d'être d'importants vecteurs (Brooks et al., 2008; Hamede et al., 2009; Perkins et al., 2009) car plus susceptibles d'être infectés et d'infecter les autres. La centralité peut aussi être corrélée avec la valeur adaptative (Formica et al., 2012; Gómez & Perfectti, 2012; Vander Wal et al., 2014) via les bénéfices de la socialité.

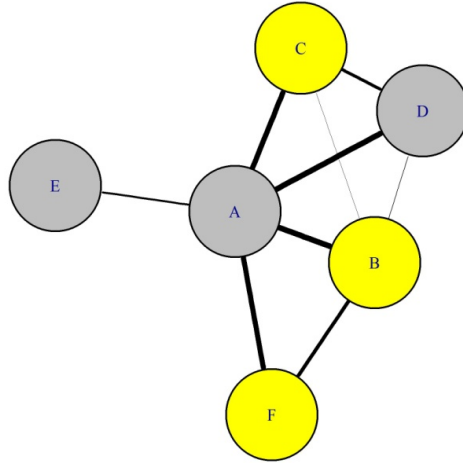


Figure 1.2 : Réseau social fictif pour les individus A à F. Les individus sont représentés par des cercles et l'épaisseur du trait entre les individus est proportionnelle à la force de leur association. Les caractéristiques des individus peuvent également être incluses dans le réseau social, dans le cas illustré les femelles sont en jaune et les mâles en gris. Dans ce réseau, l'individu le plus central est A et l'individu le plus périphérique est E.

Pour construire des réseaux sociaux, on peut utiliser tout type de données qui réfère à des liens entre des individus: association à l'intérieur des groupes (Wittemyer & Getz, 2007), associations spatiales entre individus (Lusseau, 2007), interactions directes entre dyades (Lea et al., 2010; Madden et al., 2009). Certains indices d'association sociale sont dérivés d'approximation, par exemple des localisations similaires dans un intervalle de temps donné (Aplin et al., 2012), alors que d'autres sont plus fiables, comme l'observation directe, mais ne sont pas toujours logistiquement possible. Or, le lien entre le type de données et les résultats des réseaux sociaux n'a jamais été investigué. Ceci est problématique parce que l'interprétation des résultats peut différer selon le type de données utilisées. Par exemple, les réseaux sociaux diffèrent lorsque l'on considère des interactions affiliatives par rapport à des interactions agonistiques chez les suricates (*Suricata suricatta*; Madden et al. 2009). Il est

donc important de comprendre l'influence du type de données pour être en mesure d'interpréter les résultats rigoureusement.

Les indices d'association

Il est assez commun d'utiliser des indices d'associations pour quantifier la force des associations entre deux individus ou dyade (Whitehead, 2008). Ceux-ci transforment des données de composition de groupes en une valeur qui représente l'association pour une dyade. Le plus connu et largement utilisé pour des espèces formant des groupes est le half-weight-index (HWI), mais il existe des variantes de cet indice d'association pour prendre en compte des structures sociales particulières (consulter Whitehead 2008 pour une liste exhaustive). Le HWI est une mesure standardisée entre 0 et 1 qui quantifie la proportion de temps qu'une dyade passe dans un même groupe. Cet indice d'association est relativement simple à utiliser, mais comporte le désavantage de ne pas séparer deux phénomènes participant à la socialité : l'affinité sociale qu'ont deux individus l'un pour l'autre et leur grégarité individuelle, c'est-à-dire leur propension à être dans des groupes. Dans l'optique d'avoir un indice d'association dyadique corrigé pour la grégarité des deux individus, Godde et al. (2013) ont proposé un nouvel indice dérivé du HWI, le half-weight-index corrigé pour la grégarité (HWIG). La capacité de ce nouvel indice à séparer les deux composantes des associations sociales dans des groupes a été mesurée avec des simulations (Godde et al., 2013), mais pas, à ma connaissance, avec des données empiriques. Dans ma maîtrise, je me suis intéressée à contraster des mesures de centralités dans des réseaux sociaux avec le HWI et le HWIG pour évaluer la pertinence de ce dernier pour la construction de réseaux sociaux. Ces indices d'association assument que tous les individus à l'intérieur d'un groupe s'associent de façon égale sans égard à la variabilité en distance entre eux et, par extension, à leur probabilité

d'interaction sociale. Par conséquent, je voulais aussi contraster ces résultats avec une méthode qui se base sur une échelle d'association plus fine.

Les colliers de proximité

L'utilisation des nouvelles technologies en écologie a permis de suivre les comportements des animaux de façon automatisée et de recueillir de nombreuses données qui ne sont pas biaisées par la présence d'un observateur. Pour récolter des données sur les associations sociales, on peut utiliser des colliers de proximité. Ces appareils fixés sur des animaux enregistrent un événement de proximité (certains auteurs utilisent le terme contact) lorsque deux animaux pourvus de colliers se trouvent à l'intérieur d'un certain rayon ($\leq 0,5 - 5$ mètres) les uns des autres. Les colliers sont programmés via un logiciel fourni par la compagnie Sirtrack Tracking Solution (Havelock North, Nouvelle-Zélande) de sorte que la distance maximale à laquelle un contact est enregistré peut être modifiée (Goodman, 2007). Le jour, l'heure, la durée et l'identifiant de l'autre individu sont enregistrés dans la mémoire de l'appareil. Des tests en laboratoires et sur le terrain ont montré une bonne fiabilité des appareils pour reconnaître les autres colliers (Drewe et al., 2012; Prange et al., 2006; Swain & Bishop-Hurley, 2007). Par opposition, divers facteurs peuvent diminuer la précision des appareils, à savoir la distance horizontale des colliers, l'orientation de l'antenne ou la durée de vie de la batterie (Boyland et al., 2013; Drewe et al., 2012; Walrath et al., 2011). De façon générale, l'utilisation de colliers de proximité permet d'accumuler des informations justes pour ce qui est de la distance, de la durée du contact et de l'identité des autres colliers (Prange et al., 2006; Swain & Bishop-Hurley, 2007; Walrath et al., 2011). Toutefois, il existe également des variations de performance entre les colliers et plusieurs méthodes de correction de cette hétérogénéité ont été proposées. Dans ce mémoire, la méthode proposée par Boyland et al. (2013) a été retenue. Spécifiquement, pour la reconstruction des réseaux sociaux, l'utilisation de ces appareils serait préférable à d'autres types de technologies (télémétrie et

téléométrie GPS; Walrath et al., 2011) parce que ces méthodes se basent sur une association spatiale mais pas nécessairement temporelle. Il est donc possible que l'inférence des associations sociales provenant des données ainsi obtenues contienne une proportion importante de fausses associations. Par opposition, les colliers de proximité enregistrent des associations sociales qui ont lieu à un temps donné pour une distance choisie en fonction de l'espèce à l'étude. La technologie des colliers de proximité est particulièrement utile lorsque l'on s'intéresse aux liens entre les individus d'espèces nocturnes, cryptiques ou qui sont observées difficilement (Prange et al., 2006). Par exemple, les colliers de proximité ont permis de modéliser le taux de transmission du cancer tumoral contagieux chez le diable de Tasmanie (*Sarcophilus harrisi*), qui de surcroît menace la pérennité de l'espèce (Hamede et al., 2009).

Néanmoins, le fait d'utiliser les colliers de proximité sans avoir la possibilité d'observer et de confirmer les interactions enregistrées pose problème : comment peut-on vérifier que les événements de proximité enregistrés sont avérés et quel type d'interaction le collier a-t-il enregistré ? Pour explorer cette problématique, j'ai combiné différentes approches pour recueillir des données permettant de construire des réseaux sociaux, notamment les colliers de proximité. Ainsi, l'utilisation de colliers de proximité sur une espèce facilement observable comme le mouflon d'Amérique amène une opportunité unique de vérifier si cette nouvelle technologie fonctionne correctement et si elle peut nous apporter des informations plus détaillées par rapport aux méthodes de mesure du comportement plus classiques, comme l'observation directe (Altmann, 1974).

Dans la population de Ram Mountain, nous avons muni chaque femelle adulte d'un collier de proximité. La composition des différents groupes au cours des saisons de terrain est connue pour plusieurs années et nous observons des interactions agonistiques régulièrement. Sauf pour le rut, il y a ségrégation sexuelle (Ruckstuhl et Neuhaus, 2002) et les groupes de brebis se font et se défont en une dynamique de fusion et de fission. Les mouflons sont facilement observables, ce qui permet de contraster les données des colliers avec des observations directes d'interactions et de proximité entre individus. De surcroît, ce projet à long terme nous

donne accès à une base de données qui, entre autres, mesure le succès reproducteur à vie des individus et comporte un pedigree substantiel grâce à un effort de capture et de marquage qui se fait, dans la grande majorité des cas, lors de la première année de vie des individus.

Objectifs spécifiques du projet de recherche

Pour ma maîtrise, j'ai caractérisé la structure sociale des femelles de mouflon de Ram Mountain, au cours de 3 années, en utilisant trois types de comportements : composition des groupes sociaux, fréquence d'association à une distance $\leq 1,5$ mètre et interactions agonistiques. Les trois réseaux sociaux générés ont été comparés afin d'y relever les similitudes et les différences. La contribution technique de cette recherche permet de vérifier si l'utilisation d'une nouvelle approche pour enregistrer des interactions entre animaux, les colliers de proximité, concorde avec les méthodes plus traditionnelles pour étudier les systèmes sociaux. Le chapitre 2 s'intéresse ainsi à la comparaison de 3 réseaux sociaux construits avec trois types de données d'association afin de contraster les résultats qui en découlent. Cette partie est davantage appliquée et présente des recommandations pour les chercheurs qui désirent construire des réseaux sociaux. Le chapitre 3 met l'emphase sur les déterminants de la socialité pour les brebis, aux échelles dyadique et individuelle. Il vise à identifier les variables expliquant la variation dans la fréquence d'association à fine échelle des dyades, de même que les variables qui influencent la position d'un individu dans le réseau social.

CHAPITRE 2: TESTING THE GAMBIT OF THE GROUP: A COMPARISON OF THREE SOCIAL NETWORKS FOR A GREGARIOUS UNGULATE

Introduction de l'article

Cet article traite de l'utilisation de différents indices d'association pour construire des réseaux sociaux et illustre les conséquences potentielles de ce choix sur les résultats. Plusieurs types de données dyadiques peuvent être utilisés pour construire des réseaux sociaux. Classiquement, on utilise l'association de paires d'individus dans un même groupe ou leurs interactions, mais ce type de données requiert de l'observation directe. Or, ceci n'est pas toujours possible, demande un effort d'échantillonnage conséquent et est possiblement biaisé par l'effet de l'observation. L'utilisation de colliers de proximité enregistrant ces données automatiquement peut contourner ces problématiques. Dans la littérature scientifique on retrouve des réseaux sociaux construits avec plusieurs types de données. Toutefois, aucune étude n'a quantifié comment le choix de données influence les réseaux obtenus. Cette comparaison est essentielle afin de savoir si les réseaux sociaux construits avec des interactions sociales de différente nature sont comparables. Cet article est donc novateur parce qu'il compare, pour les mêmes individus et pour une même période de temps, trois réseaux sociaux issus de l'utilisation de trois variables d'association. Nous avons utilisé trois jeux de données pour les associations entre les brebis matures sexuellement au cours de l'été 2012 : cooccurrence dans un même groupe, fréquence d'association à une distance $\leq 1,5$ mètre et interactions agonistiques. Nous avons ensuite quantifié le niveau de similitude des réseaux sociaux construits à l'aide de mesures individuelles et de réseaux par une approche de ré-échantillonnage avec remplacement (bootstrap paramétrique). Nos résultats montrent qu'il y a peu de similitude entre les réseaux, impliquant qu'il faut choisir avec discernement le type de données que l'on utilise. De plus, cet article montre un exemple des failles de l'approche du *gambit of the group* qui assume une association sociale équivalente entre les membres d'un

groupe social. Cet article s'adresse principalement aux écologistes du comportement qui voudraient utiliser le cadre conceptuel des réseaux sociaux. Il fournit des recommandations pour l'utilisation du type de données en fonction de la question biologique d'intérêt et montre les conséquences de ce choix sur l'interprétation de la structure sociale modélisée.

Ma contribution à ce travail s'est faite sur plusieurs aspects : récolte des données sur le terrain lors des étés 2012 et 2013, analyse des données et rédaction. Eric Vander Wal a été d'une aide précieuse pour l'élaboration du projet, les analyses et la rédaction. J'ai été encadrée par les professeurs Marco Festa-Bianchet et Fanie Pelletier qui ont également contribué substantiellement à la rédaction du manuscrit et dirigent le projet de recherche à Ram Mountain. La possibilité d'utiliser trois jeux de données pour ce travail a été possible dans le contexte du suivi à long terme de la population.

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TESTING THE ‘GAMBIT OF THE GROUP’: A COMPARISON OF THREE SOCIAL
NETWORKS FOR A GREGARIOUS UNGULATE

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Abstract

Social network analysis has improved our understanding of social relationships. Although social networks can be constructed with different types of behavioural data based on dyadic association, little is known about how the type of behaviour used may affect the resulting networks. We investigated this subject by constructing three social networks with different types of behaviour among bighorn sheep (*Ovis canadensis*) ewes at Ram Mountain, Alberta. We used co-occurrence in groups, frequency of proximity at ≤ 1.5 m recorded by proximity loggers and direct agonistic interactions to construct social networks for all 25 mature ewes in the population in 2012. We assessed the nature of interactions recorded by proximity loggers by comparing them with interactions seen during 83 hours of focal observations. There were few similarities in terms of either node- or network-based metrics between the three networks, suggesting that each network reveals different aspects of social structure. Our results indicate that the type of behaviour used to construct social networks has a profound influence on social networks. We highlight the importance of matching the type of behaviour and the biological question of interest when working with social networks.

Keywords: social network, social behaviour, proximity logger, gambit of the group, bighorn sheep

Our understanding of animal ecology and behaviour has recently benefited from social network techniques (Pinter-Wollman et al. 2013; Wey et al. 2008). For example, social networks can quantify population structure (Gero et al. 2013), disease transmission (Drewe 2010; Hamede et al. 2009; Corner et al. 2003), information flow (Aplin et al. 2012), population connectivity (Fletcher et al. 2011), individual fitness (Stanton & Mann 2012; McDonald 2007), and inbreeding or extinction risk (Williams & Lusseau 2006). Social networks are constructed from pairwise connections that are often derived from different behavioural data. For example, social networks were constructed with spatial associations of bottlenose dolphins (*Tursiops* sp.; Lusseau 2007), with aggressive behaviours of yellow-bellied marmots (*Marmota flaviventris*; Lea et al. 2010) and with frequency of association within 30 cm of Tasmanian devils (*Sarcophilus harrisii*; Hamede et al. 2009). However, little is known about how the type of behaviour used may affect the characteristics of resulting networks. Therefore, it is unclear whether networks constructed with different behaviours are comparable.

A common, coarse approach to network analysis is based on assuming that membership in the same group implies association (the gambit of the group; Whitehead 2008). In the context of social networks, behavioural ecologists quantify the co-occurrence of individuals in a group as a proxy of dyadic association (Franks et al. 2010). Hence, all individuals in a group are assumed to be associating equally, regardless of the distance between dyads or their probability of interacting (Whitehead 2008). A finer-scale approach examines pairwise associations, which estimate pairwise affiliations (Godde et al. 2013) where animals have

preferential dyadic bonds. Behaviours used to quantify affiliations, however, range from spatial proximity to direct interactions, which may be agonistic (Lea et al. 2010) or cooperative (Silk et al. 2010; Drewe et al. 2009; Silk et al. 2009).

Living in groups has several benefits: it can reduce the risk of being detected by predators and the risk of being killed when detected (Hoare et al. 2004; Uetz et al. 2002). In social groups, animals also benefit from shared vigilance (Roberts 1996; Lima 1995) and can allocate more time to foraging (Johnson et al. 2002; Berger 1978). Pairwise associations within groups can also benefit an individual, for example through learning from more experienced individuals (Thornton & McAuliffe 2006).

Researchers increasingly use proximity loggers (review in Cross et al. 2012), to record spatial associations between individuals. Because of precise spatial resolution and continuous monitoring, proximity loggers quantify fine-scale associations better than radio-telemetry or GPS (Walrath et al. 2011). Data from proximity loggers enable social networks to be built from spatial associations at adjustable detection distances (1 – 5 m). This technology has provided new insights on sociality (Ryder et al. 2012), but the specific nature of behaviours exhibited when animals are in close proximity remains largely unknown because loggers have primarily been used in species that are difficult to observe [e.g., raccoons, *Procyon lotor*, (Robert et al. 2013); elk, *Cervus canadensis*, (Vander Wal et al. 2013); badgers, *Meles meles* (Goodman 2007)]. Consequently, little is known about the relationships between data

collected by proximity collars and those obtained by traditional behavioural observation (but see Walrath et al. 2011).

The relationship between data from proximity loggers and agonistic interactions is also unknown. For example, agonistic interactions mediate social hierarchies and can enhance fitness (Kutsukake & Clutton-Brock 2010) by improving access to forage (Kojola 1997) and increasing mating opportunities (Pelletier & Festa-Bianchet 2006). Interactions also bear costs via increased risk of disease transmission (Drewe 2010). Classically, social interactions are quantified by direct observations, which distinguish behaviours with different costs and benefits. For example, meerkats (*Suricata suricatta*) display different proportions of cooperative and aggressive behaviours depending on group, individual, and habitat characteristics (Madden et al. 2011; Madden et al. 2009) leading to variation in disease transmission (Drewe 2010). Direct observations, however, are limited to species where individuals can be approached, observed and identified.

This study had two goals: 1) assess the nature of interactions during proximity events and 2) contrast networks constructed with group membership, associations within 1.5 m recorded by proximity loggers, and agonistic interactions. To do so, we compared metrics derived from each network, using a population of adult bighorn ewes all fitted with proximity data logger collars. Because group composition and proximity loggers are based on spatial associations, we predict that their network metrics will be similar. Proximity loggers, however, record associations at a scale of approximately one sheep body length; some ewes in a group may

not associate at < 1.5 m. Consequently, group membership is likely to over-estimate affinity for some dyads compared to proximity loggers. In turn, metrics reflecting network interconnectedness, such as cohesion or transitivity, should be higher when based on group membership than when calculated with proximity or agonistic interactions networks, if sheep discriminate with whom they associate or interact. Bighorn ewes infrequently exhibit aggressive behaviour and there is no evidence that dominance has advantages (Favre et al. 2008); therefore, we predict that agonistic networks are likely different from spatial association networks.

Methods

Study area and bighorn sheep population

The Ram Mountain bighorn sheep population has been monitored since 1971 (Jorgenson et al. 1997) and all individuals included in this study were marked as lambs (see Festa-Bianchet 1988 for details on captures). In 2012, we fitted all 25 sexually mature ewes (3 years and older) with proximity collars (Sirtrack Tracking Solutions, Havelock North, New Zealand) that recorded associations (hereafter proximity events) within 1.5 m, hereafter proximity events. We arbitrary chose this distance because it corresponds roughly to a sheep body length. Proximity collars registered the identity of the encountered animal, the date, time and

duration (seconds) of each proximity event. Visual identifiers over the collar allowed each female to be easily identified (Figure 2.1).



Figure 2.11: Two bighorn ewes with visual identifiers attached to proximity collars.

We downloaded proximity data for all females when we recaptured sheep in late May – early June and again in mid-September. Sheep were confined to a small space when in or near the trap, likely leading to proximity events different from those among free-ranging sheep. Therefore, we excluded proximity data recorded when animals were seen at the trap (~ 11% of all recorded proximity events).

Behavioural data collection

We recorded the identity of all sheep in each group (referred to as group composition) as well as the date, time and location whenever possible ($N = 226$ groups in 2012). We defined a group as sheep not separated by more than 50 meters from each other. Bighorn sheep are highly gregarious and ewes were generally within 15 m of at least one other group member. For the social network analysis, we considered all collared ewes seen within a group in 2012 and excluded any lambs, yearlings and young males present in the group.

In 2013 we conducted 1-hour focal observation on each collared ewe every month for 21 ewes present during the field season (4 hours for all except one ewe which was observed for 3 hours) to quantify proximity events and identify the type of interaction as agonistic or occurring while foraging, ruminating/resting or other. We investigated the dominance hierarchy among ewes by direct observation of six types of agonistic interactions: frontal clash, front kick, displacement without contact, horn butt, horn rubbing and mounting (see Favre et al. 2008; Pelletier & Festa-Bianchet 2006 for more details). We observed 163 interactions involving 25.4% of dyads (118 dyads, Table S4 in supplementary material).

Data analysis

We used the composition of all groups in summer 2012 to calculate the proportion of time that a dyad was in the same group using the half-weight-index (*HWI*), a common technique to convert group observations into pairwise associations:

$$HWI_{ab} = \frac{x}{\frac{1}{2}(y_a + y_b)}$$

where x is the sum of events where individuals a and b were observed associating - y_a and y_b are the sums of events when a and b were observed, respectively (Whitehead 2008). *HWI* association strength varies from 0 for animals never observed together to 1 for animals that are always together. We did not use the *HWIG*, that adjusts for individual differences in gregariousness (Godde et al. 2013), for two reasons: the *HWI* is more commonly used in behavioural ecology than the *HWIG* and in our case the *HWI* and the *HWIG* were highly correlated ($r = 0.96$; $P < 0.001$), possibly because average group size for individuals only ranged from 9 to 13.

We corrected the dataset of proximity events by calculating the mean inaccuracy of each collar following Boyland et al. (2013; Figure 2.S1 in supplementary material). We also deleted proximity events lasting only one second as recommended by Prange et al. (2006), who showed that these events likely represent recording errors. We analysed proximity events occurring between June 1st and September 15th 2012, when we recorded group membership and observed agonistic interactions. We divided the absolute frequency of proximity events

by the highest observed frequency so that all frequencies were between 0 and 1 – a scale similar to the *HWI*.

Network metrics and statistical comparisons

We represented the 3 datasets as 3 matrices (Tables S2-S4 in supplementary material). We assessed the correlation between pairs of matrices and their significance using Mantel tests implemented in library *ade4* (Dray & Dufour 2007) for *R*. With these matrices, we then constructed networks using *R* (R Development Core Team 2011) with the package *iGraph* (Csardi & Nepusz 2006). For each network, we calculated four node-based metrics: eigenvector centrality, graph strength, closeness centrality and betweenness centrality; and three network-based metrics - diameter, cohesion and transitivity (Krause et al. 2009; Wey et al. 2008). We chose these biologically meaningful metrics because they are commonly employed in animal social network studies (Table 2.1).

Table 2.1: Definitions of node- and network- based metrics used to compare social networks of bighorn ewes, with example of their use in the literature.

Metric	Definition	Examples
Degree	Number of nodes that have a connection to an individual.	(Gómez & Perfectti 2012)
Eigenvector centrality	Measure of centrality based on all edges that an	(Stanton & Mann 2012)

	individual has relative to others (Maiya & Berger-Wolf 2010; Costenbader & Valente 2003).	
Graph strength	Sum of edges weights for all edges that an individual has.	(Wey & Blumstein 2012)
Closeness centrality	Measure of centrality based on shortest paths (weighted edges) distances linking a focal individual to all others in the network. Represents the extent to which social bonds are close.	(Perkins et al. 2009) (Gómez & Perfectti 2012) (Wey & Blumstein 2012)
Betweenness centrality	Measure of centrality based on shortest paths distances linking all dyads. Indicative of the importance of a single individual as a connecting node.	(McKenzie et al. 2007) (Lea et al. 2010) (Wey & Blumstein 2012)

Diameter	Longest path length in a network.	(Lusseau 2003)
Cohesion	How resistant the network is to removal of individuals.	(Lusseau 2003) (Williams & Lusseau 2006)
Graph density	Number of observed edges divided by the number of possible edges.	
Transitivity	Measures the probability that two nodes connected to a focal individuals are themselves also connected.	(Hamede et al. 2009)

To compare results obtained with different metrics we calculated Pearson's correlation coefficient for the four node-based metrics, for each pair of networks. For significant correlations, we calculated the adjusted coefficient of determination (adjusted R^2).

To create confidence intervals for the network measures, we used the parametric bootstrap with replacement with library *boot* (Canty & Ripley 2014), keeping the number of individuals constant at 25 ewes. When one ewe was randomly removed from the network, another ewe and her associations with others were represented twice to compensate. The number of random removals ranged between 1 and 25. We then recalculated the metrics for each 1000 randomly re-sampled networks to have the upper and lower limits of the possible values. We used this method for both node- and network-based metrics; for node-based metrics, we considered the mean metric for the 25 individuals.

Results

We collected 83 focal observations of marked ewes during summer 2013 while in groups with at least 5 other ewes. On average, ewes came within 1.5 m of another ewe 26 times/hour and each ewe was involved in ~300 proximity events daily. These events involved agonistic interactions in $6\% \pm 12\%$ ($X \pm SD$); movement in $30\% \pm 19\%$; foraging in $46\% \pm 26\%$; ruminating or resting in $10\% \pm 21\%$, and $8\% \pm 11\%$ of events involved other activities such as scratching or standing (Figure 2.2).

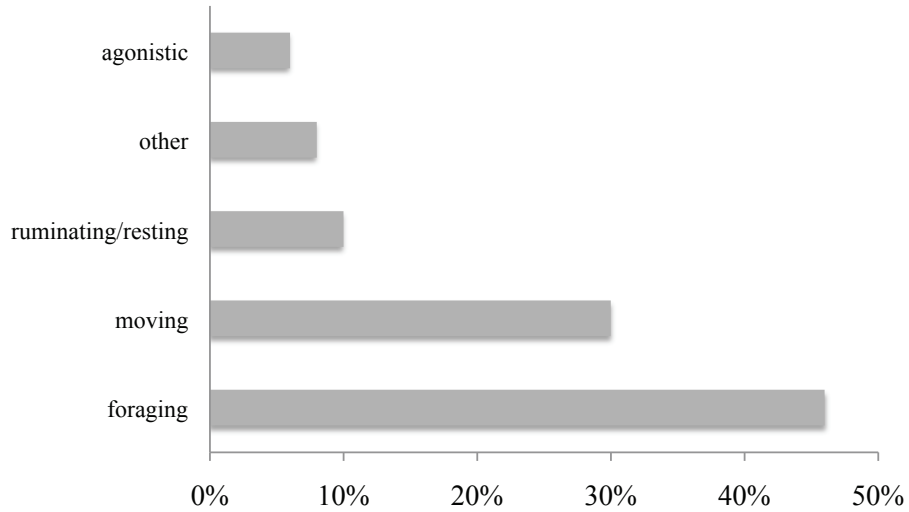


Figure 2.2: Behaviours of ewes seen within 1.5 m during 83 hours of focal observations in 2013 at Ram Mountain, Alberta. At this distance, proximity loggers recorded a proximity event in 99% of cases.

Mantel tests between matrices of the 3 networks (Figure 2.3), based on 10 000 replications, showed that the proximity and group composition matrices were correlated ($r = 0.27$, $P = 0.007$). The agonistic interactions matrix was not correlated to the group composition matrix ($r = -0.09$, $P = 0.69$) or the proximity events matrix ($r = -0.11$, $P = 0.85$).

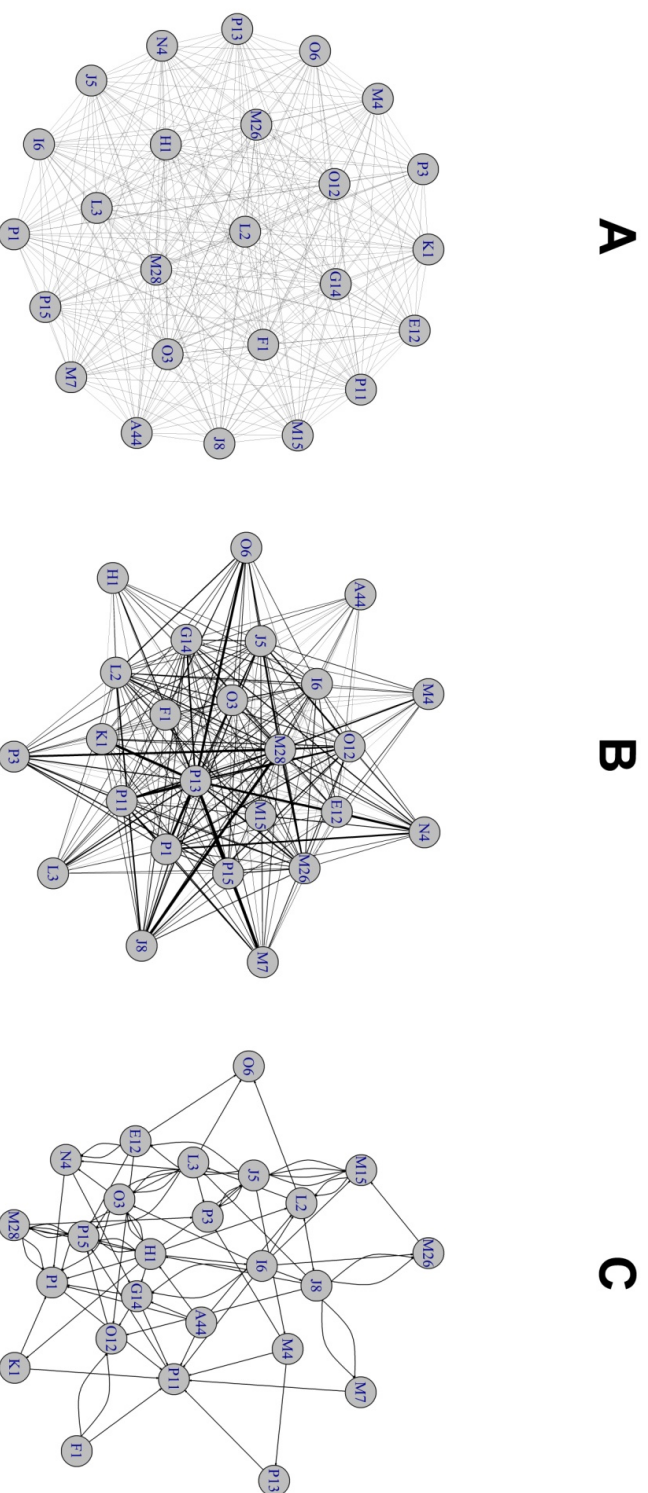


Figure 2.3: Social networks of 25 adult bighorn ewes in summer 2012 constructed from 3 types of data. A: group composition; B: proximity loggers; C: agonistic interactions. Individual ewes are represented by alpha-numeric identification codes. Thickness of lines is proportional to strength of association.

Graph density varied between the three networks (Table 2.2). Only graph strength was correlated between the group composition and the agonistic networks (adjusted $R^2 = 0.17$). All other node-based metrics were not correlated between the three networks (Table 2.3).

Table 2.2: Attributes of three social networks for 25 bighorn ewes on Ram Mountain, Alberta (2012).

Characteristic	Group composition network	Proximity Network	Agonistic network
% of dyads not interacting	None	9.14	74.62
Mean degree (\pm SD)	24 (\pm 0)	21.12 (\pm 3.92)	7.28 (\pm 3.40)
Type of network	Undirected	Undirected	Directed
Graph density	1	0.88	0.15

Table 2.3: Pearson's correlations of node-based metrics between pairs of networks for 25 bighorn ewes on Ram Mountain, Alberta (2012). Significant correlation is shown in bold.

Metric	Group composition and proximity networks	Group composition and agonistic networks	Proximity and agonistic networks
Eigenvector centrality	0.093 ($P = 0.660$)	0.116 ($P = 0.580$)	0.095 ($P = 0.653$)
Graph strength	0.131 ($P = 0.532$)	0.449 ($P = 0.024$)	-0.120 ($P = 0.567$)
Closeness centrality	0.268 ($P = 0.195$)	-0.284 ($P = 0.169$)	0.122 ($P = 0.560$)
Betweenness centrality	0.039 ($P = 0.854$)	-0.284 ($P = 0.169$)	0.096 ($P = 0.648$)

Eigenvector centrality and cohesion were similar between the group composition and the proximity events network (Table 2.4 and Table 2.S1 for details). Betweenness centralities of the group composition and agonistic networks were also correlated. Eigenvector centrality and graph strength were similar for the proximity events and agonistic interactions networks. Closeness centrality, diameter and transitivity differed among the 3 networks.

Table 2.4: Summary of pairwise comparison for three social networks for 25 bighorn ewes on Ram Mountain, Alberta (2012). Crosses indicates overlap in CI.

Node-based Metric	Group composition and proximity networks	Group composition and agonistic networks	Proximity and agonistic networks
Mean eigenvector centrality	X		X
Mean graph strength			X
Mean closeness centrality			
Mean betweenness centrality		X	
Network-based Metric			
Diameter			
Cohesion	X		
Transitivity			

Discussion

We sought to quantify the similarity among social networks derived from different types of behavioural data, contrasting node- and network-based metrics. Although the three networks represent the social structure of the same group of animals over the same period of time, metrics for individual centrality and connectedness varied among them. Therefore, the type of behaviour has a profound influence on social network metrics. No pair of networks had more than 2 similar metrics out of 10 that were compared, and no one metric was similar across all networks. This suggests that the three types of behaviours we used to construct the networks reveal different aspects of a species' social structure.

Node-based metrics should be similar if individuals have the same relative positions in different networks. The probability that a node-based metrics will be similar across network is greater for metrics whose calculation requires a high proportion of the information contained in the network (Costenbader & Valente 2003). Accordingly, our analyses suggest that metrics including both direct and indirect links such as eigenvector centrality are more similar across networks than those involving only direct links such as graph strength.

Network-based metrics should be similar between networks if the behaviour used to build them reflects the same global social structure. The group composition network is based on the gambit of the group and does not discriminate between group-level and dyadic associations. This leads to an over-estimation of network connectedness (cohesion and transitivity) and, by extension, of

dyadic association. In this study, 100% of dyads associated in the group composition network compared to 91% associating at 1.5 m in the proximity events network.

Using co-occurrence in groups as a proxy of association can over-estimate the strength of some social bonds. Although all dyads were seen in the same group, the 9% never within 1.5 m could interact. Although the group composition and proximity matrices were correlated, that correlation was rather weak at 0.27. The lack of correlation between the group composition and the agonistic networks indicates that dyads often seen in the same group will not often interact agonistically. This result underlines two potential problems when using group composition as a proxy of associations. First, the assumption that every member of a group has an equal probability of interaction (gambit of the group; Whitehead 2008; Whitehead et al. 1999) will likely be violated. Second, the assumption of transitivity in groups (Whitehead 2008) may also be violated: for a group with members A, B and C, if A and B interact and B and C interact, we should not implicitly consider that A and C have also a chance to interact. Although it is not always possible to test these assumptions (de Vries 1998; de Vries 1995), our results reinforce that group membership is a rough approximation of social associations. Because of the benefits of gregariousness, an individual may join groups even if they contain other individuals that it does not wish to associate with (Godde et al. 2013). It could then avoid those individuals at a finer spatial scale, even if it remains within the same group. We suggest that this inconsistency is more likely to be important in gregarious animals that form large groups.

Proximity loggers quantify associations between dyads better than group composition. In this study, loggers discriminated spatial association at a finer scale than that estimated at a coarser

scale by the group composition network. While they offer many advantages, proximity loggers also have an important drawback: proximity events may involve different types of behaviours that cannot be differentiated *post facto*. Our direct behavioral observations revealed that bighorn ewes displayed affiliative behaviour or tolerance when most proximity events occurred. Also, it is important to consider that loggers have an intrinsic error and imprecision that should be corrected before analysis (Boyland et al. 2013; Drewe et al. 2012; Cross et al. 2012; Prange et al. 2006), as we did in this study. The network constructed with this dataset had the greatest number (4) of similarities with the two other networks. For highly gregarious animals such as sheep, there is less variability in the strength of associations measured by group membership than in associations measured by proximity among members of each dyad. The proximity events network is better suited to identify preferential associations and its values are likely to reflect affinity among, for example, different categories of individuals.

The observation of direct interactions between individuals provides useful information about social relationships and level of associations, but it also has several limitations: not all dyads interact, interactions can be subtle or not easy to categorize, especially if they are rare. Consequently, it is very difficult to observe interactions among all possible dyads, and animals can be disturbed by the presence of an observer. For bighorn ewes, aggressive behaviours reflect the dominance hierarchy (Favre et al. 2008), but agonistic interactions are rare, resulting in a poor resolution of the agonistic interaction network. Hence, using this network limits the extent to which we can draw conclusions. Furthermore, although agonistic interactions are very useful to establish dominance hierarchies, they may not be particularly relevant to describe the social structure. Also, dyads that frequently interact agonistically may not associate spatially to avoid

injuries, as suggested for bighorn ewes by the lack of correlation between the agonistic interaction network and the other two networks. In this case, it would be very hard to disentangle the effects of avoidance and preferential association. We did not face these issues with the other networks.

Despite the popularity and promise of social networks in behavioural ecology, our work is the first to compare networks constructed with three types of behaviour for a social group where all individuals are monitored. Our results, contrasting data recorded by proximity loggers with behavioural data obtained by direct observation, suggest that the type of behaviour will affect the social network obtained. Thus, published networks built using different types of behavioural data likely are not comparable across contexts. We recommend that it should be explicitly stated in papers what behavioural data was used and what are the limitations. The common assumption that the group composition is a good proxy of dyadic associations appears inaccurate because co-occurrence in groups is very weakly associated with preferential association. Therefore, group composition data should only be used to examine the benefits and costs of gregariousness. More fine-level association data are required to investigate individual social preferences. It is critical to match the type of behavioural data used to construct networks with the biological question of interest.

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Supplementary material

Table 2.S1: Network metrics obtained with different types of behaviour, with bootstrap confidence intervals, for 25 bighorn ewes on Ram Mountain, Alberta (2012). Observed values with lower limit and upper limit (in brackets) of the 1 000 bootstrapped networks for 100% CI.

Node-based Metric	Group composition network	Proximity Network	Agonistic network
Mean eigenvector centrality	0.85 (0.75 – 0.93)	0.46 (0.34 – 0.80)	0.41 (0.13 - 0.66)
Mean graph strength	11.20 (9.56 – 12.09)	4.59 (2.11 – 7.39)	7.28 (2.88 – 12.16)
Mean closeness centrality	0.09 (0.08– 0.10)	0.38 (0.14 – 0.65)	0.005 (0.002 - 0.009)
Mean betweenness centrality	0.84 (0.32 – 3.28)	11.12 (3.96 – 13.84)	12.76 (0 – 23.76)
Network-based Metric			
Diameter	0.68 (0.64– 0.9)	0.32 (0.15 – 0.55)	-
Cohesion	24 (18 - 24)	16 (8 - 22)	0
Transitivity	1 (1 - 1)	0.90 (0.50 – 0.95)	0.27 (0 - 0.46)

Proximity loggers validation

Proximity collars are based on UHF technology and exhibit inter-collar variation (Drewe et al. 2012, Boyland et al 2013). To minimise this error in our analyses we first tested the data against visual observations, then adjusted observations to account for inter-collar variability.

(1) Comparison of visually verified proximity events and proximity collar events

We recorded field observations of ewes standing next to each other whenever individuals were approximately < 1.5 m. Subsequently, we tested whether these events were recorded by one or both proximity collars. In 83% of cases, both collars recorded the interaction; while in 16% of cases only one collar had a record. In total, 99% of the proximity events observed during visual surveys were captured by the proximity collars.

(2) Post-hoc adjustment of inter-collar variation

Proximity loggers have different detection distances and this inaccuracy is consistent over time (Boyland et al. 2013). To minimize the bias introduced by variation in collar accuracy, we corrected the proximity collar event dataset following Boyland et al. (2013). We tested the reciprocity of the proximity events matrix before and after the correction with a Mantel test. Before correction, the matrix reciprocity was 0.27. After correction, reciprocity increased to 0.89. The variation in accuracy of each proximity collars varied between -17% and 17% (Figure S1).

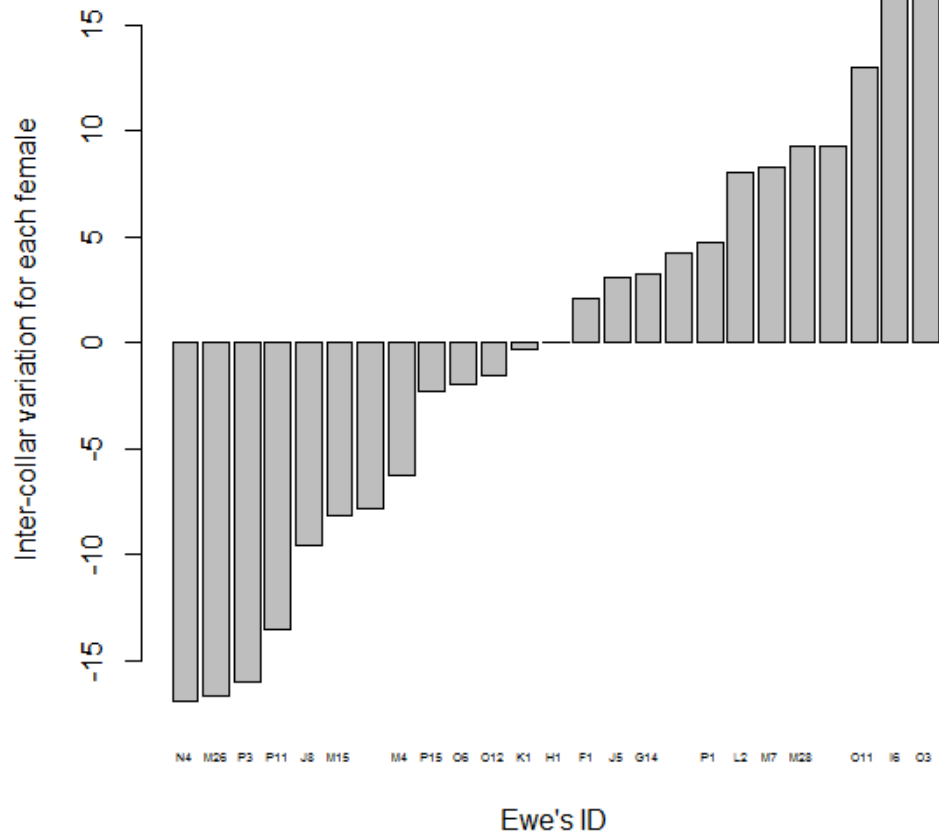


Figure 2.S1: Mean collar inaccuracy for each collared female in percentage. We calculated the variation values as the mean difference of recorded proximity events for each dyads involving a female. For more details, see Boyland et al. (2013).

Table 2.S2: Group composition network matrix for (N = 25) bighorn ewes on Ram Mountain Alberta (2012).

ID	H1	P13	E12	P11	P1	K1	M7	L3	J5	L2	O3	N4	O12	P15	J8	F1	M15	M26	O6	M28	A44	G14	M4	I6	P3
H1		0.406	0.702	0.486	0.535	0.295	0.441	0.642	0.486	0.769	0.633	0.438	0.615	0.492	0.710	0.333	0.426	0.636	0.510	0.500	0.609	0.492	0.606	0.590	0.419
P13			0.394	0.651	0.575	0.714	0.500	0.387	0.456	0.405	0.493	0.411	0.432	0.486	0.423	0.413	0.400	0.400	0.533	0.411	0.400	0.432	0.453	0.314	0.479
E12				0.507	0.471	0.310	0.429	0.520	0.388	0.742	0.596	0.525	0.484	0.414	0.542	0.196	0.345	0.476	0.458	0.393	0.558	0.355	0.571	0.552	0.305
P11					0.612	0.640	0.658	0.418	0.524	0.633	0.432	0.538	0.506	0.507	0.447	0.529	0.427	0.550	0.585	0.462	0.400	0.405	0.650	0.533	0.579
P1						0.417	0.486	0.375	0.519	0.553	0.479	0.640	0.447	0.556	0.356	0.338	0.611	0.416	0.452	0.373	0.281	0.579	0.442	0.472	0.575
K1							0.533	0.296	0.423	0.364	0.361	0.369	0.364	0.419	0.381	0.509	0.323	0.328	0.577	0.400	0.383	0.273	0.448	0.258	0.508
M7								0.423	0.435	0.500	0.339	0.508	0.250	0.300	0.393	0.453	0.333	0.338	0.480	0.254	0.400	0.313	0.400	0.433	0.426
L3									0.540	0.552	0.604	0.421	0.552	0.333	0.618	0.298	0.333	0.576	0.455	0.421	0.462	0.379	0.475	0.481	0.255
J5										0.507	0.429	0.514	0.560	0.507	0.500	0.423	0.658	0.393	0.393	0.514	0.286	0.480	0.526	0.451	0.472
L2											0.677	0.551	0.543	0.424	0.627	0.373	0.424	0.620	0.607	0.493	0.627	0.486	0.676	0.697	0.418
O3												0.469	0.615	0.459	0.548	0.296	0.393	0.545	0.549	0.469	0.565	0.369	0.576	0.525	0.323
N4													0.406	0.554	0.424	0.310	0.585	0.400	0.436	0.324	0.360	0.580	0.600	0.492	0.394
O12														0.545	0.567	0.373	0.364	0.676	0.429	0.464	0.392	0.371	0.592	0.424	0.478
P15															0.508	0.400	0.548	0.507	0.346	0.400	0.255	0.333	0.597	0.484	0.444
J8																0.429	0.317	0.647	0.453	0.636	0.458	0.388	0.676	0.508	0.375
F1																	0.400	0.533	0.489	0.483	0.400	0.373	0.367	0.436	0.500
M15																		0.388	0.385	0.338	0.340	0.545	0.418	0.516	0.413
M26																			0.456	0.543	0.462	0.479	0.639	0.537	0.500
O6																				0.364	0.703	0.357	0.491	0.423	0.453
M28																					0.320	0.377	0.571	0.400	0.485
A44																						0.392	0.462	0.426	0.333
G14																							0.451	0.455	0.358
M4																								0.567	0.412
I6																									0.286

Table 2.S3: Proximity events network matrix for (N = 23) bighorn ewes on Ram Mountain Alberta (2012).

ID	H1	P13	E12	P11	P1	K1	M7	L3	J5	L2	O3	N4	O12	P15	J8	F1	M15	M26	O6	M28	A44	G14	M4	I6	P3
H1		0.395	0.090	0.074	0.115	0.038	0.000	0.000	0.157	0.186	0.046	0.000	0.105	0.049	0.000	0.118	0.026	0.150	0.000	0.140	0.000	0.180	0.000	0.252	0.000
P13			0.360	0.702	0.810	0.849	1.000	0.447	0.355	0.251	0.210	0.738	0.589	0.627	0.405	0.291	0.327	0.492	0.780	0.274	0.184	0.553	0.227	0.274	0.351
E12				0.058	0.087	0.045	0.103	0.145	0.183	0.231	0.046	0.268	0.055	0.034	0.177	0.099	0.065	0.117	0.095	0.123	0.151	0.336	0.222	0.217	0.027
P11					0.392	0.167	0.364	0.175	0.167	0.152	0.180	0.220	0.312	0.416	0.236	0.082	0.042	0.353	0.305	0.449	0.043	0.180	0.123	0.148	0.414
P1						0.134	0.273	0.164	0.269	0.171	0.114	0.587	0.364	0.308	0.211	0.082	0.373	0.216	0.261	0.355	0.069	0.237	0.097	0.188	0.315
K1							0.258	0.075	0.227	0.154	0.055	0.113	0.339	0.097	0.214	0.065	0.036	0.153	0.202	0.205	0.040	0.151	0.079	0.139	0.116
M7								0.000	0.234	0.211	0.111	0.000	0.260	0.140	0.000	0.136	0.049	0.154	0.000	0.244	0.000	0.229	0.000	0.165	0.000
L3									0.174	0.208	0.169	0.000	0.105	0.098	0.000	0.110	0.016	0.210	0.000	0.253	0.000	0.179	0.000	0.232	0.000
J5										0.199	0.134	0.221	0.468	0.155	0.402	0.162	0.117	0.288	0.131	0.357	0.100	0.329	0.224	0.283	0.289
L2											0.283	0.261	0.287	0.125	0.491	0.225	0.125	0.313	0.404	0.431	0.180	0.222	0.181	0.335	0.140
O3												0.105	0.093	0.093	0.206	0.083	0.043	0.221	0.211	0.425	0.042	0.106	0.101	0.112	0.193
N4													0.168	0.200	0.000	0.065	0.292	0.177	0.000	0.303	0.000	0.378	0.000	0.181	0.000
O12														0.200	0.397	0.059	0.067	0.238	0.194	0.423	0.037	0.145	0.274	0.201	0.331
P15															0.136	0.063	0.046	0.309	0.233	0.241	0.027	0.138	0.075	0.085	0.404
J8																0.171	0.060	0.287	0.000	0.943	0.000	0.294	0.000	0.277	0.000
F1																	0.029	0.132	0.123	0.200	0.090	0.262	0.043	0.292	0.087
M15																		0.055	0.067	0.136	0.016	0.121	0.014	0.077	0.062
M26																			0.218	0.518	0.065	0.241	0.158	0.286	0.193
O6																				0.292	0.000	0.199	0.000	0.177	0.000
M28																					0.132	0.220	0.502	0.232	0.656
A44																						0.167	0.000	0.155	0.000
G14																							0.153	0.272	0.177
M4																								0.168	0.000
I6																									0.114

Table 2.S4: Agonistic interactions network matrix for (N = 23) bighorn ewes on Ram Mountain Alberta (2012).

ID	H1	P13	E12	P11	P1	K1	M7	L3	J5	L2	O3	N4	O12	P15	J8	F1	M15	M26	O6	M28	A44	G14	M4	I6	P3
H1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
P13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
E12	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P11	0	0	0	0	1	1	2	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	1	0
P1	1	0	0	0	0	1	0	0	1	0	2	1	0	0	0	0	0	0	0	0	2	1	1	0	0
K1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L3	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
J5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	1	0	0	1
O3	3	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
N4	0	0	2	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
O12	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0
P15	3	1	1	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	3	0	0	0	0	0
J8	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
F1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M15	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
M26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
O6	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
M28	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A44	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
G14	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
M4	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
I6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P3	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0

CHAPITRE 3: INDIVIDUAL AND DYADIC DETERMINANTS OF SOCIALITY AMONG BIGHORN EWES (OVIS CANADENSIS)

Introduction de l'article

Une des conclusions du chapitre 2 était que le réseau social construit avec les fréquences d'évènements de proximité était plus approprié pour identifier les déterminants de la socialité parce qu'il représente mieux les préférences des individus à fine échelle. Par extension, cet article traite des déterminants de la socialité des brebis du mouflon d'Amérique aux échelles de la dyade et de l'individu en utilisant les fréquences d'associations pour les étés de 2011-2013 avec les colliers de proximité. L'objectif était d'identifier quelles variables biologiques peuvent expliquer la variabilité d'association entre les dyades de brebis ainsi que le degré de socialité individuel des brebis. Pour ce faire, nous avons combiné deux analyses distinctes : une pour l'échelle dyadique avec des régressions multiples avec des matrices et une autre pour l'échelle individuelle où la socialité des brebis représentée par leur position dans le réseau social est investiguée avec des modèles mixtes. Au niveau dyadique, les brebis montrent une légère préférence à s'associer avec celles d'un statut reproducteur similaire au leur. Ceci pourrait être le reflet d'une stratégie d'association afin de minimiser les risques de prédation. Par contre, le degré d'apparement, la similarité en âge et la similarité en rang de dominance ne semblent pas affecter ces associations. Cela suggère qu'il n'y a pas d'effet de la sélection de parentèle ou du degré de familiarité sur la force des associations entre paires de brebis. À l'échelle individuelle, les brebis plus jeunes ont des mesures de centralité plus élevées que les plus âgées.

J'ai développé les objectifs de cette recherche, participé à la récolte des données sur le terrain, effectué les analyses et rédigé une première version du manuscrit. Marco Festa-Bianchet et Fanie Pelletier ont supervisé le projet et révisé le manuscrit.

Nous projetons de soumettre l'article à la revue *Behavioral Ecology and Sociobiology* à l'automne 2014.

DETERMINANTS OF DYADIC ASSOCIATIONS AND INDIVIDUAL SOCIALITY IN
BIGHORN EWES (*OVIS CANADENSIS*)

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Abstract

Social networks are a powerful tool to explore the mechanisms underlying social structure. We investigated the determinants of dyadic associations and variability in individual-based measures of sociality for adult bighorn ewes (*Ovis canadensis*) in the fully marked population at Ram Mountain, Canada. From 2011 to 2013, nearly all adult ewes were equipped with proximity logger collars, recording events when ewes were within 1.5 m of one another. Using multiple regressions with matrices, we found a weak positive effect of similarity of reproductive status on association strength for dyads. Similarity of age, dominance rank and relatedness, however did not affect the frequency of proximity among dyads. Individual-based centrality, derived from social networks, indicated that association patterns were not random; however, reproductive status and dominance had little effect on centrality derived from proximity data. Age, however, had a positive influence on centrality, where younger ewes appeared more socially connected. Variables affecting sociality for dyads are not necessarily the same variables that affect individual sociality.

Introduction

Social network analyses have improved our understanding of how social context can affect fitness. For example, in baboons (*Papio hamadryas*; Silk et al. 2010; Silk et al. 2006; Silk et al. 2003) strong and long-lasting social bonds between females increase longevity and reproductive success. Studies on sperm whales (*Physeter macrocephalus*; Gero et al., 2013) and on meerkats (*Suricata suricata*; Clutton-Brock et al., 2001, 2002; Russell et al., 2003) showed the benefits of cooperative care for juvenile survival. Although many social networks studies have focused on the quantification of the social structure, the mechanisms underlying observed patterns of association remain poorly known (Sih et al., 2009). Few studies have examined the fitness benefits of preferential associations, or what evolutionary or ecological factors shape the structure of social networks. Our understanding of how social structure may have evolved through natural selection, including kin selection, can benefit from the use of social network analyses and the emerging analytical tools that the framework provides.

Kin selection is often invoked as an evolutionary explanation of cooperation (Grafen, 1984; Hamilton, 1964), because cooperation among kin leads to direct benefits for the receiver and indirect benefits for the provider. Despite increasing reports of cooperation that cannot be explained solely through kin selection (Clutton-Brock, 2002; Foster et al., 2006; Griffin & West, 2002; Nowak et al., 2010; Strassmann et al., 2011), kin selection appears to affect the behaviour of many primates (McDonald, 2009; Silk, 2002), eusocial insects (Hughes et al., 2008), wild turkeys (*Meleagris gallopavo*; Krakauer, 2005) and carrion crows (*Corvus corone*; Baglione et al., 2003). Little is known about the role of kinship in the social behaviour of large herbivores. Some species appear to associate with kin, such as red deer (*Cervus elaphus*; Albon et al., 1992), while others do not (bighorn sheep – *Ovis canadensis*; Festa-Bianchet, 1991).

A choice of preferred associates can also be beneficial in species without cooperation. Young male bison (*Bison bison*) also prefer to associate with males of their own age class, while yearlings had more aggressive interactions with other male than with female yearlings, with whom they had more olfactory interactions (Rothstein & Griswold, 1991). These early-life social preferences appear to increase reproductive success of adult males via learning of mating tactics (Rothstein & Griswold, 1991). Associating with more familiar individuals decrease the time and energy allocated to social vigilance (Griffiths et al., 2004). Animals may select preferential partners to reduce social competition (Clutton-Brock & Huchard, 2013). For example, the social structure of African elephants (*Loxodonta africana*) is less cohesive during the dry season when food resources are scarce and competition more likely (Wittemyer et al., 2005). Similarly, avoidance of aggressive individuals can decrease the risk of injuries and the energetic cost of agonistic interactions (Ehardt & Bernstein, 1987).

Within a population, there can be substantial variability in dyadic association strength (Wey et al., 2008). The causes of this variation have rarely been explored through social network analysis (Lusseau & Newman, 2004). The aim of our study was to identify what biological variables affect the frequency of association for bighorn ewes monitored since their birth. To do so, we used the strength of association among bighorn ewes at Ram Mountain measured by proximity loggers. We have previously shown that there is much variability in strength of dyadic associations in this population: dyads had between 0 and over 2000 proximity events during one summer (Gagné-Delorme et al., in review). Thus, we sought to identify characteristics explaining variability in dyadic and individual sociality.

A common explanation for preferential associations is kin selection (Foster et al., 2006). Therefore, we wanted to test if related ewes were more likely to associate. We also expected that similarity in age or dominance rank would increase the frequency of association.

Individuals of similar age might be more familiar because they interacted from early development, and may continue to associate more often than with individuals with whom they are less familiar (Sih et al., 2009). We predicted stronger associations among individuals of similar ranks for two reasons. First, aggressive interactions between a high-ranked and a low-ranked individual may involve a risk of injury for the subordinate (Festa-Bianchet, 1991). Therefore, it might be more beneficial for a low-ranked individual to avoid risk by associating with other subordinates. Second, animals of similar ranks may benefit from winning over the other by increasing in rank in the linear dominance hierarchy (Archie et al., 2006; Smith et al., 2007).

Alternately, association rates may relate to reproductive status. Lactating ewes face a trade-off between being vigilant and acquiring food to support lactation (Rieucan & Giraldeau, 2011; Ruckstuhl et al., 2003). Ewes with lambs may benefit from forming groups of lactating females to share vigilance and increase the dilution effect among lambs in case of a predator attack. Hence we hypothesize that similarity in reproductive status will increase the frequency of association. Several studies have suggested that animals that share common characteristics might benefit from associating because they face the same trade-offs, leading to homophily, or similarity among group members (Lusseau & Newman, 2004; McPherson et al., 2001).

Several variables may influence the level of individual sociality. Some individuals are more prone to establish and maintain social bonds than others (Sih et al., 2009; Wey et al., 2008). Quantifying sociality and its potential fitness consequences can lead to new insights on its evolution (Wey et al., 2008). A recent study on our study population (Vander Wal et al., 2014) revealed fitness benefits of sociality for ewes. Here, we sought to identify what variables may explain individual differences in sociality among ewes.

Methods

Study area and bighorn sheep population

Ram Mountain is located approximately 30 km east of the main Rocky Mountain chain in Alberta, Canada. The local population of bighorn sheep has been monitored since 1971 (Jorgenson et al., 1997). Each year, from late May to late September, sheep are captured in a corral trap baited with salt (see Festa-Bianchet 1988 for details). All individuals considered in this study were first captured as lambs, therefore their age was known. A tissue sample is collected at first capture to assess paternity using molecular analyses and reconstruct the pedigree (Coltman et al., 2005). We matched mother-offspring pairs by observation of nursing behaviour. Here we use data collected from 2011 to 2013 on adult ewes. We knew both parents for 26 of 29 ewes in our study population. The remaining 3 ewes were introduced from elsewhere. Ewes were captured on average 4 times each year in 2011-2013. Female reproductive status in late May was evaluated by udder examination, allowing us to identify ewes that gave birth but lost their lamb soon afterwards.

We established the dominance hierarchy among ewes by direct observation of agonistic interactions (Favre et al. 2008; Pelletier & Festa-Bianchet 2006). To establish a linear hierarchy, we used the procedure described in De Vries (1998) implemented in *MatMan 1.1* software (De Vries et al., 1993). This procedure minimizes inconsistent interactions and their strength (De Vries, 1998). We then constructed a matrix of relative rank differences for each dyad (Table 3.1). We standardized dominance rank so that relative rank was not affected by yearly sample size.

Table 3.1: Linearity and consistency of the dominance hierarchy of bighorn ewes at Ram Mountain, 2011-2013.

Year	Females (N)	Interactions observed	% dyads observed	h'^*	P^\dagger	DCI‡
2011	18	83	12.41	0.10	0.330	0.96
2012	25	163	25.38	0.17	0.030	0.98
2013	18	318	53.66	0.32	<0.001	0.97

* Linearity index

† P -value for the linearity test

‡ Directional consistency index

Proximity loggers

We fitted adult females with proximity logger collars (Sirtrack Tracking Solutions, Havelock North, New Zealand). In 2011, 18 ewes had a proximity collar (77% of all ewes aged 2 years and older) while in 2012 (N = 25) and 2013 (N = 18), all adult ewes had loggers. Collars recorded proximity events at a distance of 1.5 m or less, or approximately one sheep body length. Proximity collars registered the identity of the encountered animal, the date, time and duration (seconds) of each event. As suggested by Prange et al. (2006), we excluded events lasting only 1 second. We also excluded from analyses events recorded when sheep were near or in the trap. We corrected the dataset for intrinsic errors of collars as proposed by Boyland et al. (2013; Figure 3. S1). For each dyad, we calculated the number of proximity events between June 1st and September 15th when all proximity loggers were able to record proximity events (Figure 3.1) and used it as a proxy of strength of association.

Statistical analyses

To test the effects of variables of interest on the frequency of proximity events, we used multiple regressions with matrices (MRM) implemented in the *R* (R Core Team, 2011) package *ecodist* (Goslee & Urban, 2007). The MRM tests the significance of explanatory variables by permutation similarly to a Mantel test, but it allows for more than one explanatory distance matrix (Legendre et al., 1994; Lichstein, 2007). For this study, the matrix of frequency of associations per year is the response variable, while explicative variables are represented as distance matrices measuring the extent of similarity between pairs of dyads (Legendre et al., 1994; Lichstein, 2007). We coded each of our variables of interest into similarity matrices. For the effect of age or dominance rank, we calculated the difference in age or rank for each dyad. We tested the effect of similarity of age and dominance rank separately because these two variables are highly correlated for bighorn ewes (Favre et al., 2008). We used the pair-wise coefficient of relatedness based on the pedigree of the population to test the effect of kinship calculated with R package *nadiv* (Wolak, 2012). For example, a mother-daughter pair would have a coefficient of relatedness of 0.5. We coded similarity of reproductive status as 1 and dissimilarity as 0. We considered ewes to be nursing a lamb during the field season when they were lactating for at least 2 weeks. Ewes that lost their lamb at birth or within the first 2 weeks after birth were considering to be not lactating. For 45 lactating ewe-years in 2011-2013, 84% (38) of lambs survived at least 3 months.

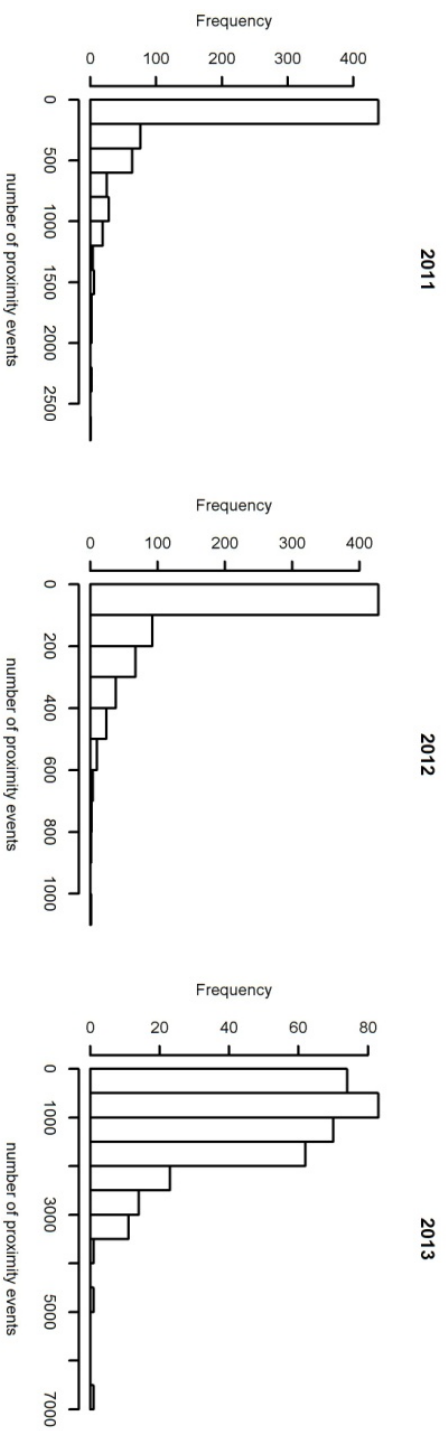


Figure 3.1.: Proximity events for dyads of bighorn ewes in 2011-2013. There were 18, 25 and 18 collared females in 2011, 2012 and 2013 respectively.

We also analysed the three years pooled. The total number of proximity events for all possible dyads over years (406 dyads) was the response matrix. We tested if similarity in age, relatedness and the number of similarities of reproductive status had an effect using MRM. We constructed an additional matrix coding for the number of years when a dyad could have proximity events as a control variable. All *P*-values for MRM analyses were calculated based on 10 000 permutations.

To test if matrices representing the social networks were correlated across years (2011-2013), we also used Mantel tests implemented in *ecodist* for dyads that were present and wearing proximity loggers for pairs of consecutive years (105 dyads monitored in 2011 and 2012; 120 dyads monitored in 2012 and 2013). We used partial Mantel test for the dyads that were present for the 3 years (36 dyads monitored over the three years). The *P*-values for the Mantel and partial Mantel tests were obtained based on 10 000 permutations.

Social networks

The number of proximity events was extremely variable across years (Figure 3.1). Thus, for analyses of individual sociality we used social networks metrics (Wey et al., 2008) and standardized the frequency of proximity events by dividing each frequency by the yearly maximum frequency. The social network framework represents social structure graphically and analyzes social structure at the individual, dyadic and network scale (Croft et al., 2011; Wey et al., 2008). We constructed a social network for each year with the frequency of association to represent the strength of social affinity among dyads with the package *igraph* (Csardi & Nepusz, 2006). These networks are undirected and weighted (Figure 3.2). From

these, we calculated the eigenvector centrality of all ewes in the network for each year, which represents their individual level of sociality. The eigenvector centrality as a proxy of individual sociality also presents several advantages: it is standardized between 0 and 1, includes both direct and indirect social bonds, is less affected by sampling bias (Costenbader & Valente, 2003) and has a near-normal distribution.

Comparison with random social networks

To test whether the observed networks differed from those formed by animals that associated at random, we created random social networks (Lusseau, 2003). To do so, we did 10 000 permutations of networks' edges (Croft et al., 2011) using package *vegan* (Oksanen et al., 2013) with the swap method. Thus, the frequency of association per dyad was swapped randomly for dyads while keeping the observed frequencies. We then calculated the mean eigenvector centrality of all individuals for each random network and compared these distributions to the value of the observed network. We considered that observed patterns of associations could not be obtained randomly when observed values were within the 5% of extreme values of the random distribution.

Determinants of individual eigenvector centrality

From the observed yearly social networks, we calculated eigenvector centrality for each ewe. We tested whether age, dominance rank and reproductive status explained why some ewes are more social as measured by their individual eigenvector centrality, using linear mixed effect models while controlling for the effect of year. The identity of the ewe was included as

random variable to control for repeated measures and we used a backward selection model. Again, because age and social rank are highly correlated (Favre et al., 2008), we tested these two variables separately.

Results

Determinants of proximity events frequency for dyads

Ewes of similar reproductive status associated more together in 2011 and 2012 (Table 3.2). Reproductive status was the only significant variable among those tested and it explained only about 1 - 2% of variability. Similarity in age, in dominance rank or relatedness did not affect associations among ewes in any year or when the three years were combined. Only the number of years that a dyad could have had proximity events was significant ($F = 11.226$; $P = 0.05$; $R^2 = 0.027$).

Stability of association strength for dyads across years

Frequency of association for dyads was inconsistently correlated across time. The correlation for the social networks of 2011 and 2012 was not significant ($r = 0.149$; $P = 0.17$). For networks in 2012 and 2013, the correlation was 0.489 ($P < 0.001$). When we only included dyads monitored for the three years there was no correlation ($r = -0.138$; $P = 0.689$).

Table 3.2: Effects of variables on the frequency of association among bighorn sheep ewes at Ram Mountain, 2011 to 2013.

Variable	2011 (N = 15)	2012 (N = 25)	2013 (N = 18)	2011-2013 combined (N = 29)
Relatedness	No effect	No effect	Marginal effect	No effect
	F = 115.651	F = -0.073	F = 4.218	F = -0.193
	P = 0.628	P = 0.517	P = 0.079	P = 0.182
	R ² = 0.001	R ² = 0.002		R ² = 0.005
Similarity of age	No effect	No effect	No effect	No effect
	F = 3.917	F = -0.001	F = -34.600	F = -0.003
	P = 0.768	P = 0.854	P = 0.145	P = 0.434
	R ² = 0.001	R ² = 0.001	R ² = 0.043	
Similarity of dominance rank	No effect	No effect	No effect	NA
	F = 6.895	F = 0.0547	F = -13.184	
	P = 0.358	P = 0.304	P = 0.368	
	R ² = 0.009	R ² = 0.009	R ² = 0.022	
Similarity of reproductive status	Positive effect	Positive effect	No effect	No effect
	F = 2.765	F = 2.835	F =	F = -0.008
	P = 0.038	P = 0.023	P =	P = 0.802
	R ² = 0.023	R ² = 0.010		R ² = 0.001

Social networks

The social networks constructed with the frequency of proximity events were not random: for all three years, the mean value of eigenvector centralities was not within the 95% CI of the

random networks (Figure 3.3). This suggested some biological driver of the patterns of association among ewes.

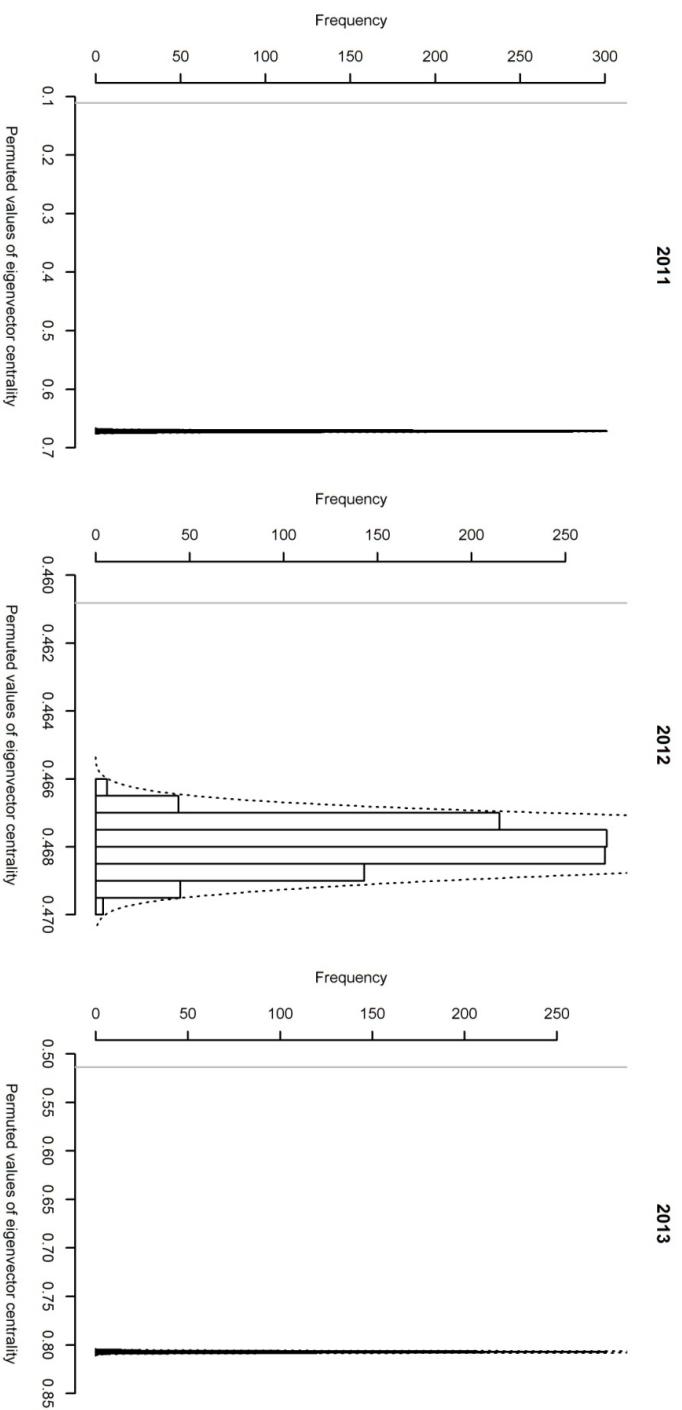


Figure 3.3: The mean permuted values of eigenvector centralities giving a random distribution of edges' weights for 2011-2013. Pale grey vertical line is the observed value of mean eigenvector centralities for the observed social network.

Variables affecting the eigenvector centrality of bighorn ewes

Social networks for each year (Figure 3.2) showed variability in strength of association and social structure. The position of every ewe in the network is measured by their eigenvector centralities. Age affected eigenvector centralities (Figure 3.3), as younger ewes appeared to be more central than older ewes. Compared to ewes aged 2-5 years, those aged 6-9 tended to have lower eigenvector centrality ($\beta = -0.094$; SE = 0.050; T-value = 1.88; $P = 0.07$) and centrality for ewes aged ten years and older was 22% lower ($\beta = -0.222$; SE = 0.069; T-value = 3.21; $P = 0.003$).

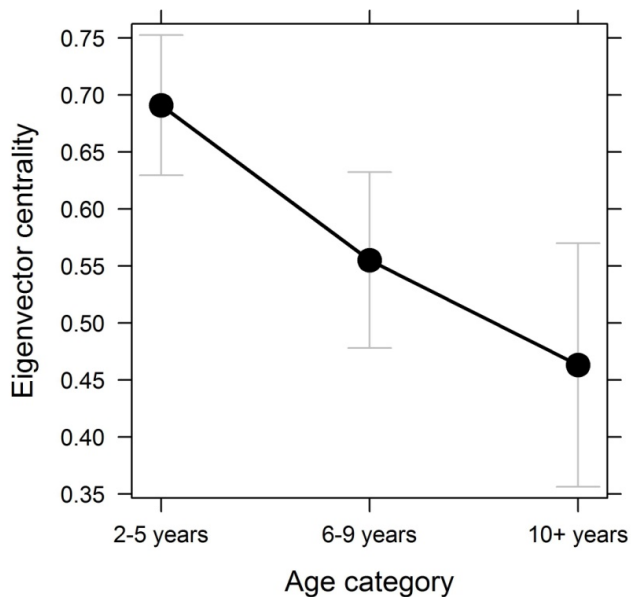


Figure 3.4: Effect of age class on eigenvector centrality of bighorn ewes for 2011-2013, controlling for ID as random effect and year as fixed effect (N = 59 observations).

Discussion

Our study revealed that the pattern of association among wild ewes was not random. Only similarity in reproductive status, however, appeared to have a weak effect on the pattern of association among bighorn ewes. We found no effect of social rank or of relatedness on fine-scale association. These results confirm that there is no genetic sub-structuring in social groups of bighorn ewes (Festa-Bianchet, 1991). The strong deviation from random associations in yearly values and the variable inter-annual stability of social associations, however, suggest that some unidentified variable drives the pattern of association. Perhaps some event that occurs during the winter, when we could not monitor our study subjects, may affect the patterns of association over the following summer.

Related ewes did not have stronger social bonds than unrelated ones. This is in contradiction with the hypothesis that in natural environments, kin selection should be stronger than for captive animals because it has the potential to provide more benefits (Nituch et al., 2008). For this population, gregariousness appears to be beneficial (Vander Wal et al., 2014), but it appears that this effect is not amplified by kinship. The main benefit of gregariousness for ungulates appears to be predator avoidance (Hunter & Skinner, 1998; Kie, 1999; Molvar & Bowyer, 1994). Selection of related individuals as group mates might not be beneficial: the anti-predator benefit of group living is not enhanced by associations with related individuals. Therefore, we would not expect to detect an effect of relatedness for a social structure that is primarily shaped by anti-predation strategies.

Our results also did not support the hypothesis of familiarity (Erhart et al., 1997; Holmes, 1984). This hypothesis states that individuals of similar age (Arnold et al., 1981; Pérez-Barbería et al., 2005) are more familiar with each other, possibly leading to more affinity. Instead our results suggest that preferential associations are somewhat stable across years, but are not more likely to occur among ewes of similar age or dominance rank. The frequent trapping in our study population regularly broke up ewe groups, as ewes that were trapped were released one at a time. Therefore it is unlikely that associations persisted simply because individuals who got together remained together over long periods. Instead, our results suggest that some individuals sought to associate with specific other individuals.

Although the positive effect of similarity of reproductive status was small and not significant in all years, this result is interesting from a behavioural and adaptive point of view. Nursing ewes experience a trade-off between acquisition of food to maintain lactation and vigilance behaviour (Rieucou & Martin, 2008). Therefore, it might be beneficial to maintain proximal social bonds among nursing ewes to share vigilance while maximizing the foraging efficiency, as suggested by the limited attention theory (Griffiths et al., 2004). Vigilance behaviour from nursing ewes can increase survival of both mothers and lambs (Rieucou & Martin, 2008). Hence, the optimal social strategy to increase a ewe's fitness would be to associate in large groups to benefit from the dilution effect and, at a finer scale, to associate with conspecifics who share the same trade-off for foraging and being vigilant. In this population, Vander Wal et al. (2014) showed that it benefits individual fitness for lactating ewes to be more central in social networks based on group membership. Here we present support for preferential associations among ewes with similar reproductive status. The extent to which these patterns of associations present an advantage remains to be investigated. Much of the variability in association strength remains unexplained.

Younger ewes are more central in social networks. We suggest that gaining social experiences early in life can provide fitness benefits. Early-life exposure to complex social behaviours

increases fitness later in life (Sachser et al., 2013; Taborsky & Oliveira, 2012) in cooperatively breeding cichlids (*Neolamprologus pulcher*; Taborsky et al. 2012), striped mice (*Rhabdomys* sp. ; Jones et al. 2010) and orange-winged Amazonia parrots (*Amazona amazonica*; Fox & Millam 2004). It is possible that ewes experiencing a diversity of social situations while young are more likely to exhibit optimal behavioural responses later in life. Further investigation is needed to identify the role that early-life sociality of ewes have in later life fitness.

Social associations are thought to accord some fitness benefit. Therefore, understanding the determinants of social behaviours should illuminate the mechanisms which result in increased reproduction or survival. In some instances social structure is kin-based. For example, another study using proximity loggers was able to identify determinants of association for dyads of another species, the raccoon (*Procyon lotor*), highlighting that kin-based social associations might be context-dependent (Robert et al., 2013). Here, associations were not kin-based; therefore inclusive fitness theory is not an explanation for social bonds. Moreover, we extend our analysis to include social networks constructed from proximity events. Social networks help us translate pair-wise relationships (dyadic associations) into individual-based measures (centrality); as a result one can quantify sociality relatively to other individuals in the network, which is more likely to affect fitness. In this study, the determinants of pair-wise social bonds and social centrality are not the same. Therefore, we argue that combining both approaches leads to a greater potential to explore animal social structure.

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Supplementary material

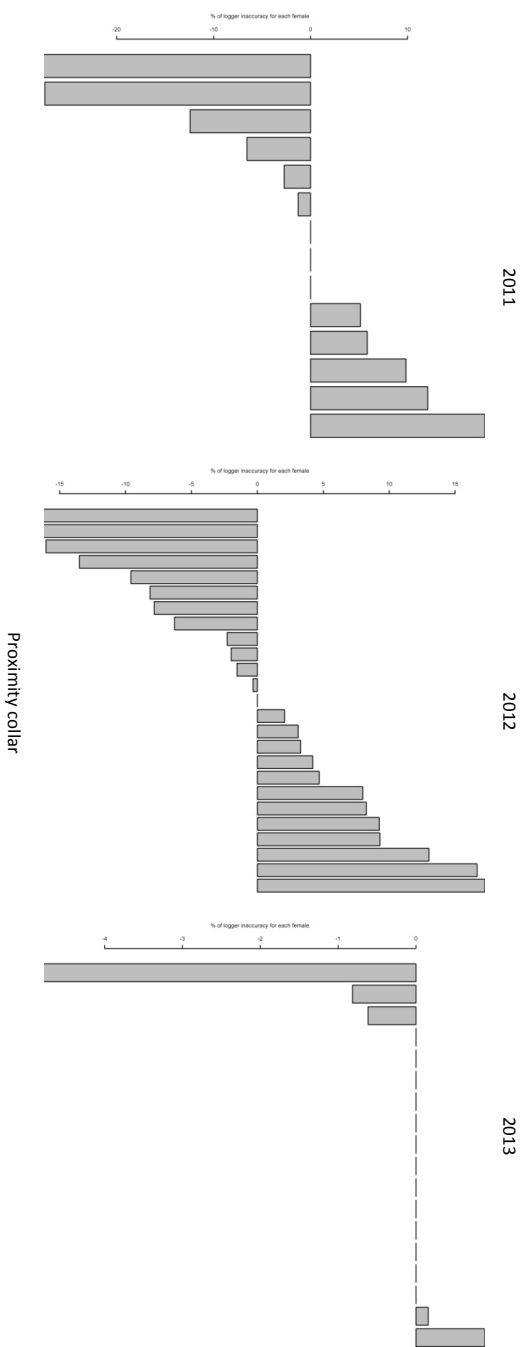


Figure 3.S1: Proximity loggers' intrinsic error for 2011-2013. We corrected our dataset for the loggers' inaccuracy following Boyland et al. (2013).

CHAPITRE 4 : DISCUSSION GENERALE ET CONCLUSION

Ma maîtrise apporte un nouveau regard sur l'utilisation des réseaux sociaux en écologie comportementale : au premier chapitre j'ai montré que le choix du type de données a une grande influence sur le réseau social construit. Il est donc primordial d'en tenir en compte et de choisir judicieusement la façon de mesurer les associations sociales pour répondre à la question d'intérêt. Ce travail est important puisqu'il est le premier à combiner des approches d'observations comportementales directes avec la technologie des colliers de proximité. Ma contribution permettra aux écologistes qui s'intéressent à l'utilisation des réseaux sociaux de bien choisir le type de données et d'analyser avec discernement les résultats. Mon projet de maîtrise est novateur également parce que je me suis intéressée aux patrons d'association à deux échelles : dyadique et individuelle. Les résultats de ces deux analyses nous renseignent sur différents aspects de la socialité des brebis : les brebis de statut reproducteur similaire s'associent davantage entre elles, mais ce sont les brebis plus jeunes qui sont les plus centrales dans les réseaux sociaux. Par ailleurs, nos résultats corroborent l'hypothèse que les individus diffèrent dans leur degré de socialité et que ceci peut également varier au cours de leur vie (Sih et al., 2009). Or, les brebis les plus centrales vivent plus longtemps et ont une descendance plus nombreuse. Le quatrième chapitre intègre les résultats des précédents chapitres pour montrer les bénéfices de la socialité en utilisant un indice d'association pertinent et en considérant à la fois les différents degrés de socialité des individus, leurs affinités sociales et leur grégarité.

Incorporer la composante sociale dans l'étude de l'écologie des espèces permet de mieux comprendre pourquoi certains individus ont une valeur adaptative plus élevée. Le degré de socialité peut varier au cours de la vie d'un animal comme c'est le cas avec les brebis du mouflon d'Amérique. La dynamique temporelle des réseaux sociaux est une avenue de recherche prometteuse. Par exemple, les brebis du mouflon d'Amérique s'isolent pour mettre

bas. Lorsque leur agneau a quelques jours, elles vont rejoindre les autres femelles possiblement pour bénéficier des avantages de la grégarité. Une approche par réseaux sociaux dans ce cas permettrait d'établir un taux de variation de la socialité entre le moment de la mise bas et le moment où la mère rejoint les autres brebis. Ceci permettrait de valider nos estimés de dates de naissance des agneaux; cette variable a le potentiel d'influencer considérablement leur probabilité de survie (Feder et al., 2008) et, par extension, le recrutement de la population.

Les mâles et les femelles ne forment pas le même type de structure sociale. Chez le mouflon d'Amérique, Ruckstuhl (1998) a montré que les différences des besoins nutritionnels est l'un des mécanismes principaux pour expliquer la ségrégation sexuelle. On connaît peu l'influence de cette ségrégation sexuelle sur les structures sociales des brebis et des béliers. Il serait intéressant de comparer comment la structure sociale varie au cours de l'année et la cohésion sociale pour les deux sexes. Il serait alors possible de tester dans quelle mesure les bénéfices et les coûts de la socialité sont différentiels entre les sexes. Ceci donnerait l'opportunité de vérifier l'hypothèse selon laquelle la structure sociale des groupes de mâles est davantage marquée par la compétition alors que la structure sociale des groupes de femelles est plus cohésive pour contrer la prédation.

Nos résultats suggèrent également que la pression de prédation a une influence importante sur la structure sociale chez le mouflon d'Amérique. On sait que la prédation par le couguar (*Puma concolor*) peut avoir un effet négatif important sur la démographie des populations de mouflons d'Amérique (Bourbeau-Lemieux et al, 2011; Festa-Bianchet et al, 2006). La grégarité semble être l'un des comportements pour éviter la prédation (Festa-Bianchet, 1991; Pelletier et al., 2006). Par le passé, la prédation par des couguars a réduit la taille de population à Ram Mountain. Il est donc possible d'identifier les années où les attaques de couguars étaient fréquentes pour comparer la structure sociale avec les années où les probabilités de prédation étaient faibles. Ceci constituerait un test avec des données

empiriques de l'hypothèse d'une augmentation de la cohésion sociale lorsque la pression de prédation augmente.

Chez le mouflon d'Amérique, il semble y avoir une taille de groupe peu variable. Dans la population à l'étude, les années de faible densité, il y a un seul groupe avec tous les individus alors qu'à forte densité, il y a plusieurs groupes d'une vingtaine d'individus. Est-ce que cette taille de groupe est optimale au sens où elle maximise les bénéfices de la socialité et minimise les coûts? Par une approche comparative avec plusieurs espèces d'ongulés faisant face à des pressions de prédation et à une compétition pour les ressources variables, il serait possible d'apporter des preuves empiriques d'une taille de groupe optimale.

Pour les espèces grégaires, on s'attend à ce que les bénéfices de la socialité soient plus grands que les coûts (Molvar & Bowyer, 1994; Riipi et al., 2001). La sociabilité peut donc avoir une valeur optimale qui serait sélectionnée (Sih et al., 2009). À ma connaissance, une seule étude à ce jour a montré, chez les marmottes à ventre jaune, que les comportements sociaux sont en partie héréditaires (Lea et al., 2010). Ceci supporte l'idée que la socialité est soumise à la sélection naturelle. Alors qu'en est-il lorsque les conditions écologiques varient? On pourrait s'attendre à ce que la sélection naturelle favorise la socialité lors d'épisodes de prédation, mais elle devrait contre-sélectionner les comportements sociaux lors d'épisodes de maladies infectieuses. La variation de l'ampleur des coûts et des bénéfices de la socialité pourrait être un mécanisme par lequel la plasticité comportementale serait favorisée plutôt qu'une sélection pour une plus grande socialité. Combiner l'utilisation de réseaux sociaux à l'étude de la plasticité comportementale est une avenue prometteuse pour comprendre la diversité de la structure sociale entre les espèces et aussi entre différentes populations d'une même espèce.

L'utilisation des réseaux sociaux en écologie comportementale bénéficie également du suivi longitudinal des individus. Une hypothèse qui n'a pu être formellement testée à ce jour est

celle que l'exposition à des conditions sociales diversifiées en bas âge permet d'avoir des comportements optimaux dans une grande diversité de situation à l'âge adulte procurant de ce fait un avantage en termes de valeur adaptative (Sih et al., 2009). Afin d'explorer cette hypothèse, il faut pouvoir mesurer la socialité en bas âge et suivre le succès reproducteur à vie des individus. Le développement de nouvelles méthodes avec les réseaux sociaux bénéficierait de l'utilisation de jeux de données basés sur le suivi à long terme d'individus.

Une application des réseaux sociaux à la conservation est la possibilité d'identifier les individus qui sont les plus importants pour maintenir la cohésion sociale (« *keystone individuals* »; Sih et al. 2009). Pour des espèces menacées et pour lesquelles le recrutement limite la croissance de la population, identifier et protéger les individus les plus centraux qui permettent de lier plusieurs groupes sociaux ensemble est une stratégie de conservation prometteuse. À ma connaissance, une seule étude sur les épaulards (*Orcinus orca*; Williams & Lusseau 2006) a utilisé une telle approche. L'intégration de l'étude des réseaux sociaux à des enjeux de gestion de population pourrait donner de précieux outils pour améliorer les pratiques de conservation de la faune.

L'utilisation de réseaux sociaux pour l'étude des comportements sociaux a beaucoup de potentiel parce que l'on peut à la fois s'intéresser aux mécanismes, aux déterminants et aux conséquences des associations sociales. Une approche intégrative de l'écologie sociale dans une perspective évolutive permet de comprendre la variabilité dans les degrés de socialité des animaux.

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ANNEXE 1: DISENTANGLING BEHAVIOURAL PATHWAYS TO NETWORK
CENTRALITY IN A FISSION-FUSION SOCIETY: IMPLICATIONS FOR INDIVIDUAL
FITNESS

Introduction de l'article

Cet article traite de l'utilisation de deux indices d'association pour construire des réseaux sociaux, le HWI et le HWIG, et de l'influence de la position dans un réseau social sur la valeur adaptative des individus. La socialité est la combinaison de la tendance d'un animal à être grégaire et de ses affinités avec d'autres individus. Le HWIG est un nouvel indice d'association découlant du HWI qui tente de contrôler pour les différences de grégarité entre les individus de sorte à représenter exclusivement les affinités. Nous avons exploré les différences entre ces deux indices en étudiant les associations dans des groupes de mouflons à Ram Mountain pour les années 1996-2011 pour construire des réseaux sociaux. Les deux indices d'associations sont fortement corrélés. Pour les femelles, la centralité mesurée avec les réseaux ajustés et non-ajustés pour la grégarité était liée positivement à leur succès reproducteur et à leur longévité. Pour les mâles, la centralité dans le réseau non-corrigé pour la grégarité (HWI) était liée à leur longévité, mais la centralité basée sur les liens directs dans le réseau corrigé pour la grégarité (HWIG) était liée négativement à leur succès reproducteur. De façon générale, la grégarité et les affinités semblent jouer un rôle dans les bénéfices de la socialité pour la valeur adaptative. Les données empiriques de Ram Mountain ne suggèrent pas que le HWIG soit en mesure de bien séparer ces deux composantes l'une de l'autre.

Eric Vander Wal a fait la majorité des analyses et de la rédaction. J'ai collaboré avec lui pour les analyses et l'interprétation des résultats. Denis Réale a apporté son expertise pour la partie

sur l'héritabilité du comportement alors que David Coltman était impliqué dans les analyses génétiques. Marco Festa-Bianchet et Fanie Pelletier ont révisé le manuscrit. Leur contribution à la recherche et au financement à Ram Mountain depuis de nombreuses années est d'autant plus majeure dans le contexte de cet article que les données utilisées s'échelonnent sur 16 ans.

L'article a été soumis à la revue *Animal Behaviour* le 20 août 2014.

DISENTANGLING BEHAVIOURAL PATHWAYS TO NETWORK CENTRALITY IN A
FISSION-FUSION SOCIETY: IMPLICATIONS FOR INDIVIDUAL FITNESS

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Abstract

Animals well-connected in social networks are hubs for information transfer and disease transmission, may have higher fitness, and may play an integral role in maintaining genetic connectivity within a population. Thus, it is critical to understand how (pathway) and why (adaptive value) an individual becomes central in a social network. In fission-fusion populations two pathways to centrality exist: associating with large groups leading to individual differences in gregariousness or having strongly preferred associates (affiliates). To test how variation in individual gregariousness and pair-wise associations affect centrality, we constructed two sets of networks: one adjusted for individual variation in gregariousness and one that did not. We built social networks from 38350 observations of group membership (N=3150 groups) in a population of wild bighorn sheep (*Ovis canadensis*) over 16 years (N=1022 sheep-years). We calculated two metrics of centrality: one accounted for indirect associations and one that did not. We tested which pathway to centrality was more likely to affect fitness, i.e., lamb production, lamb survival to age 1 and adult survival. Centrality as a function of gregariousness and affinity positively affected lamb production and adult female survival. Conversely, centrality as a function of affinity negatively affected production of lambs by adult males. Consequently, we argue that network architecture is function of both gregariousness (as an anti-predator behaviour) and affinity (as a cost of competition), but sex-specific variation in these fundamental components exists and affects the fitness-centrality landscape. Thus, antagonistic selection on social traits may maintain variation in centrality in fission-fusion animal societies.

Key words: affinity, antagonistic selection, behavioural plasticity, fitness, gregariousness, personality, sociality

Introduction

Animals that are central in social networks are hubs for information transfer (Aplin et al., 2012) and disease transmission (Perkins et al., 2009); may have higher fitness (McDonald, 2007; Stanton & Mann, 2012; Vander Wal et al., 2014); and may play an integral role in maintaining genetic connectivity within a population (Williams & Lusseau, 2006). Two behaviours, however, are pathways to becoming central in a social network: gregariousness and affinity (Godde et al., 2013). Gregariousness is an individual's tendency to aggregate or prefer to belong to group of a given size (Grassia, 1978; Pepper et al., 1999). If two individuals are gregarious and select large groups, they may be more likely to associate without necessarily having an affinity for one another. Affinities suggest that two individuals prefer to associate independently of group size. Each of these behaviours can be different routes to becoming socially connected and central in a social network. For example, a social network with edges weighted to describe pair-wise affinities, either stronger ties or more diverse number of associates, may result in a similar network architecture to one constructed via measures derived from highly gregariousness individuals. Each pathway, however, has distinct biological implications. Thus, it remains critical to ascertain which pathways individuals use to become central in a network.

Many networks are constructed from group memberships data, predicated on the assumption of 'gambit-of-the-group' (GoG, Whitehead, 2008). GoG presupposes that all individuals in a group are at least associating, if not interacting (Franks et al., 2009; Whitehead & Dufault, 1999). Variation in pair-wise associations derived from GoG rely on both pair-wise associations and individual variation in gregariousness (Godde et al., 2013). The half-weight-index (*HWT*) is a common technique to convert group observations into pair-wise association data:

$$HWI_{ab} = \frac{x}{\frac{1}{2}(y_a + y_b)} \quad [1]$$

where x is the sum of events where individuals a and b were observed associating and y_a and y_b are the sum of events where a and b were observed, respectively (Whitehead, 2008). HWI association strength varies from 0 – 1: 0 occurs when animals are never observed together and 1 when animals are always observed associating. The HWI, however, does not disentangle gregariousness and pairwise affinities (Godde et al., 2013). Therefore, fitness benefits of centrality in a network based on the HWI might be due to the benefit of an individual seeking large groups, to preferred associations, or the cumulative effects of both. To decompose these effects Pepper et al. (1999) proposed an adjustment to the HWI:

$$HWIG_{ab} = HWI_{ab} \frac{\sum HWI}{\sum HWI_a + \sum HWI_b} \quad [2]$$

Where a and b are the summed HWI values of individuals a and b and $\sum HWI$ is the sum of all HWI for all pairwise associations. The HWIG controls for classes of gregariousness, if not individual variation in gregariousness itself (Godde et al., 2013). The HWIG varies from $x > 1$ $> y$, values less than 1 suggests animals associate less than expected at random given their gregariousness and values greater than 1 suggest that animals have affinities for one another [see Godde et al. (2013) for details].

When social networks are constructed from GoG data, measures of centrality derived from HWI and HWIG networks are predicted to vary. As a result, comparing two differently derived networks may provide distinct inferences into the origins of sociality (Godde et al., 2013): HWIG networks suggest that the importance of centrality is a function of strong or variable pair-wise associations; HWI networks suggest the importance of centrality is a function of both gregariousness and pair-wise associations; and where HWI is important but HWIG is not, centrality is predominantly a function of gregariousness (Table A1.1). One

might predict the latter in fission-fusion societies where animals do not necessarily actively cooperate or form stable pair bonds (Couzin & Laidre, 2009). However, the adaptive value of

Table A1.1 Prediction scheme for comparing results from networks constructed on association data (half-weight-index, HWI) and gregariousness-adjusted affiliation networks (HWIG) based on Godde et al. (2013).

Networks		
HWI	HWIG	Interpretation
+	+	Both gregariousness and affinity are important
-	-	Neither gregariousness nor affinity are important
-	+	Affinities are important; whereas gregariousness is not
+	-	Gregariousness is important; whereas affinities are not

centralit
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also
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(Vander
Wal et
al.,
2014).

Here, we contrast sex-specific networks built using HWI and HWIG to tease apart the pathway to social centrality. Specifically, we evaluate whether sociality is advantageous because an individual has chosen to associate with larger groups or because it has chosen to associate preferentially with specific other individuals. To test which pathway to centrality is more likely to be adaptive, we created networks based on the group composition data for a population of bighorn sheep (*Ovis canadensis*). The networks differed in their edge weights: one weighted with the HWI and the other with the HWIG. Subsequently we compare the correlations between pair-wise associations from HWI and HWIG. We then derived two measures of centrality which include direct and indirect associations. We compared whether these values vary in their consistency of centrality [i.e., repeatability or ‘personality’ (Réale et al., 2010)]. Finally, we compared fitness effects (lamb production, lamb survival to age one, and adult survival) of centrality derived from the HWI and HWIG to quantify the adaptive nature of gregariousness and affiliations in fission-fusion animal societies.

Methods

Study Area and Sheep

Ram Mountain Alberta, Canada (52°N, 115°W) is approximately 30 km east of the main range of the Rocky Mountains. The sheep population has been continuously monitored since 1972 (Jorgenson et al., 1993). Bighorn sheep are highly social ungulates existing in a fission-fusion society. Animals were baited with salt into a corral trap where they were fitted with colored collars on females and plastic ear tags on males (Jorgenson et al., 1993). Maternities were assigned by visual observations of nursing. Paternity was assigned statistically using data from genotyped microsatellite loci [see Coltman et al. (2002) for details].

Group Observations and Social Networks

Sheep groups were observed between 1996-2011 ($n = 38350$ observations of sheep, 3150 groups, 1022 sheep-years). Sheep formed discrete and easily quantifiable groups. It was uncommon for individuals on the periphery of groups to be > 50 m from conspecifics. Sheep groups were relocated frequently: multiple times per week, often multiple groups per day [\pm SD): females 37 (20); males 22 (18) per year]. Bighorn sheep group sizes varied throughout the study period; however, were relatively invariant to changes in population size (Figure A1.1). Because sheep were frequently caught in the trap and then released one at a time, trapping activities affected group composition, making repeated observations of group composition more independent than in a situation where sheep may simply remain in the same group over multiple days.

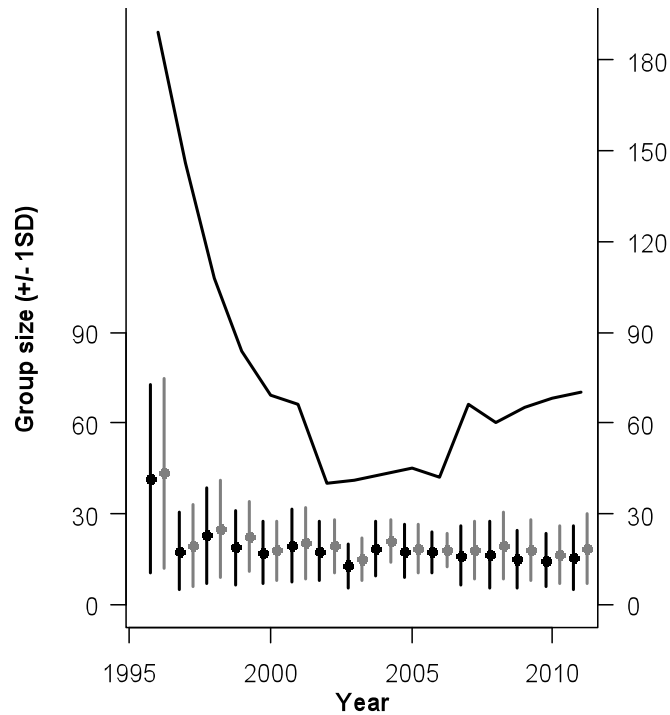


Figure A1.1 Variation in mean group size (total number of sheep 1 year and older) and standard deviation (± 1 SD) for female (gray) and male (black) bighorn sheep on Ram Mountain (AB, CAN) from 1996-2011. Solid line (black) denotes the population size through time.

We constructed social networks from group membership data, assuming that all members of the group were associating. Two networks were constructed based on the half-weight-index (HWI) or the gregariousness-adjusted half-weight-index (HWIG), see above. We constructed networks and derived their metrics using the *R* (R Development Core Team, 2011) package *igraph* (Csardi & Nepusz, 2006). We calculated two indices of centrality: eigenvector centrality and graph strength. Eigenvector centrality accounts for direct and indirect associations between individuals (Costenbader & Valente, 2003; Maiya & Berger-Wolf, 2010). Eigenvector centrality measures an individual's prominence in the network where its

centrality is proportional to the sum of centralities of individuals to which it is connected (Csardi & Nepusz, 2006; Stanton & Mann, 2012). Conversely, graph strength sums the edges of each node, thus accounting only for direct associations (Csardi & Nepusz, 2006).

Networks were built separately according to known patterns of sheep behaviour. Sheep segregate by size, and therefore by sex and age (Ruckstuhl & Neuhaus, 2002). Thus, we constructed two sets of networks. One set included all females, yearlings, and males up to 2 years old. At 2 years of age male sheep transition from predominantly female groups to bachelor groups (Ruckstuhl & Neuhaus, 2005). As a result the second set of networks included all males ≥ 2 years of age. For further details, see Vander Wal et al., 2014.

Repeatability

We tested whether eigenvector centrality and graph strength derived from HWI and HWIG networks exhibited consistent individual differences through time (i.e., repeatable). Repeatability was calculated using an inter-class coefficient (Krebs, 1970):

$$r = \frac{s_s^2}{(s_s^2 + s_{sw}^2)} \quad [3]$$

where s_s^2 is the variance among individuals and s_w^2 is the variance within individuals. Highly repeatable behaviours would have values near 1; those that are unrepeatable would not be significantly different from 0. We calculated repeatability and 95% Bayesian credible intervals for the ICC using the *R* package *MCMCglmm* (Hadfield, 2010) using uninformative priors, 500000 iterations, with a burnin period of 50000, thinned every 1000 iterations.

Generalized Linear Models

We constructed general linear mixed models (GLMMs) to test for fitness effects of eigenvector centrality or graph strength derived from HWI and HWIG networks using the *lmer4* library (Bates & Maechler, 2010). Fitness components included lamb production by adults, lamb overwinter survival and adult survival. All response variables were binomially distributed; as males could potentially sire multiple lambs, those that sired > 1 lamb were coded as 1 and those that failed to sire lambs, 0. We controlled for two random effects (individual ID and year) in all models allowing us to correct for the effect unmeasured traits that may be related to fitness. Furthermore, we accounted for an individual's mass adjusted to September 15, age and age², parental effects (size of the population when the mother or father were born), population size each year and graph density as fixed effects. Graph density is derived from the social networks; it is an indicator of social density and is the proportion of edges observed in a population in relation to the number of edges that are possible (Csardi & Nepusz, 2006). We retain the interaction between centrality and social density because it has been important in previous analyses (Vander Wal et al., 2014).

Results

The HWI indicated that bighorn sheep had variable pair-wise associations [$\text{♀} = 0.37$ (95CI: 0.06 – 0.73), $\text{♂} = 0.36$ (95CI: 0.03 – 0.82); Figures A1.2 and A1.S1]. These average values translated into HWIG values that predominantly suggested that females have pair-wise affinities (HWIG > 1 ; $\text{♀} = 5.22$, 95CI: 1.34 – 11.18; Figure A1.2). For females, 99% of HWIG values were > 1 . On average males also exhibited gregariousness-adjusted affinities ($= 1.65$, 95CI: 0.18 – 4.45; Figure A1.2). However, avoidance (HWIG < 1) was apparent in 33% of male dyads (Figure 4.S2).

When year was accounted for as a random effect in the general linear mixed model, HWI values explained considerable variation in HWIG values (Figure A1.2). As a result eigenvector centrality derived from the HWI network explained considerable variation in eigenvector centrality derived from the HWIG networks (Figure A1.3). Results were similar for graph strength (Figure A1.3). However, less variation was explained by centrality comparisons for males than females.

Being central in the HWI and HWIG networks had fitness effects, predominantly for females (Table A1.3; Tables A1.S1 and A1.S2). Centrality increased a female's probability of producing a lamb (HWIG: eigenvector centrality $\beta = 0.27$, $P = 0.11$, $AIC_w = 1$; graph strength $\beta = 0.61$ $P < 0.001$, $AIC_w = 1$; HWI: eigenvector centrality $\beta = 0.32$, $P < 0.04$, $AIC_w = 1$; graph strength $\beta = 0.50$, $P = 0.007$, $AIC_w = 1$; Tables A1.S1 and A1.S2). Results were largely indistinguishable between HWI and HWIG networks and insensitive to network metric (Table A1.3). Similarly, centrality increased adult female survival (HWIG: eigenvector centrality $\beta = 1.08$, $P < 0.001$, $AIC_w = 1$; graph strength $\beta = 0.55$ $P = 0.067$, $AIC_w = 1$; HWI: eigenvector centrality $\beta = 1.03$, $P < 0.001$, $AIC_w = 1$; graph strength $\beta = 0.50$, $P = 0.007$, $AIC_w = 1$; Tables A1.S1 and A1.S2). Generally, effect sizes and significance values were similar for gregariousness and affinity for lamb production by adult females (: eigenvector centrality = 0.81; graph strength = 0.97) and survival (eigenvector centrality = 0.95; graph strength = 2.16).

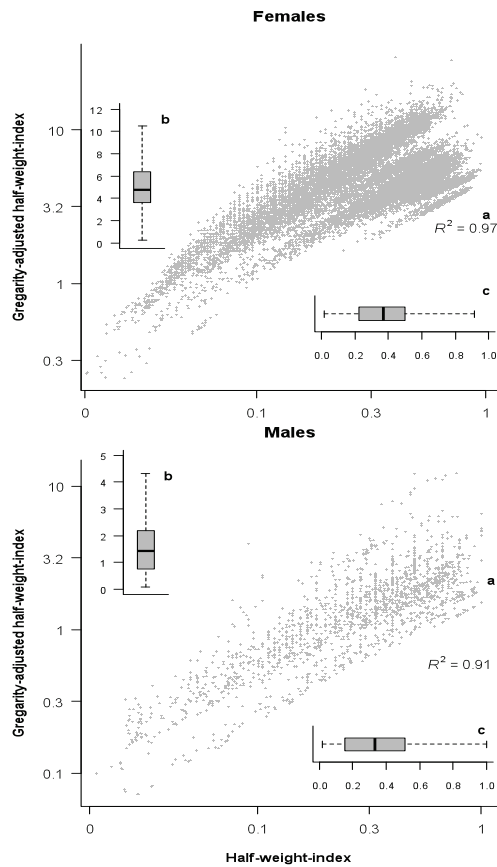


Figure A1.2 A comparison of half-weight-index (HWI) and gregariousness-adjusted half-weight-index (HWIG) values derived using gambit-of-the-group data from a fission-fusion society of female (upper panel) and male (lower panel) bighorn sheep in Ram Mountain (AB, CAN) between 1996-2011. (a) Each point illustrates the correlation between HWI and HWIG for one dyad in one year (note the $\log_{10} - \log_{10}$ scale). This highlights the variation in HWI explained by HWIG ($P < 0.001$) once year was taken into account. (b) Illustrates the distribution of values for the HWIG; whereas, (c) illustrates the distribution of pair-wise association strengths according to the HWI.

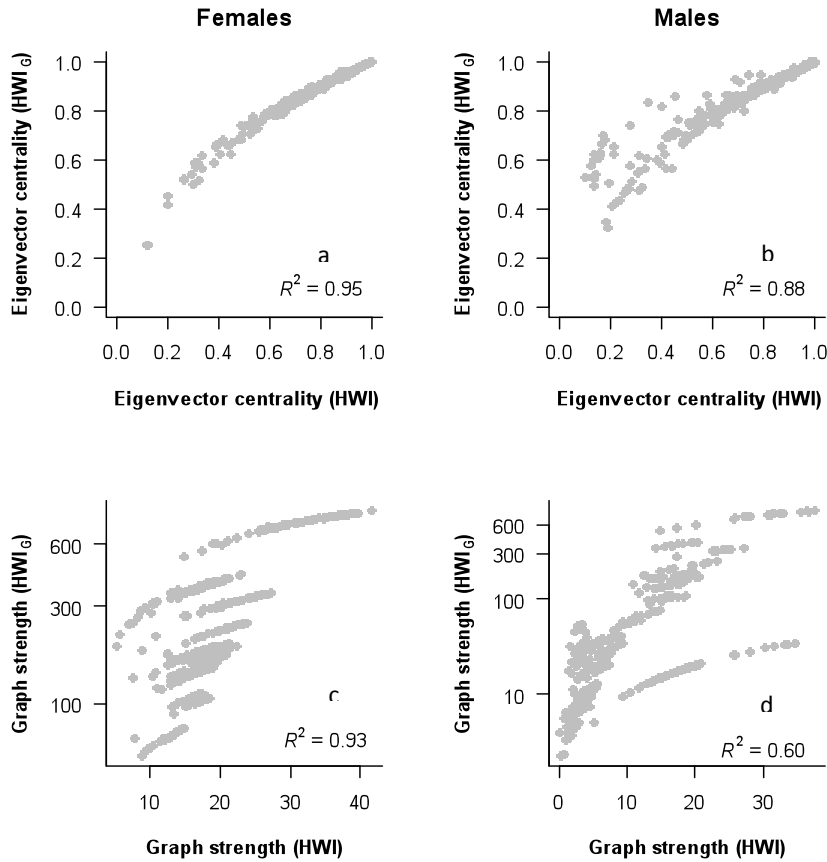


Figure A1.3 Comparison of network centrality metrics [eigenvector centrality (a, b), graph strength (c, d)] derived from sex-specific sets of social networks for female (a, c) and male (b, d) bighorn sheep on Ram Mountain (AB, CAN) between 1996-2011. Each point represents one individual in one year. One set was derived from a network with edges weighted by the half-weight-index (HWI) and the other by a network weighted by the gregariousness-adjusted half-weight-index (HWIG). Because graph strength is not standardized by population size, different population sizes resulted in distinct groups (i.e., lines of points on a \log_{10} scale for HWIG but unadjusted for HWI) in (c) and (d). As a result mixed general linear models which accounted for unequal population size across years were used to reveal statistically significant comparisons between all HWI and HWIG derived metrics ($P < 0.001$). However, the variation explained was weaker for males than females, particularly using graph strength as a metric for centrality.

Albeit Bayesian confidence intervals overlapped, eigenvector centrality as a function of HWIG had a smaller posterior mean repeatability than centrality as a function of HWI (Table A1.2). The reverse was true for graph strength, which had a larger posterior mean repeatability when derived from the HWIG than the HWI (Table A1.2). The posterior mean repeatability for graph strength was larger than eigenvector centrality for males; whereas eigenvector centrality had a larger posterior mean than graph strength for females (Table A1.2).

Table A1.2 Sex-specific comparison of inter-class correlation coefficients (posterior mean and 95% Bayesian Credible Intervals) evaluating the consistent individual differences in social centrality (eigenvector centrality and graph strength) derived from networks of bighorn sheep in Ram Mountain (AB, CAN) between 1996-2011 where pairwise association are quantified using a half-weight-index (HWI) and gregariousness-adjusted half-weight-index (HWIG).

	Metric	HWI (, 95% BCI)	HWIG (, 95% BCI)
Females	Eigenvector centrality	0.40 (0.32 – 0.50)	0.33 (0.24 – 0.42)
	Graph strength	0.08 (0.04 – 0.12)	0.31 (0.20 – 0.43)
Males	Eigenvector centrality	0.26 (0.13 – 0.42)	0.21 (0.08 – 0.36)
	Graph strength	0.38 (0.20 – 0.55)	0.46 (0.31 – 0.60)

Table A1.3 Results from networks constructed on association data (half-weight-index, HWI) and gregariousness-adjusted pairwise social affinity networks (HWIG) for eigenvector centrality and graph strength in a population of bighorn sheep on Ram Mountain (AB, CAN) from 1996 – 2011. *P*-value, direction of effect (+ or –) and individual variable weights (AIC_w) are presented to weigh two lines of evidence suggesting whether gregariousness or affinities were more important for fitness components (detailed model results can be found in Tables A1.S1 and A1.S2). Key findings are emboldened.

		Networks			
		Eigenvector centrality		Graph strength	
Fitness component	HWI	HWIG	HWI	HWIG	Interpretation
Lamb production	0.04, +, 1.00	0.10, +, 1.00	0.01, +, 1.00	<0.001, +, 1.00	Gregariousness and affinities are important routes to centrality for lamb production.
Lamb survival	0.33, +, 0.13	0.14, +, 0.14	NA ^a	0.10, –, 0.58	Neither individual variation in gregariousness nor affinities were important for female lamb survival.
Females					Individual variation in gregariousness was
Adult survival	<0.001, +, 1.00	<0.001, +, 1.00	<0.001, +, 1.00	0.07, +, 1.00	likely more important than pair-wise affinities for attaining a central position and consequently affecting survival.

					Some evidence for pair-wise affinities negatively influencing individual centrality and consequently centrality negatively affecting the probability of producing a lamb.
Lamb production	0.62, +, 0.44	0.47, +, 0.61	0.19, -, 0.76	0.04, -, 1.00	
Lamb survival	0.22, +, 0.10	0.16, +, 0.46	0.22, +, 0.35	0.32, -, 0.22	Neither individual variation in gregariousness nor affinities were important for female lamb survival.
Adult survival	0.19, -, 0.81	0.12, +, 0.86	0.24, +, 0.80	0.08, +, 1.00	Very weak support for pair-wise affinity affecting centrality and consequently survival.

^a variable dropped in all-possible model selection

Conversely, for males centrality had a largely equivocal effect on lamb production when considering both eigenvector centrality and graph strength for the HWI ($P > 0.05$; Tables A1.S1 and S2). However, male graph strength derived from the HWIG networks appeared to have a negative, significant, and important influence on lamb production (graph strength $\beta = -9.07$, $P = 0.044$, $AIC_w = 1$; Table A1.3 and A1.S2). Here, pair-wise affinities appear to reduce the probability of producing a lamb (Table A1.3). There was, however, marginal evidence for affinities increasing adult male survival (HWIG graph strength: $\beta = 7.64$, $P = 0.078$, $AIC_w = 1$; Table A1.3 and A1.S2).

Discussion

As network centrality is adaptive (McDonald, 2007; Stanton & Mann, 2012; Vander Wal et al., 2014), it is important to disentangle the pathways individuals use to maximize their social connectedness relative to conspecifics. Our study shows that both gregariousness and affiliations influenced an individual's centrality in the networks, with implications for fitness. For example, for adult female survival both individual variation in gregariousness and pair-wise affinities clearly affected social connectedness and consequently fitness. Furthermore, the gregariousness adjustment may have revealed a previously undetected negative effect of affiliation for lamb production by males (see Vander Wal et al., 2014). Our results suggest that in some contexts, one can cautiously use the HWIG adjustment as a post-hoc means to disentangle gregariousness and pair-wise affinity from gambit-of-the-group data.

The HWIG accounts for individual variation in gregariousness (Godde et al., 2013; Pepper et al., 1999). In our fission-fusion population of bighorn sheep the dyadic HWI and HWIG

values were strongly correlated. This might appear to create uncertainty as to whether the HWIG can adjust for gregariousness; particularly, as Godde et al. (2013) suggest that the HWIG might not perfectly remove the influence of group size. A high correlation between HWI and HWIG results when the variance in the gregariousness adjustment (element 2, equation [1]) is not large compared to the among-individual variance in HWI (Godde et al., 2013). Indeed, here there was less variation in the gregariousness adjustment than the HWI (Figure 4.S1), likely due to limited variation in sheep group size. Nevertheless, the HWIG did generate variation among dyads for a given HWI (note Figure A1.2 is on a $\log_{10} - \log_{10}$ scale). The HWI and HWIG measures of centrality were also correlated; albeit, for any given HWI derived centrality there appears to be less variation in HWIG derived centrality. These relationships differed between sexes. The correlation between HWI and HWIG derived centrality was weaker in males than females. For males there was no correlation between the annual coefficients of variation in HWI and the gregariousness adjustment of the HWIG (element 2, equation [1], Figure A1.S1). Therefore a weaker correlation between HWI and HWIG occurred for males. Increased variance in these elements resulted in increased variance in centrality and thus we detected differences in downstream effects on fitness – if not repeatability. Ultimately, suggesting that the HWIG was contributing novel information.

It is increasingly being recognized that personality (e.g., boldness) influences network position (Aplin et al., 2013; Pike et al., 2008). However, network position may itself be a personality trait (Krause et al., 2010; Wilson et al., 2012). Here, eigenvector centrality and graph strength derived from HWI and HWIG weighted networks were repeatable behaviours. The degree to which behaviours are repeatable may be indicative of their adaptive value (Dingemanse & Réale, 2005; Réale et al., 2010). Our observations of repeatability were similar to behaviours reported in the literature (Bell et al., 2009), including those derived from social networks (e.g., Fowler et al., 2009; Lea et al., 2010). Repeatability occurred despite individual-based measures of centrality being contingent on the social environment, e.g., social connectedness of conspecifics (Krause et al., 2010). The highest measures of repeatability arose when considering specific logical combinations of network edge weights

and metric. Inasmuch as we detected no significant differences among combinations of sex and network metric (i.e., all had overlapping Bayesian credible intervals), the posterior means for HWIG were larger while only considering direct associations. This may suggest that the HWIG and graph strength better capture information from pair-wise affinities and were arguably less affected by gregariousness. Conversely, HWI, which does not account for gregariousness and eigenvector centrality, and accounts for indirect links among network nodes, may better reflect individual variation in gregariousness. As such, gregariousness appears more important for females and affinity for males.

Previous research on a different bighorn sheep population suggests sheep do not have stable group structure (Festa-Bianchet, 1991) or pair-wise affinities. For example, mothers and weaned daughters do not preferentially associate under most circumstances (L'heureux et al., 1995). This contrasts with our findings for females, where most dyads technically were affiliates (*sensu* Godde et al., 2013) because the vast majority of HWIG values were > 1 . Bighorn sheep exhibit a fission-fusion dynamics and group mixing is expected, and in years where population size was small all individuals had pair-wise associations, suggesting considerable mixing (Vander Wal et al., 2014). If all dyads have HWIG values >1 , however, it becomes unclear which of those affiliations are 'preferential'. As a result, we caution against interpreting the HWIG as an index of preferential associations. For example, it may be more appropriate to identify as preferential those dyads with HWIG that exhibit affiliations greater than the population mean.

Centrality, which included individual variation in gregariousness and affinities, had a positive impact on lamb production and survival of adult females. Grouping is a common anti-predator behaviour in ungulates, particularly those that occupy open habitats and rely on visual detection of their predators (Geist, 1971). Its direct benefits include diluting individual risk of being killed (Hamilton, 1971; Wrona & Dixon, 1991) and avoiding detection (Ioannou et al., 2011). Indirect effects include collective vigilance (Beauchamp et al., 2012; Pays et al.,

2013). In bighorn sheep, predator-sensitive foraging has been shown to be affected by group size where small groups were less efficient foragers (Berger, 1978). For females, it might be beneficial to maximize direct and indirect associations to lower the probability of being depredated. Similarly for males, being in bigger groups may improve survival presumably through the dilution effect. Surprisingly, however, our results suggested that males with more pair-wise affinities had a lower probability of producing a lamb. Similarly aged (and sized) sheep may be more likely to have affinities because they have synchronous patterns of foraging and ruminating (Ruckstuhl & Neuhaus, 2002). Here, dyads of similar age and presumably social rank were more likely to have affinities – especially young males which are unlikely to produce lambs (Figure 4.S2a) – than individuals who differed in age. Altogether, these sex-specific differences in gregariousness and affinities suggest that natural selection on social traits may differ between males and females.

We capitalized on a gregariousness-adjustment index proposed by Pepper et al. (1999) and validated in simulations by Godde et al. (2013) to test which pathways to centrality confer fitness benefits through lamb production, survival of lambs to one-year of age one and adult survival. We show that despite the inferential nature of post-hoc gambit-of-the-group networks, in some instances we can decompose the pathways to centrality based on two different social behaviours: gregariousness and affinities. We establish this by contrasting the results of two indices (HWI and HWIG) and two centrality metrics (eigenvector centrality and graph strength). Consequently, our results provide novel insights into social behaviours that indirectly confer fitness benefits via social centrality. However, it is apparent that the fission-fusion society of bighorn sheep does not involve an either-or scenario for gregariousness and affinity: both gregariousness and affinity are adaptive. In general, network architecture that is function of both gregariousness and affinity may arise from sex-specific variation in these fundamental components which appear to affect the fitness-centrality landscape. As a result, antagonistic selection on social traits may maintain variation in centrality in fission-fusion animal societies.

References

Supplementary material

Table A1.S1. Model averaged results from the global model explaining the variation in different measures of fitness in bighorn sheep on Ram Mountain, Alberta. Models constructed with eigenvector centrality, see Tables S2 for results using graph strength. We standardized all variable to their z-scores prior to analysis. Emboldened numbers report either $P < 0.05$ or relative variable importance values ($AIC_w = 1$). Results are reported for networks that account for individual variation in gregariousness (HWI^a) and those that report gregariousness-adjusted pairwise affinities (HWIG).

	HWI ^a					HWIG							
	Fixed Effects	β	SE	z-value	P-value	AIC_w	R^2	β	SE	z-value	P-value	AIC_w	R^2
Females													
Lamb production ($n = 556$ animal-years, 147 individuals)													
Intercept	-0.15	0.34	0.46	0.648	NA	-0.20	0.34	0.59	0.553	NA			
Eigenvector centrality	0.32	0.16	2.05	0.040	1.00	0.27	0.17	1.62	0.105	1.00			
Social density	0.40	0.17	2.30	0.021	1.00	0.44	0.18	2.44	0.015	1.00			
Centrality*Social density	-0.37	0.15	2.50	0.012	1.00	-0.37	0.16	2.25	0.024	1.00			
Mass	0.56	0.39	1.43	0.154	0.49	0.56	0.39	1.42	0.155	0.49			0.44
Maternal effect	-0.74	0.18	4.20	<0.001	1.00	-0.72	0.18	4.13	<0.001	1.00			
Age	3.04	0.45	6.71	<0.001	1.00	3.02	0.45	6.71	<0.001	1.00			
Age ²	-1.23	0.19	6.57	<0.001	1.00	-1.23	0.19	6.61	<0.001	1.00			
Population density	0.73	0.24	3.10	0.002	1.00	0.68	0.24	2.86	0.004	1.00			
Intercept	-0.41	0.55	0.74	0.458	NA	-0.41	0.55	0.74	0.458	NA			0.21
Eigenvector centrality	0.31	0.32	0.98	0.328	0.13	0.39	0.36	1.08	0.281	0.14			
Social density													
Centrality*Social density													
Mass	0.68	0.83	0.83	0.409	0.18	-0.45	0.22	2.05	0.040	0.86			
Lamb survival ($n = 96$)													

		Adult survival (n = 557 animal-years, 144 individuals)					Males Lamb production (n = 353 animal-years, 138 individuals)					Lamb survival (n = 113)				
Maternal effect	-0.45	0.22	2.05	0.040	0.85	0.26	0.34	0.77	0.442	0.13	0.26	0.34	0.77	0.442	0.13	
Age	0.26	0.34	0.77	0.442	0.13	0.21	0.18	1.14	0.252	0.24	0.21	0.18	1.14	0.252	0.24	
Age ²	0.21	0.18	1.14	0.255	0.23	-0.49	0.30	1.64	0.100	0.49	-0.49	0.30	1.64	0.100	0.49	
Population density	-0.49	0.3	1.64	0.100	0.50	0.68	0.83	0.83	0.409	0.18	0.68	0.83	0.83	0.409	0.18	
Intercept	2.23	0.28	7.97	<0.001	N/A	2.22	0.26	8.37	<0.001	N/A	2.22	0.26	8.37	<0.001	N/A	
Eigenvector centrality	1.03	0.15	6.92	<0.001	1.00	1.08	0.16	6.78	<0.001	1.00	1.08	0.16	6.78	<0.001	1.00	
Social density	0.03	0.17	0.21	0.836	0.54	0.09	0.15	0.61	0.542	0.48	0.09	0.15	0.61	0.542	0.48	
Centrality*Social density	-0.20	0.12	1.66	0.097	0.41	-0.20	0.13	1.49	0.137	0.26	-0.20	0.13	1.49	0.137	0.26	
Mass	0.82	0.32	2.59	0.010	1.00	0.71	0.28	2.52	0.012	1.00	0.71	0.28	2.52	0.012	1.00	
Maternal effect	-0.28	0.15	1.94	0.053	0.80	-0.32	0.14	2.22	0.027	1.00	-0.32	0.14	2.22	0.027	1.00	
Age	-0.59	0.17	3.42	0.001	0.41	-0.58	0.17	3.37	0.001	0.16	-0.58	0.17	3.37	0.001	0.16	
Age ²	-0.22	0.06	3.44	0.001	0.59	-0.23	0.06	3.59	<0.001	1.00	-0.23	0.06	3.59	<0.001	1.00	
Population density	0.58	0.20	2.91	0.004	1.00	0.56	0.19	2.93	0.003	0.84	0.56	0.19	2.93	0.003	0.84	
Intercept	-3.71	0.73	5.09	<0.001	N/A	-3.69	0.73	5.06	<0.001	N/A	-3.69	0.73	5.06	<0.001	N/A	
Eigenvector centrality	0.12	0.23	0.50	0.616	0.44	0.18	0.25	0.73	0.467	0.61	0.18	0.25	0.73	0.467	0.61	
Social density	0.27	0.33	0.83	0.409	0.79	0.28	0.33	0.85	0.393	0.79	0.28	0.33	0.85	0.393	0.79	
Centrality*Social density	0.28	0.16	1.77	0.076	0.23	0.33	0.16	2.03	0.042	0.40	0.33	0.16	2.03	0.042	0.40	
Mass	2.60	0.43	5.99	<0.001	1.00	2.57	0.40	6.42	<0.001	1.00	2.57	0.40	6.42	<0.001	1.00	
Age	-0.11	0.33	0.33	0.744	0.08	b	b	b	b	b	b	b	b	b	b	
Age ²	-0.04	0.09	0.43	0.670	0.09	b	b	b	b	b	b	b	b	b	b	
Population density	-0.74	0.40	1.82	0.068	0.73	-0.77	0.39	1.96	0.050	0.69	-0.77	0.39	1.96	0.050	0.69	
Intercept	-1.59	0.59	2.69	0.007	N/A	-1.39	0.50	2.79	0.005	N/A	-1.39	0.50	2.79	0.005	N/A	
Eigenvector centrality	0.48	0.40	1.22	0.222	0.35	0.42	0.30	1.42	0.156	0.46	0.42	0.30	1.42	0.156	0.46	
Social density	0.30	0.30	0.98	0.327	0.04	0.31	0.30	1.05	0.296	0.06	0.31	0.30	1.05	0.296	0.06	
Centrality*Social density	b	b	b	b	0.04	-0.58	0.37	1.58	0.114	0.03	-0.58	0.37	1.58	0.114	0.03	

	0.45	0.25	1.79	0.073	0.77	0.45	0.25	1.82	0.070	0.74
Mass	0.45	0.25	1.79	0.073	0.77	0.45	0.25	1.82	0.070	0.74
Maternal effect	-0.37	0.21	1.75	0.081	0.63	-0.37	0.21	1.76	0.078	0.65
Age	-0.18	0.58	0.31	0.753	0.29	-0.18	0.58	0.31	0.757	0.26
Age ²	0.30	0.21	1.44	0.151	0.54	0.31	0.20	1.55	0.120	0.61
Population density	-0.92	0.47	1.94	0.052	1.00	-0.71	0.33	2.13	0.033	0.90
Intercept	1.87	0.34	5.57	<0.001	N/A	1.88	0.34	5.58	<0.001	N/A
Eigenvector centrality	0.22	0.17	1.31	0.189	0.81	0.24	0.15	1.56	0.118	0.86
Social density	-0.2	0.25	0.77	0.439	0.49	-0.17	0.24	0.71	0.480	0.42
Centrality*Social density	^b	^b				^b	^b			
Mass	0.81	0.49	1.65	0.100	0.38	0.79	0.49	1.62	0.106	0.36
Maternal effect	-0.27	0.2	1.36	0.174	1.00	-0.27	0.2	1.37	0.170	1.00
Age	-0.80	0.44	1.83	0.068	0.67	-0.75	0.43	1.75	0.081	0.67
Age ²	-0.20	0.10	2.10	0.036	0.40	-0.19	0.10	2.02	0.044	0.41
Population density	^b	^b				^b	^b			

Adult survival
(n = 227 animal-years,
87 individuals)

^a Reproduced from Vander Wal et al., 2014

^b Variable dropped during 'all-possible-model' selection

Table A1.S2. Model averaged results from the global model explaining the variation in different measures of fitness in bighorn sheep on Ram Mountain, Alberta. Models constructed with graph strength, see Table S1 for results using eigenvector centrality. We standardized all variable to their z-scores prior to analysis. Emboldened numbers report either $P < 0.05$ or relative variable importance values (AIC_w) = 1. Results are reported for networks that account for individual variation in gregariousness (HWI⁶) and those that report gregariousness-adjusted pairwise affinities (HWIG).

Fixed Effects	β	SE	z-value	P-value	AIC_w	R^2	HWI ⁶					HWIG															
							β	SE	z-value	P-value	AIC_w	R^2	β	SE	z-value	P-value	AIC_w	R^2									
Lamb production (n = 556 animal-years, 147 individuals)																											
Intercept	-0.88	0.32	2.73	0.006	NA		-0.88	0.24	3.61	<0.001	NA		-0.88	0.24	3.61	<0.001	NA										
Graph strength	0.50	0.18	2.71	0.007	1.00	0.19	0.61	0.17	3.64	<0.001	1.00	0.1	0.61	0.17	3.64	<0.001	1.00										
Social density	0.15	0.16	0.94	0.349	1.00		0.44	0.14	3.09	0.002	1.00		0.44	0.14	3.09	0.002	1.00										
Centrality*Social density	-0.55	0.23	2.38	0.017	1.00	0.45	^b																				
Mass	0.56	0.39	1.43	0.152	0.5		0.53	0.39	1.35	0.176	0.47	0.4	0.53	0.39	1.35	0.176	0.47										
Maternal effect	-0.77	0.16	4.77	<0.001	1.00		-0.76	0.18	4.24	<0.001	1.00		-0.76	0.18	4.24	<0.001	1.00										
Age	3.04	0.45	6.76	<0.001	1.00		3.01	0.44	6.81	<0.001	1.00		3.01	0.44	6.81	<0.001	1.00										
Age ²	-1.22	0.18	6.63	<0.001	1.00		-1.24	0.18	6.77	<0.001	1.00		-1.24	0.18	6.77	<0.001	1.00										
Population density	0.28	0.26	1.09	0.278	0.39		^c						^c														
Intercept	-0.45	0.57	0.79	0.432	NA		-0.18	0.44	0.40	0.690	NA		-0.18	0.44	0.40	0.690	NA										
Graph strength	^b	^b	^b	^b	^b		-0.41	0.25	1.66	0.098	0.58		-0.41	0.25	1.66	0.098	0.58										
Social density	^b	^b	^b	^b	^b		^b	^b	^b	^b	^b		^b	^b	^b	^b	^b										
Centrality*Social density	^b	^b	^b	^b	^b	0.19	^b	^b	^b	^b	^b	0.1	^b	^b	^b	^b	^b										
Mass	0.68	0.83	0.83	0.409	0.21		0.67	0.81	0.83	0.404	0.21	0.1	0.67	0.81	0.83	0.404	0.21										
Maternal effect	-0.45	0.22	2.00	0.046	0.83		-0.44	0.22	1.99	0.046	0.83	8	-0.44	0.22	1.99	0.046	0.83										
Age	0.26	0.34	0.77	0.442	0.15		0.25	0.34	0.73	0.468	0.15		0.25	0.34	0.73	0.468	0.15										
Age ²	0.19	0.18	1.09	0.277	0.20		0.67	0.81	0.83	0.404	0.21		0.67	0.81	0.83	0.404	0.21										
Population density	-0.49	0.30	1.64	0.100	0.58		^e	^e	^e	^e	^e		^e	^e	^e	^e	^e										
Intercept	1.12	0.33	3.37	0.001	NA		1.46	0.26	5.60	<0.001	NA		1.46	0.26	5.60	<0.001	NA										
Graph strength	1.19	0.26	4.57	<0.001	1.00		0.55	0.30	1.83	0.067	1.00		0.55	0.30	1.83	0.067	1.00										
Social density	-0.34	0.21	1.66	0.096	0.64		0.20	0.20	1.02	0.304	0.93		0.20	0.20	1.02	0.304	0.93										
Centrality*Social density	-0.41	0.20	1.99	0.046	0.64	0.29	-1.07	0.58	-1.82	0.068	0.77	0.1	-1.07	0.58	-1.82	0.068	0.77										
Mass	0.66	0.23	2.94	0.003	1.00		0.53	0.21	2.50	0.012	0.79	6	0.53	0.21	2.50	0.012	0.79										
Maternal effect	-0.40	0.14	2.76	0.006	1.00		-0.40	0.19	-2.06	0.038	0.82		-0.40	0.19	-2.06	0.038	0.82										
Age	^b	^b	^b	^b	^b		^b	^b	^b	^b	^b		^b	^b	^b	^b	^b										
Age ²	-0.25	0.06	3.94	<0.001	1.00		0.31	0.07	-4.07	<0.001	0.83		0.31	0.07	-4.07	<0.001	0.83										
Population density	-0.71	0.29	2.45	0.014	1.00		^c	^c	^c	^c	^c		^c	^c	^c	^c	^c										
Intercept	-3.78	0.75	5.05	<0.001	NA	0.61	-7.62	2.11	3.62	<0.001	NA		-7.62	2.11	3.62	<0.001	NA										

Lamb survival (n = 113)											
Graph strength	-0.83	0.64	1.31	0.191	0.76	-9.07	4.50	2.02	0.044	1.00	0.6
Social density	0.37	0.31	1.20	0.228	0.80	-1.63	0.98	1.68	0.094	1.00	1
Centrality*Social density	-0.30	0.48	0.63	0.529	0.09	-4.44	2.15	2.07	0.039	1.00	
Mass	2.49	0.46	5.38	<0.001	1.00	2.58	0.46	5.67	<0.001	1.00	
Age	-0.14	0.38	0.36	0.719	0.08	^b	^b				
Age ²	-0.05	0.10	0.46	0.647	0.08	^b	^b				
Population density	-0.66	0.42	1.57	0.116	0.44	-0.53	0.80	0.66	0.509	0.31	
Intercept	-1.59	0.59	2.69	0.007	NA	-1.34	0.56	2.40	0.016	NA	
Graph strength	0.48	0.40	1.22	0.222	0.35	-0.34	0.68	0.51	0.612	0.22	
Social density	0.30	0.30	0.98	0.327	0.04	0.30	0.30	0.98	0.327	0.05	
Centrality*Social density	^b	^b	^b	^b	^b	^b	^b	^b	^b	^b	
Mass	0.45	0.25	1.79	0.073	0.77	0.45	0.25	1.79	0.073	0.83	0.2
Maternal effect	-0.37	0.21	1.75	0.081	0.63	-0.36	0.21	1.74	0.082	0.68	4
Age	-0.18	0.58	0.31	0.753	0.29	-0.27	0.57	0.47	0.635	0.29	
Age ²	0.30	0.21	1.44	0.151	0.54	0.29	0.21	1.36	0.174	0.53	
Population density	-0.92	0.47	1.94	0.052	1.00	-0.78	0.43	1.81	0.070	0.83	
Intercept	1.96	0.47	4.15	<0.001	NA	4.84	1.91	2.53	0.011	NA	
Graph strength	0.50	0.42	1.19	0.235	0.80	7.64	4.34	1.76	0.078	1.00	
Social density	-0.77	0.63	1.22	0.223	0.83	-1.06	1.15	0.92	0.359	0.20	
Centrality*Social density	-0.89	0.48	1.86	0.063	0.57	-3.72	2.44	1.53	0.127	0.09	
Mass	1.02	0.64	1.59	0.111	0.49	0.76	0.54	1.42	0.156	0.24	0.5
Maternal effect	-0.31	0.22	1.40	0.162	1.00	-0.24	0.21	1.15	0.249	1.00	5
Age	-1.11	0.59	1.87	0.061	0.73	-0.7	0.41	1.68	0.094	0.75	
Age ²	-0.16	0.20	0.80	0.424	0.33	-0.19	0.11	1.80	0.073	0.33	
Population density	-0.53	0.41	1.30	0.193	0.23	-0.84	0.45	1.87	0.062	0.75	
Adult survival (n = 227 animal-years, 87 individuals)											

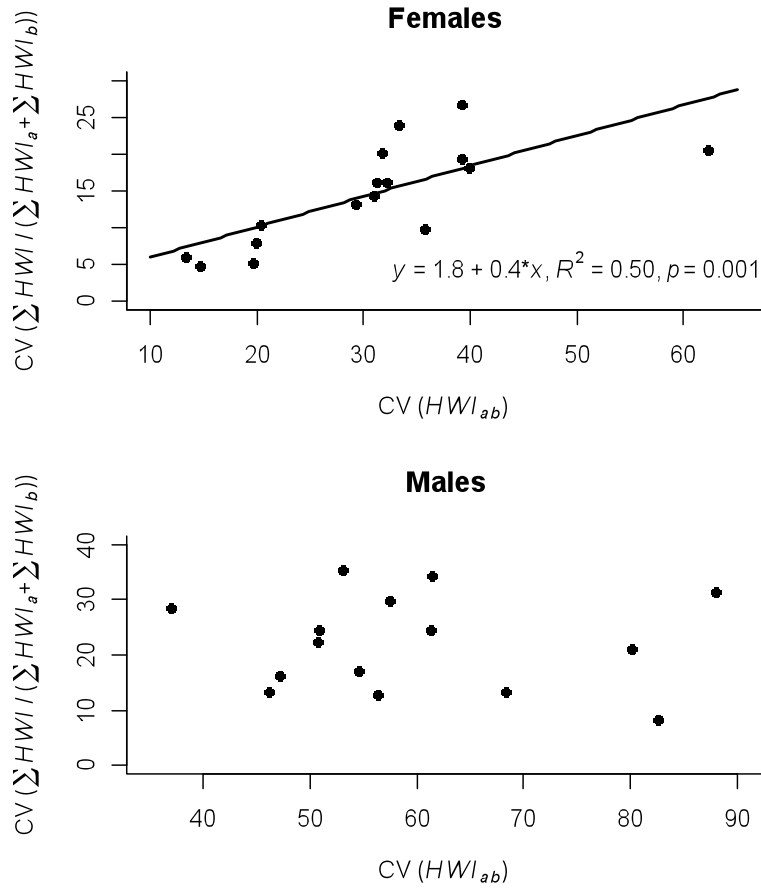


Figure A1.S1. A comparison of the annual coefficients of variation (CV) for dyadic values of the half-weight-index (HWI_{ab}) and the gregariousness adjustment (element 2 in equation [1] main text:) of the HWI_G derived using gambit-of-the-group data from a fission-fusion society of female (upper panel) and male (lower panel) bighorn sheep in Ram Mountain (AB, CAN) between 1996-2011. Variation in HWI_{ab} was typically larger than variation in . $CV(HWI_{ab})$ significantly explains variation in for females but not males.

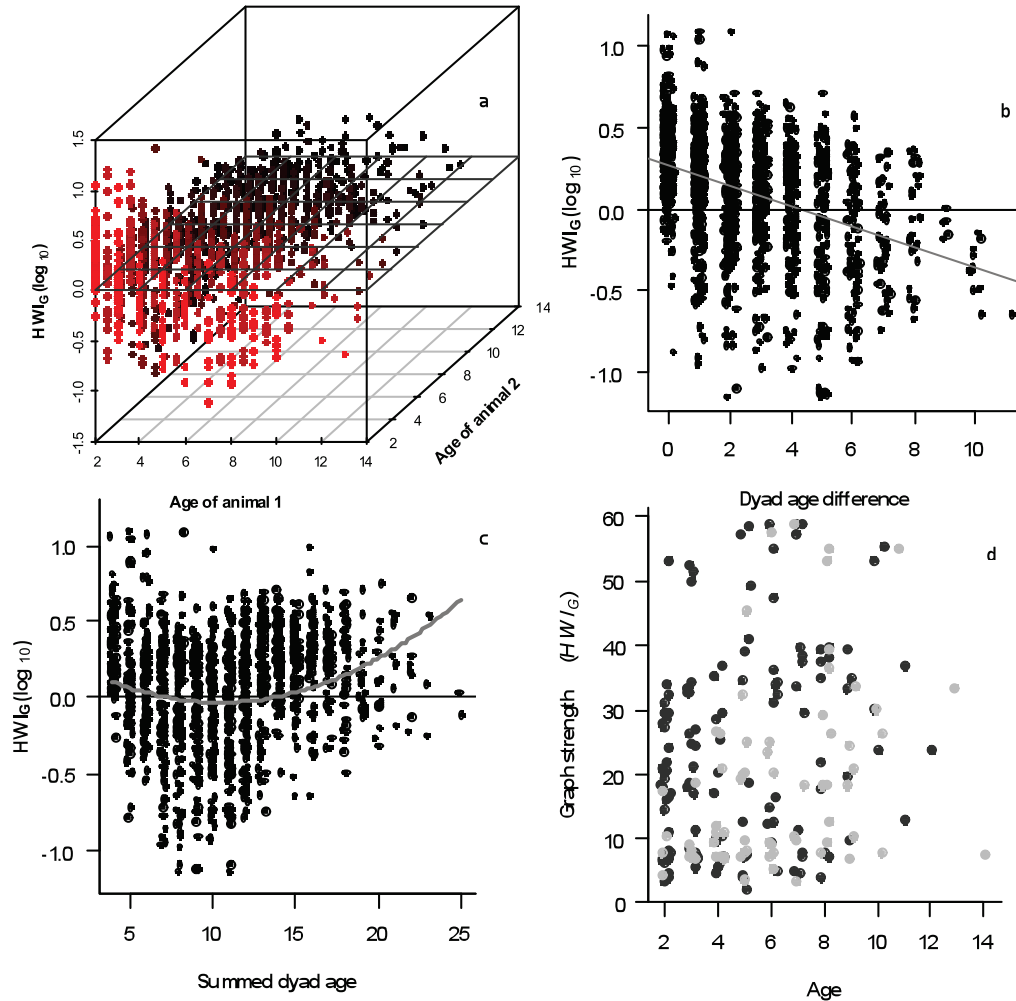


Figure A1.S2. A comparison gregariousness-adjusted half-weight-index (HWIG) values derived using gambit-of-the-group data from a fission-fusion society of male bighorn sheep in Ram Mountain (AB, CAN), 1996-2011. (a) \log_{10} transformed HWIG values as a function of each age of individual in the dyad. The lattice at $\log_{10}(\text{HWIG}) = 0$ corresponds to an HWIG value = 1 or random associations of members in the dyad. Values < 0 therefore indicate avoidance and values > 0 affinity between members of the dyad. Shading is added to provide depth, where darker points fall behind lighter points. Difference in animal age (b) explained 42% of the variation (R^2) in HWIG ($P < 0.01$) according to a mixed general linear model that

accounted for year as a random effect. The grey line indicates the trend from the regression. A first order polynomial spline in age (c, grey line) explained 32% of the variation in HWIG (age and age²: $P < 0.01$) while accounting for year as a random effect. The black lines (b and c) denote the transition from avoidance (below) to affinity (above). HWIG values were then translated into measures of graph strength from male-only networks (d). Dark grey points indicate individuals that failed to produce a lamb; whereas, light grey points indicate individuals that did produce a lamb at each age. Age did not explain a meaningful amount of variation in graph strength ($R^2 = 0.02$).

