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**FACTORES QUE ESTABLECEN LA DINÁMICA DE LOS SISTEMAS
SOCIALES: EFECTO DE LA PERSONALIDAD Y EL AMBIENTE**

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Factores que establecen la dinámica de los sistemas sociales:

efecto de la personalidad y el ambiente

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RESUMEN

En esta tesis se investigó la personalidad y su influencia en el establecimiento de relaciones interindividuales que definen la estructura social de los grupos. Nosotros usamos a *Porcellio scaber* (Isópoda) como modelo de estudio debido a que los individuos muestran personalidad y que presentan gregariedad social basada en preferencias individuales. En el capítulo I, se introduce el sistema de estudio con el cual esta tesis fue planteada. En esta sección se describen los conceptos utilizados y como es que se integran para construir el marco teórico. En el capítulo II, se exploró la relación entre personalidad, la responsividad social y los atributos que describen la sociabilidad antes y después de la exposición a un ambiente social. Se encontró que la personalidad y la responsividad social de los individuos tiene influencia sobre los atributos de sociabilidad. Además, se evidenció que la responsividad social se encuentra influenciada por los tipos de personalidad. También se mostró que el ambiente social determinado por el ensamble de personalidades establece las relaciones que se dan entre individuos. En el capítulo III, se examinó la consistencia de los nichos sociales basados en asociación e interacciones agonísticas, incluyendo estatus de dominancia, y su relación con la personalidad de los individuos utilizando la aproximación de la hipótesis de nicho social. Se evidenció consistencia en los roles sociales a nivel de individuo a través de diferentes entornos sociales. Asimismo, se mostró que la personalidad, en conjunto con otras conductas influenciadas socialmente, tienen influencia sobre los roles sociales y las relaciones interindividuales que definen el estatus de dominancia. En el capítulo IV, se indagó acerca de la influencia de las relaciones interindividuales entre personalidades y atributos intrínsecos de los individuos sobre la dinámica grupal a nivel asociaciones.

diádicas, comportamiento del grupo basado en modularidad y los atributos basados en la membresía de los individuos a los agregados. Se evidenció que el tiempo que los individuos gastan en un entorno social, el tamaño de los agregados y la personalidad influyen en la manera en que los individuos se agregan. Además, se encontró que el estado reproductivo y el sexo de los individuos determinan la membresía de los individuos a un agregado social en particular.

ABSTRACT

In this thesis, we presented a series of studies investigating personality and its influence on the establishment of interindividual relationships that define the social structure of groups. We use *Porcellio scaber* (Isopoda) as a study model because individuals show personality and social gregariousness based on individual preferences. In Chapter I, we introduce the study system with which this thesis was proposed. In this section we described the concepts used and how they are integrated to build the theoretical framework. In Chapter II, we explored the relationship between personality, social responsiveness, and attributes describing sociability before and after exposure to a social environment. We found that the personality and social responsiveness of individuals have an influence on the attributes of sociability. Also, we noted that social responsiveness is influenced by personality types, and that the social environment determined by the set of personalities determines in a certain way the relationships that occur between individuals. In Chapter III, we examined the consistency of association-based social roles and agonistic interactions, including dominance status, and their relationship to the personality of individuals using the social niche hypothesis approach. We evidenced consistency in social roles at the individual level across different social settings. We also showed that personality, in combination with other socially influenced behaviors, has an influence on the social roles and interindividual relationships that define dominance status. In Chapter IV, we investigated the influence of interindividual relationships between personalities and intrinsic attributes of individuals on group dynamics at the level of dyadic associations, group behavior based on modularity, and attributes based on individuals' membership in aggregates. We evidenced that the time individuals spend in a

social environment, aggregate size and personality influence the way individuals aggregate.

In addition, we found that the reproductive status and sex of individuals determine the membership of individuals to a particular social aggregate.

CAPÍTULO I

INTRODUCCIÓN GENERAL

INTRODUCCIÓN GENERAL

Un sistema social puede ser entendido como un conjunto de animales conespecíficos que cohabitan e interactúan regularmente en mayor medida entre ellos que con miembros de otras sociedades (Kappeler & Van Schaik, 2002; Whitehead, 2008). Esto implica que un sistema social se constituye de al menos dos componentes fundamentales (Kappeler & Van Schaik, 2002): la organización social, que describe el tamaño, proporción de sexos y cohesión espaciotemporal del sistema social; y la estructura social, que consiste en los patrones de interacción social y las relaciones resultantes entre miembros del sistema social. Este último puede ser caracterizado a partir de rasgos consistentes que surgen de las diferencias en la naturaleza de las interacciones o asociaciones entre individuos. En este sentido, Hinde (1976) propone un marco funcional que permite estudiar la estructura social como un proxy de las sociedades animales basándose en tres niveles jerárquicos, el cual es aplicable en diversos tipos de sistemas sociales que van desde sociedades complejas de insectos y primates (Aureli *et al.*, 2012; Brent *et al.*, 2011; Corradino, 1990; Kasper & Voelkl, 2009), hasta organismos con sociedades aparentemente más simples como roedores, peces e insectos coloniales (Kasper & Voelkl, 2009; Lihoreau *et al.*, 2012; Sunobe, 2000). Bajo el modelo de Hinde, el nivel fundamental se establece en base a las Interacciones que se entablan entre individuos (por simplicidad basado en diadas), entendiendo la interacción como la conducta de un individuo que está dirigido directamente hacia otro o afecta la conducta del otro. Un nivel intermedio se basa en las Relaciones que involucran las interacciones entre diadas que conforman un grupo, que incluyen el contenido, calidad y patrones de las interacciones con respecto a conductas específicas entre individuos en el tiempo. Finalmente, el nivel superior

corresponde a la Estructura social, que está definida por la generalización de la naturaleza, calidad y patrones de las relaciones sociales en una población (Whitehead, 2008). Una de las limitantes de este sistema es que las interacciones no siempre pueden ser observadas, por lo que una forma de sobrellevar esta limitante es utilizando Asociaciones interindividuales en lugar de interacciones. Una asociación puede ser entendida como una situación o estado en el que se suelen producir interacciones (Whitehead & Dufault, 1999).

Si bien a partir de este modelo se han realizado múltiples aproximaciones al estudio de los sistemas sociales, hasta ahora existen muy pocos trabajos que exploren los mecanismos involucrados en la diferenciación de interacciones entre individuos, y los posibles mecanismos o rasgos intrínsecos individuales que podrían explicar cómo se forma la estructura social, y cómo se mantiene su estabilidad. Uno de los factores intrínsecos de los individuos es la Personalidad Animal, que puede ser definida como las diferencias interindividuales en la expresión de conductas que manifiesta un individuo y que son consistentes en el tiempo y en diferentes contextos (Figura 1) (Dall *et al.*, 2004; Réale & Dingemanse, 2010). El grado de percepción y la capacidad de generar respuestas conductuales asociadas de cada individuo permiten que se erijan combinaciones únicas de rasgos conductuales que definen una personalidad propia (Réale & Dingemanse, 2010). En términos operacionales, la personalidad es comúnmente evidenciada mediante una alta repetibilidad de conductas, entre las que resaltan atrevimiento, agresividad, exploración, sociabilidad y neofobia (Réale *et al.*, 2007). En este sentido, la personalidad puede ser interpretada como un gradiente que incluye los valores cuantificados de un comportamiento en un grupo o población. Uno de los ejes claves de la personalidad animal es la variación del eje tímido-atrevido, el cual mide la capacidad exploratoria de los individuos (Wilson *et al.*,

1993). De esta forma, la personalidad podría ser uno de los mecanismos clave en la dinámica de interacciones que establecen la estructura social dentro de un grupo, y las relaciones entre grupos.

En este sentido, Bergmüller & Taborsky (2010) proponen el concepto de Nicho Social para explicar cómo el ambiente social (constituido en base a interacciones) conduce el mantenimiento de las diferencias en los tipos de personalidades y, en consecuencia, como los grupos resultantes quedan determinados por complementariedad de personalidades. De este modo, el ambiente social determina un ordenamiento de personalidades no aleatorio, que lleva a que los grupos se ordenen por personalidades complementarias, reduciendo conflictos entre individuos con rasgos de personalidad similares (Figura 2). Esto quiere decir, que un individuo se mantendrá como miembro de un grupo solo si adquiere un Rol Social diferenciado dentro del grupo, o si tiene la capacidad de ajustar su personalidad a las necesidades del grupo (Montiglio *et al.*, 2013; Wolf & Weissing, 2010).

En base a lo anterior, Wolf *et al.* (2011) proponen el concepto de Responsividad Social, entendido como la capacidad de ajustar las conductas en respuesta a la personalidad de los otros miembros del grupo (Figura 3). De esta forma, en base al nivel de responsividad social, los individuos pueden modificar la expresión de su personalidad en función del contexto social (Wolf & Krause, 2014). Por ejemplo, si un individuo presenta alta responsividad social podrá modular el nivel de coordinación en sus conductas y alcanzar un mayor grado de asociación con los miembros del grupo modulando su personalidad (McNamara & Leimar, 2010). Complementariamente, es conocido que el ambiente social influye fuertemente sobre el desempeño conductual de los individuos (Webster & Ward, 2011), ya sea por restricción de la expresión de las respuestas conductuales mediada por procesos de Conformidad

(Tendencia positivamente dependiente de la frecuencia a adoptar el comportamiento de la mayoría de sus compañeros de grupo - Efferson *et al.*, 2008), o también por estimulación o potenciación de dichas respuestas mediadas por procesos de Facilitación social (Tendencia a desempeñar conductas en una proporción diferente a la que lo harían estando aislados - Zajonc, 1965).

De esta forma, el establecimiento de relaciones y de vínculos sociales entre diferentes personalidades producen propiedades emergentes que definen la complejidad de los sistemas sociales en cada uno de sus componentes (estructura y organización sociales). Consecuentemente, la responsividad social de los individuos conllevará a dinámicas de formación y estabilidad de grupos que serán caracterizadas en última instancia por el tamaño de grupo, la fidelidad de los miembros y la tasa de intercambio de individuos entre grupos (Croft *et al.*, 2003; Hoare *et al.*, 2004; Ward *et al.*, 2002; Webster & Ward, 2011).

Otro aspecto que repercute en la dinámica y mantenimiento de grupos es el efecto de los cambios en las condiciones ambientales. Esto ocurre debido a que los atributos del ambiente no solo influyen en las respuestas conductuales de los individuos, sino también modifican los procesos derivados de las interacciones ecológicas que se dan entre los miembros de las poblaciones (Dingemanse & Wolf, 2013; Krause & Ruxton, 2002; Whitehead, 2008). De esta forma, los factores condicionales pueden afectar o modificar el tipo de interacciones que se manifiestan entre individuos, repercutiendo sobre el cambio o la estabilidad de la estructura social. Por ejemplo, las condiciones ambientales pueden modificar el nivel de gregariedad por medio de la alteración en los niveles de depredación. Otro ejemplo es el nivel de inversión de energía en la búsqueda y defensa de recursos, donde el oportunismo o la cooperación que

muestren los individuos dependerá de la disponibilidad de tales recursos (Dosmann & Mateo, 2014; Henzi *et al.*, 2009).

Pese a que existe evidencia de que la personalidad afecta las interacciones interindividuales en los grupos, determinando la estructura social e influenciando la propensión a tomar roles sociales específicos (Wolf & Krause, 2014), y que el contexto social tiene efectos cualitativos y cuantitativos sobre la expresión de rasgos de personalidad en los individuos (Webster & Ward, 2011), aún no se ha analizado en forma integral como la personalidad puede ser un forzante sobre la estructuración y organización social. En este sentido, la personalidad y su responsividad social debe abarcar las interacciones interindividuales que definen las conductas afiliativas al interior de los grupos, las dinámicas de conformación y mantenimiento de grupos, y el efecto de las condiciones ambientales sobre las dinámicas sociales de los individuos. La importancia de generar conocimiento acerca de cómo los individuos responden al ambiente social en función de su personalidad radica en la posibilidad de poder generalizar aspectos poblacionales a partir atributos individuales fácilmente cuantificables. Desde un punto de vista aplicado, considerar las interacciones sociales dependientes de los patrones de personalidad en un contexto de reintroducción o cautiverio puede permitir mejoras en los planes de conservación de animales sociales (Aureli *et al.*, 2008; Herbert-Read, 2017; Westneat *et al.*, 2011).

En este contexto, el presente trabajo busca determinar cómo influye la personalidad sobre la estructuración social a través de diferentes contextos sociales. En el segundo capítulo, se explora sobre la dinámica social al interior de los grupos basándose en atributos de personalidad y responsividad social. En esta etapa se estudia acerca de los patrones de asociación entre diferentes tipos de personalidades y si estos ocurren de manera no aleatoria.

En el tercer capítulo, se evalúa la consistencia de los roles sociales basados en atributos de asociación y agresión con la intención de conocer si existen evidencias que sugieran una especialización de nicho social. Esto se realizó con la finalidad de comprender si las respuestas conductuales y los patrones sociales son consistentes cuando las condiciones ambientales cambian. Además, se investigó la relación entre los roles sociales y la personalidad de los individuos. En el cuarto capítulo se describe la dinámica de agregación social haciendo uso de tres métricas que definen la intensidad y la identidad de las asociaciones, estas son el índice de asociación diádico, la modularidad y la identificación de clusters como proxy de membresía local. En este capítulo se busca comprender como la personalidad, la espacio temporalidad de los eventos de asociación y los atributos individuales influyen en la dinámica de agregación. Finalmente, en el quinto capítulo se realiza una discusión general. Además, se especifican limitantes y desafíos en la conducción de la tesis.

APROXIMACION UTILIZADA EN EL ESTUDIO

El análisis de redes sociales es una herramienta comúnmente usas para investigar las causas y consecuencias de interacciones sociales y ecológicas complejas en comunidades animales (Farine & Whitehead, 2015). Este provee un sistema flexible, basado en datos de asociación e interacción, para responder preguntas biológicas que consideren aspectos de afiliación social, sistemas reproductivos, relaciones genéticas y vínculos a nivel comunitario (Croft *et al.*, 2008; Lusseau, 2003; Olesen *et al.*, 2008). La potencialidad del análisis de redes sociales radica en que permite un entendimiento de como los procesos locales conducen las propiedades a diferentes escalas de organización a través de un enfoque individual (Aplin *et al.*, 2013; Jacoby *et al.*, 2014; Strandburg-Peshkin *et al.*, 2013). En términos de redes

sociales, los individuos están representados por nodos y la calidad de las interacciones por los enlaces. Cada nodo tiene una serie de propiedades que lo caracteriza dentro de una red social en función de la calidad y cantidad de enlaces con los que cuenta, estas características pueden ser descritas a partir de las métricas de redes. Comúnmente, las métricas de redes se definen como una medida ponderada o binaria. Por ejemplo, las métricas nodelas más utilizadas son el grado y la fuerza, cuales son la suma del numero de enlaces que cada nodo tiene o de todos los enlaces ponderados conectados a este, respectivamente. Asimismo, el promedio o distribución de estas medidas puede ser usado para describir propiedad globales de red social, como por ejemplo la distribución del grado de todos los nodos que hacen parte de la red (Farine & Whitehead, 2015).

En este sentido, las métricas de redes permiten diferenciar a los individuos y su ubicación dentro de una red social. Los estudios en sociedades animales suelen utilizar métricas basadas en centralidad para identificar a aquellos individuos quienes están conectados en mayor medida que los otros (Newman, 2018). Debido a que las métricas de centralidad permiten caracterizar la capacidad de asociación e interacción de los nodos, estas suelen ser utilizadas para caracterizar la sociabilidad de los individuos teniendo en consideración el entorno social en que los individuos están inmersos (Aplin *et al.*, 2013; Croft *et al.*, 2008; Lusseau, 2003).

Bajo la misma lógica, en esta tesis se propone el uso de las métricas globales de redes para describir los atributos de organización social de los grupos bajo el enfoque de redes sociales, contribuyendo en sumar nuevos atributos que sean útiles en la descripción de las sociedades animales más allá de las métricas tradicionales, como el tamaño de grupo. Entre estas métricas globales se propone el uso de la densidad, la assortatividad, la transitividad y la modularidad para describir los atributos de la organización social.

MODELO DE ESTUDIO

El modelo de estudio de este trabajo es *Porcellio scaber*. Son crustáceos que pertenecen al orden Isópoda, al suborden Oniscidea, y a la familia Porcellionidae (Schmalfuss, 2003). Estos organismos, principalmente detritívoros, se alimentan de hojarasca, madera descompuesta, hongos y bacterias. Estos tienen gran importancia en los procesos de descomposición y participan activamente en la dispersión de microbiota por medio de la evacuación de pellets fecales (Zimmer & Zimmer, 2002). Esta especie es comúnmente utilizada como modelo de estudio para investigar respuestas conductuales a estímulos ambientales, como la sensibilidad de los individuos a ambientes novedosos o la actividad exploratoria a nivel grupal en Oniscideos (Anselme, 2013, 2015; Pálková, 2013). Otros trabajos han explorado la respuesta individual a gradientes de humedad (Gunn, 1937), de recurso alimenticio (Hassall *et al.*, 2002) y de temperatura (Lardies *et al.*, 2004).

Con respecto al eje central de este estudio, existe un trabajo que comprueba la consistencia de conductas a nivel individual en *Porcellio scaber* mediante la evaluación de respuestas conductuales antidepredatorias tales como reactividad, sensibilidad y duración de la inmovilidad tónica (Tuf *et al.*, 2015). Adicionalmente, se ha logrado evidenciar que las condiciones ambientales modifican los patrones de agrupamiento y aspectos de sociabilidad en este grupo (Devigne *et al.*, 2011). En función de esto, se ha podido observar el surgimiento de propiedades sociales emergentes producto de la agregación de individuos de *Porcellio scaber*, como por ejemplo la ocurrencia de conductas de autoorganización (Broly *et al.*, 2012, 2013, 2014, 2016; Broly & Devigne, 2011).

En Chile, *Porcellio scaber* es una especie introducida asociada a ambientes intervenidos por el hombre y es común encontrarla en jardines, campos de cultivo y hasta en el interior de estructuras edificadas. Los individuos de esta especie pueden ser identificados porque presentan una superficie dorsal granulada, a diferencia de *Porcellio laevis* que presentan un dorso liso, un margen posterior cóncavo a los lados en el primer pereionito y ángulos posterolaterales agudos en las coxas 2-3 (Pérez-Schultheiss, 2010).

HIPÓTESIS

HIPÓTESIS GENERAL

La personalidad por medio de la responsividad social influye directamente sobre la estructura social y la dinámica de los sistemas sociales, por lo que los atributos sociales de los individuos estarán limitados por la personalidad y aspectos relacionados a rasgos de historia de vida de la especie.

HIPÓTESIS ESPECÍFICAS

1. El agrupamiento no aleatorio de personalidades y la estructura social resultante se dan a través de dos procesos sociales no excluyentes que dependen de la responsividad social: complementariedad basada en procesos de facilitación social y similitud de personalidades por conformidad.
2. Los roles sociales están modulados por la personalidad y la capacidad de competencia de los individuos. Por lo que la posición y características de los individuos dentro de los grupos es consistente a través de diferentes contextos sociales estableciendo nichos sociales.
3. Las relaciones interindividuales entre personalidades y atributos intrínsecos tales como el sexo y el estado reproductivo conducen la dinámica de los grupos, de modo que la intensidad de las asociaciones diádicas, el grado de modularidad en los grupos y la composición de agregados variaran en función del tiempo y del ensamble de personalidades.

PREDICCIONES

1. Se espera que individuos asociados a personalidades con bajo nivel de exploración y alto nivel de neofobia tiendan a asociarse por similitud de personalidades a través de un proceso de conformidad, y en el lado opuesto del eje, aquellos individuos que presenten personalidades con alto nivel de exploración y bajo nivel de neofobia buscarán complementariedad en los grupos ajustando sus conductas a través de procesos de facilitación social. Por otro lado, se espera que personalidades tímidas presenten mayor fuerza de asociación en relación con personalidades atrevidas. Con respecto a la responsividad social, se espera que esta sea acotada a los niveles de expresión de conductas asociados a cada tipo de personalidad sin importar el ambiente social, es decir que individuos tímidos siempre sean tímidos e individuos atrevidos siempre sean atrevidos. En consecuencia, es esperado que los roles sociales (nicho social realizado) estén relacionados directamente con los tipos de personalidades.

2. Se espera que los roles sociales y los patrones de agrupamiento se mantengan en el tiempo y a través de los contextos sociales. Adicionalmente, la labor de relacionar los grupos o limitar el acceso a recursos mediante eventos de interacción agonística debería darse como una función de roles sociales específicos relacionados a personalidades más atrevidas (alto nivel de exploración y bajo nivel de neofobia).

3. Las preferencias individuales y la transmisión de información modulan la ubicación de los agregados sociales, mientras que las dinámicas de agregación y la toma de decisiones

colectivas con respecto al grupo están controladas por la personalidad y la habilidad de los individuos para expresar conductas desencadenantes en otros individuos. Además, la cohesión grupal está gobernada por conductas amplificadas por la facilitación social, la cual depende de la densidad de individuos y el tiempo que estos gastan en el grupo.

OBJETIVOS

OBJETIVO PRINCIPAL

Determinar cómo influye la personalidad mediada por la responsividad social sobre la estructuración y dinámica social a través de diferentes contextos.

OBJETIVOS ESPECÍFICOS

1. Determinar los procesos sociales basados en la personalidad que influyen en la estructuración de grupos.
2. Evaluar la consistencia de los roles sociales basados en asociación e interacciones agonísticas y su relación con la personalidad.
3. Evaluar la influencia de la personalidad y atributos intrínsecos en la dinámica de los grupos.

LITERATURA CITADA

Anselme, P. (2013). Sensitivity to tactile novelty in the terrestrial isopod, *Porcellio scaber*.

Behavioural Processes, 92, 52–59. <https://doi.org/10.1016/j.beproc.2012.10.007>

Anselme, P. (2015). Enhanced exploratory activity in woodlice exposed to random visuo-

tactile patterns. Learning and Motivation, 50, 48–58.

<https://doi.org/10.1016/j.lmot.2014.09.002>

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cole, E. F., Cockburn, A., & Sheldon, B. C.

(2013). Individual personalities predict social behaviour in wild networks of great tits

(*Parus major*). Ecology Letters, 16(11), 1365–1372.

<https://doi.org/10.1111/ele.12181>

Aureli, F., Fraser, O. N., Schaffner, C. M., & Schino, G. (2012). The regulation of Social

Relationships. In J. Cary. Mitani, Josep. Call, P. M. Kappeler, R. A. Palombit, & J.

B. Silk (Eds.), The evolution of primate societies. The University of Chicago Press.

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor,

R., Fiore, A. D., Dunbar, R. I. M., Henzi, S. P., Holekamp, K., Korstjens, A. H.,

Layton, R., Lee, P., Lehmann, J., Manson, J. H., Ramos-Fernandez, G., Strier, K. B.,

& Schaik, C. P. van. (2008). Fission-Fusion Dynamics. Current Anthropology, 49(4),

627–654. <https://doi.org/10.1086/586708>

Bergmüller, R., & Taborsky, M. (2010). Animal personality due to social niche

specialisation. Trends in Ecology and Evolution, 25(9), 504–511.

<https://doi.org/10.1016/j.tree.2010.06.012>

Brent, L. J. N., Lehmann, J., & Ramos-Fernández, G. (2011). Social network analysis in the study of nonhuman primates: A historical perspective. *American Journal of Primatology*, 73(8), 720–730. <https://doi.org/10.1002/ajp.20949>

Broly, P., Deneubourg, J. L., & Devigne, C. (2013). Benefits of aggregation in woodlice: A factor in the terrestrialization process? *Insectes Sociaux*, 60(4), 419–435. <https://doi.org/10.1007/s00040-013-0313-7>

Broly, P., & Devigne, C. (2011). Aggregation in woodlice: Analysis of social component of the process. June 2011.

Broly, P., Devigne, L., Deneubourg, J.-L., & Devigne, C. (2014). Effects of group size on aggregation against desiccation in woodlice (Isopoda: Oniscidea). *Physiological Entomology*, 39(2), 165–171. <https://doi.org/10.1111/phen.12060>

Broly, P., Mullier, R., Deneubourg, J. L., & Devigne, C. (2012). Aggregation in woodlice: Social interaction and density effects. *ZooKeys*, 176(SPECIAL ISSUE), 133–144. <https://doi.org/10.3897/zookeys.176.2258>

Broly, P., Mullier, R., Devigne, C., & Deneubourg, J.-L. (2016). Evidence of self-organization in a gregarious land-dwelling crustacean (Isopoda: Oniscidea). *Animal Cognition*, 19(1), 181–192. <https://doi.org/10.1007/s10071-015-0925-6>

Corradino, C. (1990). Proximity structure in a captive colony of Japanese monkeys (*Macaca fuscata fuscata*): An application of multidimensional scaling. *Primates*, 31(3), 351–362. <https://doi.org/10.1007/BF02381106>

- Croft, D. P., Arrowsmith, B. J., Bielby, J., Skinner, K., White, E., Couzin, I. D., Magurran, A. E., Ramnarine, I., & Krause, J. (2003). Mechanisms underlying shoal composition in the Trinidadian guppy, *Poecilia reticulata*. *Oikos*, 100(3), 429–438. <https://doi.org/10.1034/j.1600-0706.2003.12023.x>
- Croft, D. P., James, R., & Krause, J. (2008). Exploring animal social networks. Princeton University Press. <https://www.jstor.org/stable/j.ctt7sfqv>
- Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters*, 7(8), 734–739. <https://doi.org/10.1111/j.1461-0248.2004.00618.x>
- Devigne, C., Broly, P., & Deneubourg, J. L. (2011). Individual preferences and social interactions determine the aggregation of woodlice. *PLoS ONE*, 6(2), e17389. <https://doi.org/10.1371/journal.pone.0017389>
- Dingemanse, N. J., & Wolf, M. (2013). Between-individual differences in behavioural plasticity within populations: Causes and consequences. *Animal Behaviour*, 85(5), 1031–1039. <https://doi.org/10.1016/j.anbehav.2012.12.032>
- Dosmann, A., & Mateo, J. M. (2014). Food, sex and predators: Animal personality persists with multidimensional plasticity across complex environments. *Animal Behaviour*, 90, 109–116. <https://doi.org/10.1016/j.anbehav.2014.01.011>
- Efferson, C., Lalive, R., Richerson, P. J., McElreath, R., & Lubell, M. (2008). Conformists and mavericks: The empirics of frequency-dependent cultural transmission.

Evolution and Human Behavior, 29(1), 56–64.

<https://doi.org/10.1016/j.evolhumbehav.2007.08.003>

Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology*, 84(5), 1144–1163.

<https://doi.org/10.1111/1365-2656.12418>

Gunn, D. L. (1937). The Humidity Reactions of the Woodlouse, *Porcellio scaber* (Latreille).

Journal of Experimental Biology, 14(2), 178–186.

Hassall, M., Tuck, J. M., Smith, D. W., Gilroy, J. J., & Addison, R. K. (2002). Effects of spatial heterogeneity on feeding behaviour of *Porcellio scaber* (Isopoda: Oniscidea).

European Journal of Soil Biology, 38(1), 53–57. [https://doi.org/10.1016/S1164-5563\(01\)01124-4](https://doi.org/10.1016/S1164-5563(01)01124-4)

Henzi, S. P., Lusseau, D., Weingrill, T., Van Schaik, C. P., & Barrett, L. (2009). Cyclicity in

the structure of female baboon social networks. *Behavioral Ecology and*

Sociobiology, 63(7), 1015–1021. <https://doi.org/10.1007/s00265-009-0720-y>

Herbert-Read, J. E. (2017). Social Behaviour: The Personalities of Groups. *Current Biology*,

27(18), R1015–R1017. <https://doi.org/10.1016/j.cub.2017.07.042>

Hinde, R. A. (1976). Interactions, Relationships and Social Structure. *Man*, 11(1), 1–17.

<https://doi.org/10.2307/2800384>

Hoare, D. J., Couzin, I. D., Godin, J.-G. J., & Krause, J. (2004). Context-dependent group

size choice in fish. *Animal Behaviour*, 67(1), 155–164.

<https://doi.org/10.1016/J.ANBEHAV.2003.04.004>

Jacoby, D. M. P., Fear, L. N., Sims, D. W., & Croft, D. P. (2014). Shark personalities? Repeatability of social network traits in a widely distributed predatory fish. *Behavioral Ecology and Sociobiology*, 68(12), 1995–2003.
<https://doi.org/10.1007/s00265-014-1805-9>

Kappeler, P. M., & Van Schaik, C. P. (2002). Evolution of primate social systems. *International Journal of Primatology*, 23(4), 707–740.
<https://doi.org/10.1023/A:1015520830318>

Kasper, C., & Voelkl, B. (2009). A social network analysis of primate groups. *Primates*, 50(4), 343–356. <https://doi.org/10.1007/s10329-009-0153-2>

Krause, J., & Ruxton, G. D. (2002). Living in groups. Oxford University Press.
https://books.google.pt/books?id=HAoUFFfVFtMcC&dq=Krause,+J.+%26+Ruxton,+G.D.+2002.+Living+in+Groups.+Oxford:+Oxford+University+Press.&lr=&hl=es&source=gbs_navlinks_s

Lardies, M. a, Bacigalupe, L. D., & Bozinovic, F. (2004). Testing the metabolic cold adaption hypothesis: An intraspecific latitudinal comparison in the common woodlouse. *Evolutionary Ecology Research*, 6(May), 567–578. <https://doi.org/10.1139/Z04-033>

Lihoreau, M., Costa, J. T., & Rivault, C. (2012). The social biology of domiciliary cockroaches: Colony structure, kin recognition and collective decisions. *Insectes Sociaux*, 59(4), 445–452. <https://doi.org/10.1007/s00040-012-0234-x>

Lusseau, D. (2003). The emergent properties of a dolphin social network. Proceedings of the Royal Society B: Biological Sciences, 270(Suppl_2), S186–S188.
<https://doi.org/10.1098/rsbl.2003.0057>

McNamara, J. M., & Leimar, O. (2010). Variation and the response to variation as a basis for successful cooperation. Philosophical Transactions of the Royal Society B: Biological Sciences, 365(1553), 2627–2633. <https://doi.org/10.1098/rstb.2010.0159>

Montiglio, P. O., Ferrari, C., & Réale, D. (2013). Social niche specialization under constraints: Personality, social interactions and environmental heterogeneity. Philosophical Transactions of the Royal Society B: Biological Sciences, 368(1618), 20120343. <https://doi.org/10.1098/rstb.2012.0343>

Newman, M. (2018). Networks (Vol. 1). Oxford University Press.
<https://doi.org/10.1093/oso/9780198805090.001.0001>

Olesen, J. M., Bascompte, J., Elberling, H., & Jordano, P. (2008). Temporal Dynamics in a Pollination Network. Ecology, 89(6), 1573–1582. <https://doi.org/10.1890/07-0451.1>

Pálková, R. (2013). Space activity and sheltering behaviour of terrestrial isopods. Palacký University in Olomouc.

Pérez-Schultheiss, J. (2010). FAMILIAS DE ISÓPODOS TERRESTRES (CRUSTACEA: ISOPODA: ONISCIDEA) DE CHILE: SINOPSIS Y CLAVE DE IDENTIFICACIÓN. BOLETÍN DE BIODIVERSIDAD DE CHILE, 4, 63–82.

Réale, D., & Dingemanse, N. J. (2010). Personality and individual social specialisation. In T. Székely, A. J. Moore, & J. Komdeur (Eds.), *Social Behaviour* (pp. 417–441). Cambridge University Press. <https://doi.org/10.1017/CBO9780511781360.033>

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2), 291–318. <https://doi.org/10.1111/j.1469-185X.2007.00010.x>

Schmalfuss, H. (2003). World catalog of terrestrial isopods (Isopoda: Oniscidea). Stuttgart. Beitr. Naturk. Ser. A. (Biol.), 654, 1–341. <https://doi.org/63648>

Strandburg-Peshkin, A., Twomey, C. R., Bode, N. W. F., Kao, A. B., Katz, Y., Ioannou, C. C., Rosenthal, S. B., Torney, C. J., Wu, H. S., Levin, S. A., & Couzin, I. D. (2013). Visual sensory networks and effective information transfer in animal groups. *Current Biology*, 23(17). <https://doi.org/10.1016/j.cub.2013.07.059>

Sunobe, T. (2000). Social Structure, Nest Guarding and Interspecific Relationships of the Cichlid Fish (*Julidochromis marlieri*) in Lake Tanganyika. *Afr. Study Monogr.*, 21.

Tuf, I. H., Drábková, L., & Šipoš, J. (2015). Personality affects defensive behaviour of *Porcellio scaber* (Isopoda, Oniscidea). *ZooKeys*, 2015(515), 159–171. <https://doi.org/10.3897/zookeys.515.9429>

Ward, A. J. W., Botham, M. S., Hoare, D. J., James, R., Broom, M., Godin, J.-G. J., & Krause, J. (2002). Association patterns and shoal fidelity in the three-spined stickleback. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269(1508), 2451–2455. <https://doi.org/10.1098/rspb.2002.2169>

Webster, M. M., & Ward, A. J. W. (2011). Personality and social context. *Biological Reviews*, 86(4), 759–773. <https://doi.org/10.1111/j.1469-185X.2010.00169.x>

Westneat, D. F., Hatch, M. I., Wetzel, D. P., & Ensminger, A. L. (2011). Individual Variation in Parental Care Reaction Norms: Integration of Personality and Plasticity. *The American Naturalist*, 178(5), 652–667. <https://doi.org/10.1086/662173>

Whitehead, H., & Dufault, S. (1999). Techniques for analysing vertebrate social structure using identified individuals: Review and recommendations. *Advances in the Study of Behavior*, 28, 33–74.

Whitehead, Hal. (2008). *Analyzing Animal Societies: Quantitative Methods For*. University of Chicago Press.

Wilson, D. S., Coleman, K., Clark, A. B., & Biederman, L. (1993). Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): An ecological study of a psychological trait. *Journal of Comparative Psychology*, 107, 250–260. <https://doi.org/10.1037/0735-7036.107.3.250>

Wolf, M., Doorn, G. S. V., Weissing, F. J., Van Doorn, G. S., & Weissing, F. J. (2011). On the coevolution of social responsiveness and behavioural consistency. *Proceedings of the Royal Society B: Biological Sciences*, 278(1704), 440–448. <https://doi.org/10.1098/rspb.2010.1051>

Wolf, M., & Krause, J. (2014). Why personality differences matter for social functioning and social structure. *Trends in Ecology and Evolution*, 29(6), 306–308. <https://doi.org/10.1016/j.tree.2014.03.008>

Wolf, M., & Weissing, F. J. (2010). An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 3959–3968. <https://doi.org/10.1098/rstb.2010.0215>

Zajonc, R. B. (1965). Social Facilitation. *Science*, 149(3681), 269–274. <https://doi.org/10.1126/science.149.3681.269>

Zimmer, M., & Zimmer, M. (2002). Nutrition in terrestrial isopods (Isopoda: Oniscidea): An evolutionary-ecological approach. 455–493.

FIGURAS

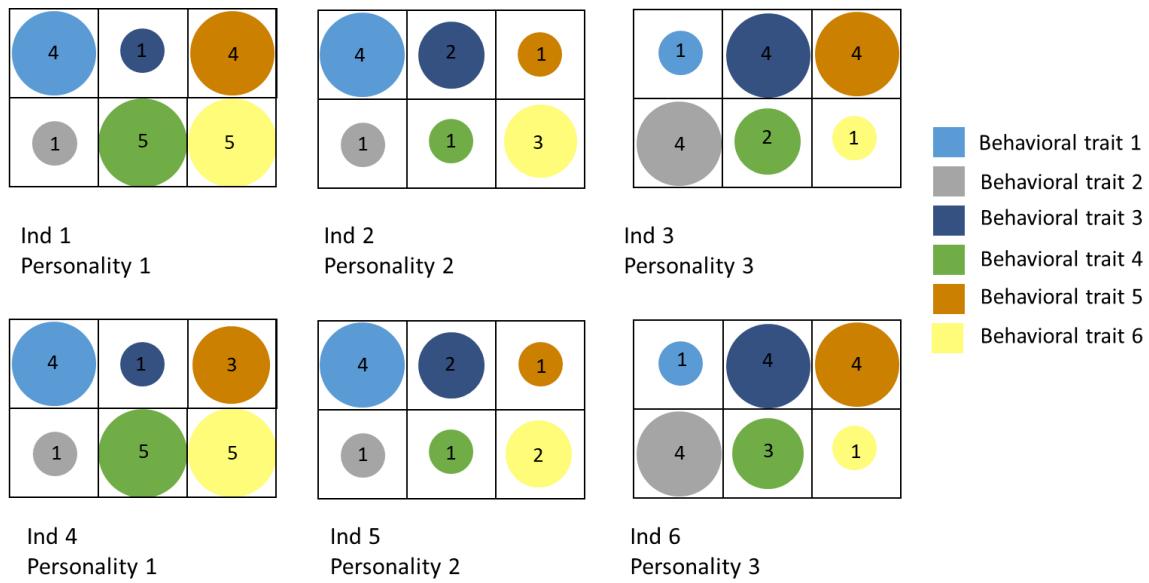


Figure 1. Representación de la personalidad Animal. Cada individuo expresa consistentemente una combinación de rasgos conductuales que definen su personalidad.
Basado en el trabajo de Dall *et al.* 2004.

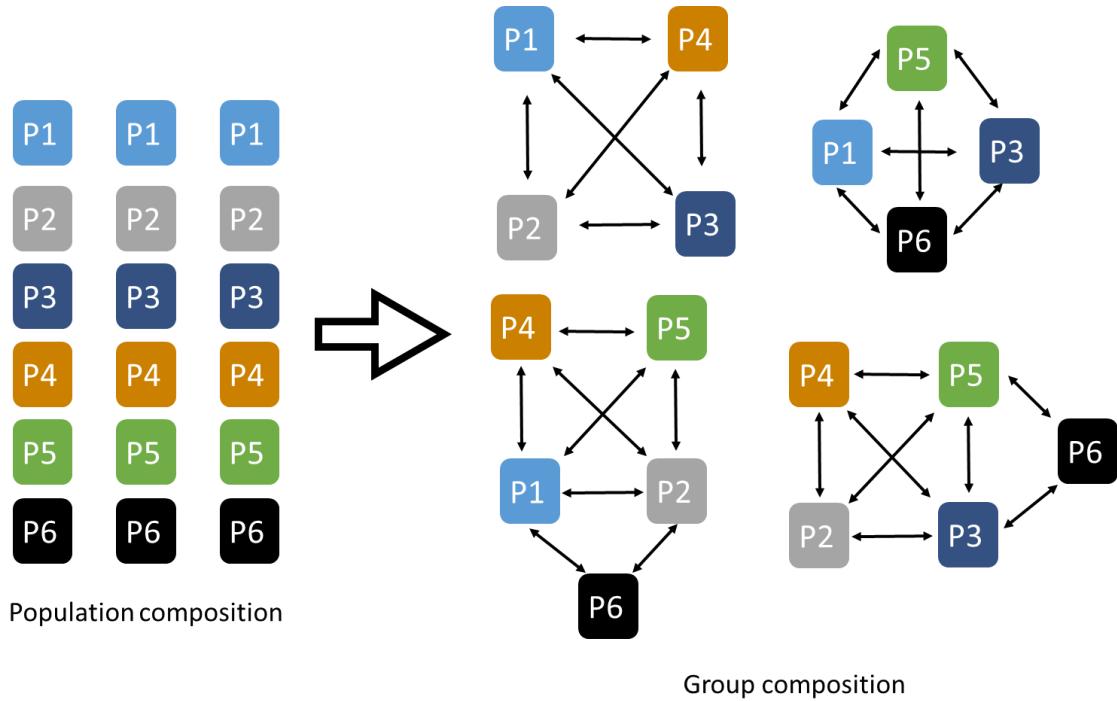


Figure 2. Representación de la hipótesis de ordenamiento no aleatorio de personalidades. Los grupos se ordenarán por personalidades complementarias, evitando conflictos entre individuos con rasgos de personalidad similares. Basado en el trabajo de Wolf & Weissing, 2010.

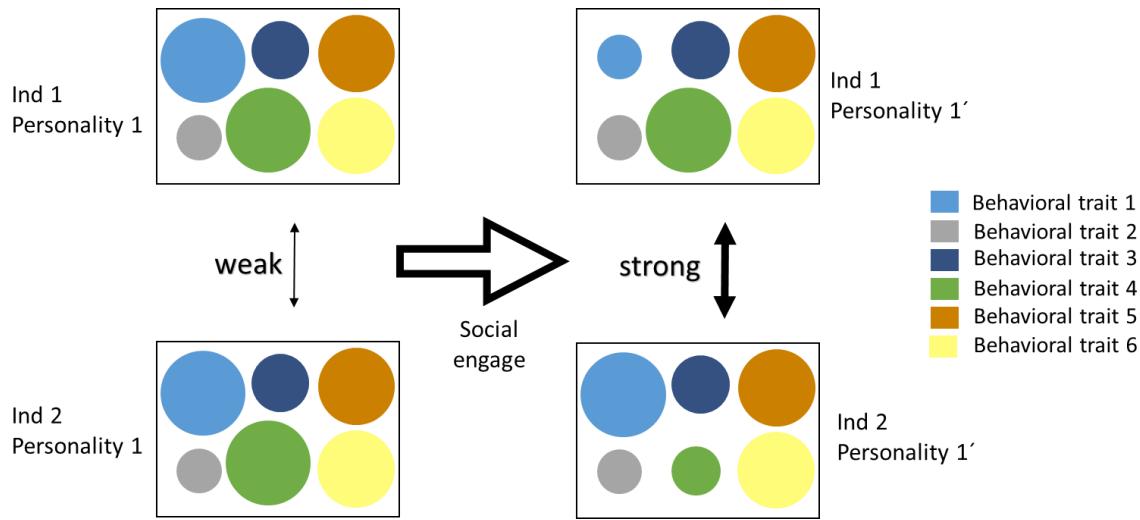


Figure 3. Representación de la responsividad social. La responsividad social señala que los individuos pueden modificar la expresión de su personalidad en función del contexto social.

Basado en el trabajo de Wolf & Krause, 2014.

CAPÍTULO II

PERSONALITY AND SOCIAL CONTEXT: WHO LEADS WHOM? A case study with terrestrial isopod *Porcellio scaber*

J. Romero-Herrada, M. Soto-Gamboa

Manuscrito sometido a Animal Behaviour

ABSTRACT

Animal personality is defined as interindividual differences in the expression of behaviors that are consistent over time and in different contexts. In a social environment, it is possible to observe that individuals interact differently among themselves, establishing asymmetrical relationships characteristic of the set of individuals and types of personalities that make up the groups. Therefore, the social environment influences behavioral performance through social processes such as conformity and facilitation, while personality can drive the nature, frequency, and intensity of interindividual interactions as a function of their social behavioral responsiveness. In this paper, we explore the relationship between personality and social environment, and their effect on individuals' social attributes using social network analysis in the terrestrial isopod *Porcellio scaber*. We find that the personality and social responsiveness of individuals influence their sociability attributes based on aggregation processes. We also show that social responsiveness, and thus the social processes that define behavioral reactivity, are driven by personality types. Finally, we show that the social environment, determined by the set of personalities, modulates the associational relationships between individuals. Our results demonstrate that both personality and social environment modulate social aggregation and behavioral performance in *Porcellio scaber*.

INTRODUCTION

Animal personality is commonly defined as the inter-individual differences in the expression of behaviors that are temporally and contextually consistent (Dall *et al.*, 2004; Dingemanse *et al.*, 2010). Under this definition, this concept has been described in several taxa, including invertebrates (Amat *et al.*, 2018; Briffa *et al.*, 2013; Mather & Logue, 2013; Modlmeier *et al.*, 2015), fishes (Conrad *et al.*, 2011; Croft *et al.*, 2009; Magnhagen & Bunnefeld, 2009; Webster *et al.*, 2007), amphibians (Kelleher *et al.*, 2018; Koenig & Oosterhout, 2018), reptiles (Cote & Clobert, 2007; Horváth *et al.*, 2017; Waters *et al.*, 2017), avians (Groothuis & Carere, 2005; Van Oers & Naguib, 2013), and mammals (Boon *et al.*, 2007; Eccard & Rödel, 2011; Frick *et al.*, 2017; Gosling, 2001). Inter-individual differences in behavior are consistently under different contexts, including habitat use, predation threat, social interactions, and neophobia (Réale *et al.*, 2007), and used as a phenotypic trait (Dingemanse & Réale, 2005; Sih *et al.*, 2004; Sih & Bell, 2008).

In a social context, it is possible to perceive that some individuals tend to interact constantly to extent than other members of the group, either by performing cooperation, aggression, or maintaining their social position without apparent conflicts (Favati *et al.*, 2013; McNamara & Leimar, 2010; Wolf *et al.*, 2011). Social interactions are considered the fundamental level of social structure (Hinde, 1976) and are closely related to personality (Aplin *et al.*, 2013; Webster & Ward, 2011). In this sense, how everyone behaves and interacts with others can substantially affect social processes at the group or population level (Bergmüller & Taborsky, 2010; Dingemanse & Wolf, 2010; McElreath *et al.*, 2007; McNamara *et al.*, 2009; Wolf *et al.*, 2007; Wolf & Krause, 2014). Moreover, social influence may determine how individuals respond to the environment, and personality may restrict them (Webster & Ward, 2011).

Social influence can occur mainly through two processes: Conformity and Social Facilitation. Conformity describes individuals' positively frequency-dependent tendency to perform behaviors disproportionately generalized by the group and is often an important strategy in species that gain fitness from grouping (Efferson *et al.*, 2008). Social Facilitation refers to changes in the frequency at which individuals perform certain behaviors when they are in the presence of group mates, allowing them to perform behaviors they would not do alone (e.g., decrease investment in defensive behaviors, increase exploratory or competitive behaviors) (Zajonc, 1965). A suggested way to show how the social environment impacts the expression of behaviors are through a behavioral reaction norm, that includes the personality of individuals and intra-individual responsiveness to environmental variation as a measure of plasticity (Favati *et al.*, 2013; McNamara & Leimar, 2010; Wolf *et al.*, 2011). This approach includes information on how an animal behaves on average and how its behavior changes along a gradient, precisely specifying the relationship between the magnitude of the response through the contexts (Dingemanse *et al.*, 2010).

Additionally, sociality promotes the rise of differentiated social relationships between personalities due to consistency in patterns of association over time, which is expressed as the probability of interaction or social preference between individuals (McPherson *et al.*, 2001; Schino & Aureli, 2017; Weinstein & Capitanio, 2012). The understanding the role of personality in social systems, it is necessary to consider not only immediate interactions but also indirect interactions and the different ways in which an animal can perform in population contexts (Krause *et al.*, 2009, 2010; Sih *et al.*, 2009; Strandburg-Peshkin *et al.*, 2013). In this regard, social network analysis provides a theoretical framework where it is possible to examine the totality of interactions that occur in a population and to characterize the fine

structure through specific metrics (Farine & Whitehead, 2015; Krause *et al.*, 2010; Webber & Vander Wal, 2019; Wilson & Krause, 2014).

We studied how personality and social behaviors can influence social structure in the common rough woodlouse *Porcellio scaber* (Crustacea; Isopoda; Oniscidea), using the exploratory capacity and stereotyped behaviors as a descriptor of the reactive-proactive gradient (Coppens *et al.*, 2010; Hall *et al.*, 2017; Koolhaas *et al.*, 1999; Smith & Blumstein, 2008). Previous studies have described that proactive-reactive personality can be characterized using behavioral assays in novel environments (Tuf *et al.*, 2015). The explorative ability (Anselme, 2015, 2018; Yli-Renko *et al.*, 2018), foraging (Hassall *et al.*, 2002), rearing up (Anselme, 2013, 2015), sheltering (Hassall & Tuck, 2007; Pálková, 2013), antenna movements (Schmalfuss, 2018), and tonic immobility (Quadros *et al.*, 2012; Tuf *et al.*, 2015), are behaviors that pay more attention in behavioral studies in terrestrial isopods. These behaviors are expected to be subject to selection (Rojas *et al.*, 2014), involve life-history traits (Lardies, *et al.*, 2004a; Lardies, *et al.*, 2004b), and be heritable (Lardies & Bozinovic, 2008).

The aggregation in woodlice has a social component and results from a trade-off between individual preferences and the strong attraction between individuals (Devigne *et al.*, 2011). Densities do not impact aggregation patterns (Broly *et al.*, 2012). Social aggregation in woodlice is so strong that it can form aggregates in complicated locations, such as dry, bright, or polluted areas, which appear to be disadvantageous for survival (Broly *et al.*, 2013; Zidar *et al.*, 2012). The aggregation has a mechanism that prevents water loss and allows the transfer of bacterial biota (Bell *et al.*, 2007), predisposes to the development of other forms

of cooperation, and could be a social step in the evolution (Brockett & Hassall, 2005; Broly *et al.*, 2016; Krause *et al.*, 2010).

This work evaluates how personality establishes social processes that influence group aggregation/self-organization and structuring. We expect non-random aggregation of personalities (and social structure) to occur mainly through the social processes depending on the social responsiveness capacity of individuals. Therefore, conformity and social facilitation, evidence possible association patterns, either by personality similarity (Koski & Burkart, 2015; McPherson *et al.*, 2001; Pike *et al.*, 2008) or by the complementarity of social niche based on types of behavior (Carter *et al.*, 2014; Laskowski & Bell, 2014; Montiglio *et al.*, 2013; Saltz *et al.*, 2016). Using video recordings, isolated and grouped individuals were analyzed. We first assessed the personality of individuals based on the repeatability of behaviors before and after exposure to the social environment. Second, we evaluate the strength of associations between personalities. Third, we used social network analysis to describe group formation, organization, and structure. Finally, we assessed the non-randomness of social behaviors based on node centrality metrics and the effect of personality on them. We propose an integrative approach between dyad analysis to understand the preference of individuals and social network analysis to describe aspects of the combination of personalities in the assemblage of individuals.

MATERIALS AND METHODS

Collect and housing conditions

We collected ninety woodlice (*P. scaber*) from fourteen localities in Valdivia, Chile. Localities maintained the individuals in plastic containers provided with organic matter in different states of decomposition (barks, roots, and leaves) and wet soil. We maintained the

substrate constantly kept humid to avoid the desiccation of the individuals. Similarly, ventilation was allowed through perforations in the upper part of the containers to prevent mold formation. The individuals were acclimatized for three days under controlled conditions (temperature = $16 \pm 3^{\circ}\text{C}$ and humidity = $80 \pm 10\% \text{ RH}$). Before group formation, everyone was sexed and marked with a unique identification code using white non-toxic acrylic marker "ONE4ALL - MOLOTOW" (Supplementary material 1, Figure S1-A) and isolated in a 95 mm diameter Petri dish with wet plaster as substrate and provided with decomposing organic matter. All individuals remained isolated for 24 h before the personality test and social contests.

Personality test

First, to determine the effect of personality on the social context, we estimated personality traits under isolation. The personality test consisted of five minutes of recording in a 94 mm Petri dish with a homogeneous novel substrate (sterilized paper filter) inside a dark chamber (Supplementary material 1, Figure S1-B). This experiment was repeated three times, once per day, for three consecutive days. The behavioral variables we quantified from the video recordings were: (a) distance traveled, as the linear distance covered; (b) the number of stops, the number of times the individual stopped; (c) immobility time, a sum of all time intervals that the individual remains immobile or with the low sensory activity of the antennae; (d) Escape attempts, the number of escape attempts on the arena side walls; (e) mobility intervals, the average duration of mobility intervals; f) Escape interval, the average time interval between two events of escape attempt; g) speed, the average speed of displacement; h) average direction angle, the average direction of displacement based on the sexagesimal system; i) directional deviation, the angle of deviation of displacement; and j) the number of

turns, indicates the number of times the individual changed direction by more than 45° (modified from Anselme, 2015, 2018). We used the free software BORIS (Friard & Gamba, 2016) and the R packages "pathtrackR" (Harmer & Thomas, 2019). At the end of the social contest experiment (see below), we repeated the personality test to evaluate possible personality changes influenced by the social context.

We determined the expression of personality in individuals by assessing behavioral repeatability across each replicate controlling for sex and reproductive status in females. The standard measure of repeatability can be defined as the proportion of the total variance accounted for by differences among groups (Sokal & Rohlf, 1995). We repeat the procedure in a second test (after the social contest experiment) and compared personality changes using a Hotelling test on the behavioral variables before and after the social contest. Sequentially, we took the behavioral variables that showed significant repeatability before and after the social contest and reduced them by eliminating those correlated. To evaluate the correlation between behaviors and body size we used Kendall correlation analysis. We found no correlation between behaviors and body size (Supplementary material, Figure S2). Finally, we define personality scores as a function of the selected behaviors. The personality score helps us place the individuals within a reactivity-proactivity spectrum, where the individuals who expressed these behaviors to a lesser extent correspond to a reactive type, and those who performed them to a greater extent are proactive. All analyses were realized in R software (R Development Core Team, 2012), and in a particular "rptR" package to quantify the repeatability of behaviors (Nakagawa & Schielzeth, 2010).

Social contest experiment

To evaluate the effect of personality on the social context, we assembled three groups of 30 individuals, which included three individuals by locality (ten different localities per group). We placed each group in an arena of 40 cm diameter containing black painted plaster as substrate and flexible PVC sheet walls. We recorded all interindividual associations that occurred at five minutes intervals every 2 hours, from 00:00 to 04:00 hours, for three consecutive days (modified from Drahokoupilová & Tuf, 2012). Each evaluation day represents one observation and consists of three video recordings. All records were realized using EZVIZ network video recorder model EZWIRELESS X5C and EZVIZ cameras model C3W (Supplementary material 1, Figure S1-C).

Social network analysis

We constructed dyadic association matrices from the video records based on the individuals' time spent together in each observation. To perform the networks analysis, first, we estimated the association index (AI) between pairs of individuals (dyad) using a simple ratio index (Whitehead, 2008), scaled between 0 (never associated) to 1 (always associated) (Ginsberg & Young, 1992). We considered an association when two individuals are close to one body length of distance (approximately 10 mm). To establish network attributes, we considered network analysis estimators: Density (as the proportion of links present in the network relative to the total number of possible links), Path Length Mean (as the average of all the geodesics between nodes, and Diameter (as the longest geodesic distance, length of the shortest path between two nodes). These three metrics allow quantifying how close nodes are in terms of the number of links (Croft *et al.*, 2008). In addition, we estimated Transitivity (or clustering coefficient) as a measure of the probability that the adjacent nodes are connected

(Watts & Strogatz, 1998), and Modularity as the level of division of a network into clusters (Newman, 2003). We included two modularity estimators, the first based on edge betweenness (Newman & Girvan, 2004), and the second based on Greedy optimization (Newman, 2004). Social individual attributes were measured using three commonly employed node measures; degree centrality, betweenness centrality, and average association strength (Croft *et al.*, 2008). To build the network and obtain the metrics, we will use the R packages called “sna” (Butts, 2015) and “igraph” (Csardi & Nepusz, 2005).

Social influence of personality

To determine if personality directly influences dyadic association weights, we performed a Bayesian multilevel model with a gaussian distribution that included multi-membership random effects (modified from Hart *et al.*, 2021). As fixed factors, we include Euclidean dyadic distance of personality variables (behavioral variables distinguishing between pre-social exposure and post-social exposure), sex dissimilarity (0: same sex and 1: different sex), and locality dissimilarity (0: same origin and 1: different origin) and multi membership considering observation days. Details of the models in Appendix 1

In addition, we developed null models based on permutation of network and pre-networks, establishing random values of degree centrality, betweenness centrality, and average association strength. Null models consider non-social factors that affect the co-occurrence of individuals assuming non-independence of observations and can evidence emergent properties of the groups (Farine, 2017). We consider personality variables as predictor variables in the null models to evaluate these centrality measures. Subsequently, Bayesian multilevel models were used to compare these centrality measures to personality variables while adding as random effects individual, original location, and observation by the group.

Finally, to know the nature of the variation of the variables that influence the centrality measures, we will perform reaction norms and analyze behavioral plasticity concerning personality. We calculated Euclidean distances using R software (R Development Core Team, 2012), and models were performed using R "brms" (Bürkner, 2017) and "mm" packages (Altham & Hankin, 2012).

RESULTS

We found high individual repeatability of behaviors (41% - 7% in variables that present repeatability). The directional deviation was the only behavioral variable that did not show significative repeatability when analyzed independently of the social exposure stage (Repeatability: $R = 0.02$, CI [0, 0.08], $P = 0.21$). When analyzed as a function of social exposure, the repeatability of behaviors is expressed in greater intensity after social exposure (Paired t -test: $t_9 = -4.0608$, $P = 0.003$). In this condition, the repeatability values ranged from 64% to 21%. Regarding the repeatability of behaviors before social exposure, we observed that distance, stops, immobility, escape attempts, mobility intervals, escape intervals, speed, and directional deviation have repeatability values ranging from 46% to 11%. In contrast, average direction (Repeatability: $R = 0.08$, CI [0, 0.19], $P = 0.1$) and turns (Repeatability: $R = 0.07$, CI [0, 0.20], $P = 0.14$) have low average repeatability values (Table 1).

We observed significant differences in the expression of behaviors before and after social exposure (Hotelling's test: $t^2_{10, 513} = 13.78$, $P < 0.001$). In addition, we found a strong correlation between distance traveled and travel speed (Kendall correlation, $\tau = 0.84$, $P < 0.001$) and with the number of turns (Kendall's correlation, $\tau = 0.51$, $P < 0.01$). Additionally, we observed that the mean displacement direction is slightly correlated with distance (Kendall correlation, $\tau = 0.36$, $P = 0.02$) and speed (Kendall correlation, $\tau = 0.34$, $P = 0.02$).

Knowing the degree of correlation between these variables, we can assume that they are part of a behavioral syndrome linked to exploration ability. On the other hand, we observed that the number of escape attempts was strongly correlated with the time intervals between escape attempts as expected. (Kendall correlation, $\tau = 0.55$, $P < 0.001$). We did not find considerable correlations between these variables and behaviors linked to individuals' exploratory abilities, so we can assume that they represent another behavioral syndrome represented by individuals' stereotyped behaviors. In this case, stereotyped behavior can be understood as any behavior that is repetitive and seemingly functionless and can be performed in artificial or abnormal environments (Jeppesen *et al.*, 2004; Mason, 1993). We note that the number of stops and the cumulative immobility time because these two variables are positively correlated with each other (Kendall correlation, $\tau = 0.50$, $P < 0.001$), and they are slightly correlated with behaviors linked to the exploratory ability and stereotyped behaviors. It is known that tonic immobility is not usually a generalized reaction in this species but instead may represent a stereotyped behavior that is part of a trade-off based on defensive strategies (Schmalfuss, 2018; Tuf *et al.*, 2015). The relationship between the number of stops and immobility is profoundly complex because there will be individuals who will perform fewer stops but remain in states of tonic immobility as a defense mechanism, while on the other hand there will be individuals who will perform a greater number of shorter stops as a process of individual decision making (Supplementary material 1, Table S1).

From these results, we operationally defined personality using four behavioral variables (distance, stops, escape attempts and average direction), distinguishing between pre and post social exposure. These variables were selected because they presented greater repeatability in both social contexts and because they represented those other variables with which they

were correlated. We did not find generalized behavioral repeatability at the locality origin (Supplementary material 1, Table S2).

Concerning the structure measures based on network analysis, we found that the ensembles formed within the three groups presented high link density and transitivity, close to the maximum value in both cases. Likewise, the three groups presented high connectance represented by an average path length of one step. The diameter of the networks ranged from one to two steps in groups. Modularity based on betweenness presented values close to zero for the three sets of individuals, while modularity based on Greedy optimization presented low values that did not exceed 0.2 (Table 2).

Regarding the effect of personality on the patterns and intensity of association, we found an effect of the interindividual difference in personality on the dyadic association index in the three groups evaluated. We observed that the between-pair difference in the number of stops before social exposure and the between-individual difference in the number of escape attempts after social exposure positively affected the dyadic association index weight. In contrast, the between-individual difference in the distance traveled after social exposure had a negative effect. In addition, we found a marginally positive effect of interindividual differences on the average direction of travel. We found no effect of the difference in sex or the difference in the locality of origin (Table 3 and Figure 1).

Concerning centrality measures of individuals, From the null models, groups 1 and 2 were distributed differently than expected by network permutation for degree centrality and betweenness centrality. In the case of average association strength, groups 2 and 3 were distributed differently than expected by the permutation of networks. None of the groups were distributed differently than expected by a pre-network permutation to centrality

measures (Supplementary material 1, Table S3, Figure S3 and S4). When we evaluated the influence of personality on betweenness centrality we found a negative effect on the number of stops performed before the social contest. The same phenomenon was observed in average association strength but to a lesser magnitude. We did not notice any effect of personality on degree centrality (Table 4 and Figure 2). Details of the random effects conditional modes in the models are shown in Appendix 2.

When we evaluated the relationship between the expression of the number of stops and the social context, we observed that despite not having a generalized tendency, it depends on the individuals participating in the groups and their personality types (Table 5). Additionally, we found a negative relationship between the personality score (described by the number of stops before the social contest) and social responsiveness independently of the set of individuals. In this case, proactive individuals (individuals who performed the greatest number of stops) tended to decrease the expression of the behavior, and reactive individuals (individuals who performed the fewest number of stops) increased such expression (Table 6 and Figure 3).

DISCUSSION

We found that behavioral variables defining personality in *P. scaber* were correlated even after individuals were subjected to the social contest. These variables included exploratory attributes and stereotypic behaviors that allowed us to establish a gradient reactivity-proactive describing the personality of individuals. This phenomenon involving the exploratory behaviors correlation generally tends to be linked to aggressiveness and dominance (Dingemanse & de Goede, 2004; Verbeek *et al.*, 1996), foraging (Marchetti & Drent, 2000; Verbeek *et al.*, 1994), stress responses (Carere *et al.*, 2001; Carere & Van Oers, 2004), risk-taking behavior (Van Oers *et al.*, 2004) and dispersal (Dingemanse *et al.*, 2003).

In the specific case of terrestrial isopods, correlations have been found between travel speed and certain defense mechanisms such as conglobation in *Armadillium vulgare* (Matsuno & Moriyama, 2012). In most animals, individual performance is closely linked to life history traits (Wolf & Weissing, 2012), and phenotypic attributes could be linked to age (body size) and sex, therefore, may impact individuals' exploratory behaviors, and the relationship between body size and defensive behaviors in *P. scaber* (Hals & Beal, 1982; Tuf *et al.*, 2015) and in *Porcellio dilatatus* (Quadros *et al.*, 2012). We found no correlation between body size or sex on any of the behavioral variables evaluated, so we can assume that these traits do not impact the expression of individual behavior in *P. scaber*.

Because we assessed the performance of individuals in isolation before and after exposure to a freely interacting social environment, it was possible to visualize whether behavioral expression could be plastic. We found differences in how individuals behaved after exposure to the social environment. We noticed that the behaviors associated with being proactive increased after being exposed to the social contest. In contrast, the stereotyped behaviors are maintained or slightly reduced.

These results are similar to those of Anselme (2018), who found modifications in the expression of behavior when individuals move from a stressful condition to a recognizable condition. A recognizable environment can relax the expression of stereotyped or sensitized behaviors due to conformity processes (Efferson *et al.*, 2008). Likewise, it can also influence the expression of habituated behaviors, such as displacement, and defensive or alerting behaviors, such as tonic immobility, through social facilitation processes (Zajonc, 1965). A similar case was reported by Magnhagen & Bunnefeld (2009) in perch (*Perca fluviatilis*) when they assessed risk-taking in open water. Fish tended to behave more boldly when in

groups, spending more time in open water compared to when alone. The variation between individuals was greater when alone, suggesting that sociality may restrict the diversity of individual responses due to a conformity process, which has a greater impact on more sensitive individuals. Van Oers and collaborators (2005) found a directional facilitation effect on personality in individuals with lower exploratory ability when they assessed the exploratory behavior across an asocial and social context in great tit (*Parus major*). A similar case occurs with three-spined sticklebacks (*Gasterosteus aculeatus*) when assessing the ability of focal fishes within a group to compete for prey, activity in a novel environment and latency to resume foraging after a simulated predator attack. Here, high variability was evident in how individuals performed when in isolation compared to when in groups, suggesting an assemblage-dependent facilitatory effect (Webster *et al.*, 2007). These studies demonstrate that the influence of sociality on personality expression is complex and dependent on the context in which it is analyzed. This fact reveals that the relationships between different behavioral expressions can be modified multidimensionally, evidencing the true nature of behavioral plasticity and its limitations (Webster & Ward, 2011).

The fact that there is behavioral plasticity across social contexts implies differences in the expression of behaviors around a reaction norm (Dingemanse *et al.*, 2010), and consequently, in most cases, behavioral repeatability at the inter-contextual level will be lower than at the intra-contextual level (Garamszegi *et al.*, 2012). Bell and collaborators (2009) point out that the average repeatability in the expression of behaviors is 40%. In our case, the average individual repeatability values, regardless of the social context, are below this value. The same pattern is observed for behavioral performance before social exposure, while a remarkable increase was observed in the case of behavioral expression after social exposure.

Presumably, this process is maintained and facilitated by the protective effect induced by the social environment in the same way as behavioral plasticity. Behavioral consistency in *P. scaber* is not new, because it has been reported in the duration of tonic immobility between different types of treatments over time (Tuf *et al.*, 2015).

Concerning group attributes in a social context, we noted a high cohesion where individuals, had direct interaction when forming aggregates (high transitivity and a low number of steps between nodes). In this case, the high cohesion could respond to desiccation avoidance, therefore increasing probability of individual survival by spatial centralization (Allee, 1926; Broly *et al.*, 2014; Takeda, 1984). Additionally, the average density of aggregated individuals was found to be 83% (replicate/observation per day), similar to previous values reported (~80%) in experiments estimating the proportion of individuals seeking refuge (Broly *et al.*, 2012). To understand why the proportion of individuals aggregating was constant Broly and collaborators (2016) proposed three possible hypotheses. The first argues for a maximum aggregation size that rarely depends on system heterogeneities or constraints. The second proposes that aggregation of individuals occurs by amplification with positive feedback, which at some point collapses due to competition generating the aggregate to break up. The third points out that aggregates break up due to the rapid dynamics in the establishment process. Own results suggest that constant aggregation is related to the fact that reactive individuals tend to stay more time in the same environment (as protection perception). In contrast, proactive individuals are less represented in the groups and on the periphery. Even when optimization methods forced modularity, it was close to zero. However, the results suggest that there is strong aggregation, either by physiological-environmental restrictions (Dias *et al.*, 2012; Warburg, 1965) or by positive amplification feedback dynamics (Bridges

& Chittka, 2019; Camazine *et al.*, 2001; Didham *et al.*, 2007; Jeanson *et al.*, 2012; Sumpter, 2006). The concentration of reactive individuals in the center of the group and the peripheral proactive individuals cannot discard the complementary niche hypothesis (Bergmüller & Taborsky, 2010).

Regarding the strength of dyadic associations, we found that interindividual personality difference influences differently. We noted that differences in the expression of stereotyped behaviors (e.g., number of stops and escape attempts) influence the strength of dyadic associations through heterophily. In this case, individuals with more significant behavioral dissimilarity tend to associate more strongly. Additionally, we observed that the directionality of the influence of stereotyped behaviors on dyadic association patterns is independent of the social context. On the other hand, we noted that inter-individual differences in the expression of behaviors linked to exploratory ability (distance and direction) presented a marginal effect of homophily on the weight of dyadic associations. This marginal effect was only observed in the performance after the social contest. It could be evidence of conformity or habituation in behaviors linked to exploratory ability in individuals who remained more associated. Moreover, we found that inter-individual differences in the behaviors performed after the social contest had a greater impact on the weight of dyadic associations. This fact demonstrates the prevalence of a feedback process between personality and the social organization of individuals. Therefore, the aggregation properties in the self-organizing system of *P. scaber* may not only emerge from amplification processes based on positive feedback loops between the generalized expression of behaviors (Camazine *et al.*, 2001; Jeanson *et al.*, 2012; Sumpter, 2006), but also from the affinity between personality types and it is environment confer (Grand & Dill, 1999; Webster &

Ward, 2011; Zajonc, 1965). In addition, we must consider the presence of chemical signals (Beauché & Richard, 2013; Takeda, 1984) and the presence of places that provide better environmental conditions (Broly *et al.*, 2016) strongly influence the spatial establishment of the groups.

When we assessed social structuring based on measures of node centrality, we noticed that degree centrality, betweenness centrality and average association strength differed from the values expected by randomization at the network level. This result means that the structuring and association of individuals do not occur randomly in self-organization processes but responds to emergent processes provided by the behavioral types of individuals in the assemblage (Farine, 2017). Additionally, we found a negative effect of the number of stops before social exposure on betweenness centrality and average association strength. Thus, we can deduce that betweenness and the average duration of everyone's associations are linked to personality attributes. Individuals who have fewer stops (reactive) in a neutral and asocial environment are those who will tend to associate more intensely. As we found no effect of personality on degree centrality, the number of conspecifics in aggregates could be attributed to the assembly's characteristics, inherent properties of self-organization, or the transmission of local information at the individual level (Bonabeau *et al.*, 1997; Camazine *et al.*, 2001; Jeanson *et al.*, 2012; Theraulaz *et al.*, 2003). We also note that the directionality of the effect of the number of stops after the social contest tends to be positive (in all models) to assess centrality measures, contrary to the observed effect of this behavior before the social contest. The difference in the effect of this behavior may evidence the existence of social responsivity as a plastic attribute of personality regulated by the presence of conspecifics.

In invertebrates, it is known that individuals are chronically located in places where aggregates are established and that this phase is characterized by relative periods of behavioral immobility or pauses (Alves-dos-Santos *et al.*, 2009; Finkbeiner *et al.*, 2012; Hölldobler, 1976; Pearson & Anderson, 1985; Teng *et al.*, 2012). In a social environment this behavior can be regulated by the priority activity of individuals, as well as by the presence or behavior of conspecifics (Eban-Rothschild & Bloch, 2012; Tobler, 1983). Broly and Deneubourg (2015) suggest that the process of aggregation during the retention phase of individuals may promote behavioral quiescence or sleep-like states collectively, and that this state may explain why clustered individuals, corresponding to the reactive personality spectrum, can be observed for long periods in apparently unfavorable locations (high light incidence and no cover) when isolated individuals with proactive personalities flee quickly in similar conditions. At this point, we suggest that there is a differential effect on how social facilitation and conformity influence different personality types in *P. scaber*. Individuals that are more reactive in their personality spectrum will tend to associate more strongly and perform collective behaviors with other members of the aggregate due to conformity processes (e.g. quiescence as a collective behavior in invertebrates) (Hendricks *et al.*, 2000; Stephenson & Lewis, 2011). Conversely, those individuals with more proactive personalities will tend to have more ephemeral associations but not fewer associations. This fact is important to highlight because we found no differentiation or effect of personality on the degree in the network analysis. Because proactive individuals are more exposed to stressful conditions than those on a reactive spectrum, the social environment has a differential influence on them by motivating signal amplification and social facilitation (Broly *et al.*, 2012, 2016). In this study, we attempt to describe and evaluate the direct and indirect relationships between individuals of *P. scaber* to gain more insight into their social system.

We recommend conducting trials that allow a random and arbitrary combination of personalities, outside the natural relationship of personalities in population samples, to assess the impact of personality on social types and better understand personality's effect on self-organization and group structuring.

In conclusion, we could observe the consistency in the expression of behaviors regardless of whether it was isolated in a novel environment or part of a social aggregate, so we can reinforce the idea that *P. scaber* individuals have personality. The personality was not completely rigid and presented plasticity motivated by the social environment. Regarding dyadic association, we found that the proportion of time that two individuals spend in the association is influenced by the difference between the personalities that compose the dyad and the social influence of the environment. On the other hand, we present evidence that individual attributes of sociability are mainly driven by personality and by the social environment, being able to establish a reactivity-proactivity spectrum that defines personality and its role in structuring groups. Finally, we show that social responsiveness is differential concerning to the personality of individuals and consequently suggest that the social processes that influence the expression of behaviors differ between reactive and proactive individuals.

REFERENCES

- Allee, W. C. (1926). Studies in animal aggregations: Causes and effects of bunching in land isopods. *Journal of Experimental Zoology*, 45(1), 255-277.
<https://doi.org/10.1002/jez.1400450108>

Altham, P. M. E., & Hankin, R. K. S. (2012). Multivariate generalizations of the multiplicative binomial distribution: Introducing the MM package. *Journal of Statistical Software*, 46(12), 1-23. <https://doi.org/10.18637/jss.v046.i12>

Alves-dos-Santos, I., Gaglianone, M. C., Naxara, S. R. C., & Engel, M. S. (2009). Male sleeping aggregations of solitary oil-collecting bees in Brazil (Centridini, Tapinotaspidini, and Tetrapediini; Hymenoptera: Apidae). *Genetics and Molecular Research*, 8(2), 515-524. <https://doi.org/10.4238/VOL8-2KERR003>

Amat, I., Desouhant, E., Gomes, E., Moreau, J., & Monceau, K. (2018). Insect personality: What can we learn from metamorphosis? *Current Opinion in Insect Science*, 27, 46-51. <https://doi.org/10.1016/J.COIS.2018.02.014>

Anselme, P. (2013). Sensitivity to tactile novelty in the terrestrial isopod, *Porcellio scaber*. *Behavioural Processes*, 92, 52-59. <https://doi.org/10.1016/j.beproc.2012.10.007>

Anselme, P. (2015). Enhanced exploratory activity in woodlice exposed to random visuo-tactile patterns. *Learning and Motivation*, 50, 48-58. <https://doi.org/10.1016/j.lmot.2014.09.002>

Anselme, P. (2018). Rotational stress influences sensitized, but not habituated, exploratory behaviors in the woodlouse, *Porcellio scaber*. *Learning & Behavior* 2018 46:3, 46(3), 294-305. <https://doi.org/10.3758/S13420-018-0315-4>

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cole, E. F., Cockburn, A., & Sheldon, B. C. (2013). Individual personalities predict social behaviour in wild networks of great

tits (*Parus major*). *Ecology Letters*, 16(11), 1365-1372.
<https://doi.org/10.1111/ele.12181>

Beauché, F., & Richard, F.-J. (2013). The Best Timing of Mate Search in *Armadillidium vulgare* (Isopoda, Oniscidea). *PLOS ONE*, 8(3), e57737.
<https://doi.org/10.1371/journal.pone.0057737>

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: A meta-analysis. *Animal Behaviour*, 77(4), 771-783.
<https://doi.org/10.1016/j.anbehav.2008.12.022>

Bell, W. J., Roth, L. M., & Nalepa, C. A. (2007). Cockroaches: Ecology, Behavior, and Natural History. Johns Hopkins University Press.
<https://doi.org/10.1353/book.3295>

Bergmüller, R., & Taborsky, M. (2010). Animal personality due to social niche specialisation. *Trends in Ecology and Evolution*, 25(9), 504-511.
<https://doi.org/10.1016/j.tree.2010.06.012>

Bonabeau, E., Theraulaz, G., Deneubourg, J.-L., Aron, S., & Camazine, S. (1997). Self-organization in social insects. *Trends in Ecology & Evolution*, 12, 188.

Boon, A. K., Réale, D., & Boutin, S. (2007). The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecology Letters*, 10(11), 1094-1104. <https://doi.org/10.1111/j.1461-0248.2007.01106.x>

Bridges, A. D., & Chittka, L. (2019). Animal Behaviour: Conformity and the Beginnings of Culture in an Insect. *Current Biology*, 29(5), R167-R169.
<https://doi.org/10.1016/j.cub.2019.01.023>

Briffa, M., Bridger, D., & Biro, P. A. (2013). How does temperature affect behaviour? Multilevel analysis of plasticity, personality and predictability in hermit crabs. *Animal Behaviour*, 86(1), 47-54. <https://doi.org/10.1016/j.anbehav.2013.04.009>

Brockett, B. F. T., & Hassall, M. (2005). The existence of an Allee effect in populations of *Porcellio scaber* (Isopoda: Oniscidea). *European Journal of Soil Biology*, 41(3-4), 123-127. <https://doi.org/10.1016/j.ejsobi.2005.09.004>

Broly, P., & Deneubourg, J. L. (2015). Behavioural Contagion Explains Group Cohesion in a Social Crustacean. *PLoS Computational Biology*, 11(6), e1004290. <https://doi.org/10.1371/journal.pcbi.1004290>

Broly, P., Deneubourg, J. L., & Devigne, C. (2013). Benefits of aggregation in woodlice: A factor in the terrestrialization process? *Insectes Sociaux*, 60(4), 419-435. <https://doi.org/10.1007/s00040-013-0313-7>

Broly, P., Devigne, L., Deneubourg, J.-L., & Devigne, C. (2014). Effects of group size on aggregation against desiccation in woodlice (Isopoda: Oniscidea). *Physiological Entomology*, 39(2), 165-171. <https://doi.org/10.1111/phen.12060>

Broly, P., Mullier, R., Deneubourg, J. L., & Devigne, C. (2012). Aggregation in woodlice: Social interaction and density effects. *ZooKeys*, 176(SPECIAL ISSUE), 133-144. <https://doi.org/10.3897/zookeys.176.2258>

- Broly, P., Mullier, R., Devigne, C., & Deneubourg, J.-L. (2016). Evidence of self-organization in a gregarious land-dwelling crustacean (Isopoda: Oniscidea). *Animal Cognition*, 19(1), 181-192. <https://doi.org/10.1007/s10071-015-0925-6>
- Bürkner, P. C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, 80(1), 1-28. <https://doi.org/10.18637/jss.v080.i01>
- Butts, C. T. (2015). Social Network Analysis with sna. *Journal of Statistical Software*, 24(6). <https://doi.org/10.18637/jss.v024.i06>
- Camazine, S., Deneubourg, J.-L., Franks, N. R., Sneyd, J., Theraula, G., & Bonabeau, E. (2001). Self-Organization in Biological Systems. Princeton University Press. <https://doi.org/10.1515/9780691212920>
- Carere, C., & Van Oers, K. (2004). Shy and bold great tits (*Parus major*): Body temperature and breath rate in response to handling stress. *Physiology & Behavior*, 82(5), 905-912. [https://doi.org/10.1016/S0031-9384\(04\)00312-9](https://doi.org/10.1016/S0031-9384(04)00312-9)
- Carere, C., Welink, D., Drent, P. J., Koolhaas, J. M., & Groothuis, T. G. G. (2001). Effect of social defeat in a territorial bird (*Parus major*) selected for different coping styles. *Physiology & Behavior*, 73(3), 427-433. [https://doi.org/10.1016/S0031-9384\(01\)00492-9](https://doi.org/10.1016/S0031-9384(01)00492-9)
- Carter, A. J., English, S., & Clutton-Brock, T. H. (2014). Cooperative personalities and social niche specialization in female meerkats. *Journal of Evolutionary Biology*, 27(5), 815-825. <https://doi.org/10.1111/jeb.12358>

Conrad, J. L., Weinermith, K. L., Brodin, T., Saltz, J. B., & Sih, A. (2011). Behavioural syndromes in fishes: A review with implications for ecology and fisheries management. *Journal of Fish Biology*, 78(2), 395-435.

<https://doi.org/10.1111/j.1095-8649.2010.02874.x>

Coppens, C. M., De Boer, S. F., & Koolhaas, J. M. (2010). Coping styles and behavioural flexibility: Towards underlying mechanisms. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 4021-4028.

<https://doi.org/10.1098/rstb.2010.0217>

Cote, J., & Clobert, J. (2007). Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society B: Biological Sciences*, 274(1608), 383-390.

<https://doi.org/10.1098/rspb.2006.3734>

Croft, D. P., James, R., & Krause, J. (2008). Exploring animal social networks. Princeton University Press. <https://www.jstor.org/stable/j.ctt7sfqv>

Croft, D. P., Krause, J., Darden, S. K., Ramnarine, I. W., Faria, J. J., & James, R. (2009). Behavioural trait assortment in a social network: Patterns and implications. *Behavioral Ecology and Sociobiology*, 63(10), 1495-1503.

<https://doi.org/10.1007/s00265-009-0802-x>

Csardi, G., & Nepusz, T. (2005). The Igraph Software Package for Complex Network Research. *InterJournal, Complex Systems*, 1695.

Devigne, C., Broly, P., & Deneubourg, J. L. (2011). Individual preferences and social interactions determine the aggregation of woodlice. PLoS ONE, 6(2), e17389.
<https://doi.org/10.1371/journal.pone.0017389>

Dias, A. T. C., Krab, E. J., Mariën, J., Zimmer, M., Cornelissen, J. H. C., Ellers, J., Wardle, D. A., & Berg, M. P. (2012). Traits underpinning desiccation resistance explain distribution patterns of terrestrial isopods. Oecologia 2012 172:3, 172(3), 667-677.
<https://doi.org/10.1007/S00442-012-2541-3>

Didham, R. K., Lawton, J. H., & Mar, N. (2007). Edge Structure Determines the Magnitude of Changes in Microclimate and Vegetation Structure in Tropical Forest Fragments
Edge Structure Determines the Magnitude of Changes in Microclimate and Vegetation Structure in Tropical Forest Fragments1. 31(1), 17-30.

Dingemanse, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L., & Drent, P. J. (2003). Natal dispersal and personalities in great tits (*Parus major*). Proceedings of the Royal Society of London. Series B: Biological Sciences, 270(1516), 741-747.
<https://doi.org/10.1098/rspb.2002.2300>

Dingemanse, N. J., & de Goede, P. (2004). The relation between dominance and exploratory behavior is context-dependent in wild great tits. Behavioral Ecology, 15(6), 1023-1030. <https://doi.org/10.1093/beheco/arh115>

Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: Animal personality meets individual plasticity. Trends in Ecology and Evolution, 25(2), 81-89. <https://doi.org/10.1016/j.tree.2009.07.013>

Dingemanse, N. J., & Réale, D. (2005). Natural selection and animal personality. *Behaviour*, 142(9), 1159-1184. <https://doi.org/10.1163/156853905774539445>

Dingemanse, N. J., & Wolf, M. (2010). Recent models for adaptive personality differences: A review. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 3947-3958. <https://doi.org/10.1098/rstb.2010.0221>

Drahokoupilová, T., & Tuf, I. H. (2012). The effect of external marking on the behaviour of the common pill woodlouse *Armadillidium vulgare*. *ZooKeys*, 176(SPECIAL ISSUE), 145-154. <https://doi.org/10.3897/zookeys.176.2375>

Eban-Rothschild, A., & Bloch, G. (2012). Social influences on circadian rhythms and sleep in insects. *Advances in Genetics*, 77, 1-32. <https://doi.org/10.1016/B978-0-12-387687-4.00001-5>

Eccard, J. A., & Rödel, H. G. (2011). Optimizing temperament through litter size in short-lived, iteroparous mammals in seasonal environments. *Developmental Psychobiology*, 53(6), 585-591. <https://doi.org/10.1002/dev.20547>

Efferson, C., Lalive, R., Richerson, P. J., McElreath, R., & Lubell, M. (2008). Conformists and mavericks: The empirics of frequency-dependent cultural transmission. *Evolution and Human Behavior*, 29(1), 56-64. <https://doi.org/10.1016/j.evolhumbehav.2007.08.003>

Farine, D. R. (2017). A guide to null models for animal social network analysis. *Methods in Ecology and Evolution*, 8(10), 1309-1320. <https://doi.org/10.1111/2041-210X.12772>

Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology*, 84(5), 1144-1163.
<https://doi.org/10.1111/1365-2656.12418>

Favati, A., Leimar, O., Radesäter, T., & Løvlie, H. (2013). Social status and personality: Stability in social state can promote consistency of behavioural responses. *Proceedings of the Royal Society B: Biological Sciences*, 281(1774).
<https://doi.org/10.1098/rspb.2013.2531>

Finkbeiner, S. D., Briscoe, A. D., & Reed, R. D. (2012). The benefit of being a social butterfly: Communal roosting deters predation. *Proceedings of the Royal Society B: Biological Sciences*, 279(1739), 2769-2776.
<https://doi.org/10.1098/RSPB.2012.0203>

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, 7(11), 1325-1330. <https://doi.org/10.1111/2041-210X.12584>

Frick, E. E., Vere, A. J. de, & Kuczaj, S. A. (2017). What Do We Want to Know About Personality in Marine Mammals? *Personality in Nonhuman Animals*, 237-253.
https://doi.org/10.1007/978-3-319-59300-5_12

Garamszegi, L. Z., Markó, G., & Herczeg, G. (2012). A meta-analysis of correlated behaviours with implications for behavioural syndromes: Mean effect size, publication bias, phylogenetic effects and the role of mediator variables.

Evolutionary Ecology, 26(5), 1213-1235. <https://doi.org/10.1007/s10682-012-9589-8>

Ginsberg, J. R., & Young, T. P. (1992). Measuring association between individuals or groups in behavioural studies. Animal Behaviour, 44, 377-379. [https://doi.org/10.1016/0003-3472\(92\)90042-8](https://doi.org/10.1016/0003-3472(92)90042-8)

Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? Psychological Bulletin, 127(1), 45-86. <https://doi.org/10.1037/0033-2909.127.1.45>

Grand, T. C., & Dill, L. M. (1999). The effect of group size on the foraging behaviour of juvenile coho salmon: Reduction of predation risk or increased competition? Animal Behaviour, 58(2), 443-451. <https://doi.org/10.1006/anbe.1999.1174>

Groothuis, T. G. G., & Carere, C. (2005). Avian personalities: Characterization and epigenesis. Neuroscience and Biobehavioral Reviews, 29(1 SPEC. ISS.), 137-150. <https://doi.org/10.1016/J.NEUBIOREV.2004.06.010>

Hall, M. L., Parson, T., Riebel, K., & Mulder, R. A. (2017). Personality, plasticity, and resource defense. Behavioral Ecology, 28(1), 138-144. <https://doi.org/10.1093/beheco/arw104>

Hals, G., & Beal, K. (1982). The death feint and other responses of the terrestrial isopod *Porcellio scaber* to a jarring stimulus. Ohio Journal of Science, 82(94).

Harmer, A. M. T., & Thomas, D. B. (2019). pathtrackr: An r package for video tracking and analysing animal movement. *Methods in Ecology and Evolution*, 2041-210X.13200. <https://doi.org/10.1111/2041-210X.13200>

Hart, J. D. A., Weiss, M. N., Brent, L. J. N., & Franks, D. W. (2021). Common Permutation Methods in Animal Social Network Analysis Do Not Control for Non-independence. *bioRxiv*, 2021.06.04.447124. <https://doi.org/10.1101/2021.06.04.447124>

Hassall, M., & Tuck, J. M. (2007). Sheltering behavior of terrestrial isopods in grasslands. *Invertebrate Biology*, 126(1), 46-56. <https://doi.org/10.1111/j.1744-7410.2007.00075.x>

Hassall, M., Tuck, J. M., Smith, D. W., Gilroy, J. J., & Addison, R. K. (2002). Effects of spatial heterogeneity on feeding behaviour of *Porcellio scaber* (Isopoda: Oniscidea). *European Journal of Soil Biology*, 38(1), 53-57. [https://doi.org/10.1016/S1164-5563\(01\)01124-4](https://doi.org/10.1016/S1164-5563(01)01124-4)

Hendricks, J. C., Finn, S. M., Panckeri, K. A., Chavkin, J., Williams, J. A., Sehgal, A., & Pack, A. I. (2000). Rest in Drosophila is a sleep-like state. *Neuron*, 25(1), 129-138. [https://doi.org/10.1016/S0896-6273\(00\)80877-6](https://doi.org/10.1016/S0896-6273(00)80877-6)

Hinde, R. A. (1976). Interactions, Relationships and Social Structure. *Man*, 11(1), 1-17. <https://doi.org/10.2307/2800384>

Hölldobler, B. (1976). The behavioral ecology of mating in harvester ants (Hymenoptera: Formicidae: Pogonomyrmex). *Behavioral Ecology and Sociobiology*, 1(4), 405-423. <https://doi.org/10.1007/BF00299401>

Horváth, G., Mészáros, B., Urszán, T. J., Bajer, K., Molnár, O., Garamszegi, L. Z., & Herczeg, G. (2017). Environment-dependence of behavioural consistency in adult male European green lizards (*Lacerta viridis*). *PLoS ONE*, 12(11), e0187657. <https://doi.org/10.1371/journal.pone.0187657>

Jeanson, R., Dussutour, A., & Fourcassié, V. (2012). Key factors for the emergence of collective decision in invertebrates. *Frontiers in Neuroscience*, 0(AUG), 121. <https://doi.org/10.3389/fnins.2012.00121>

Jeppesen, L. L., Heller, K. E., & Bildsøe, M. (2004). Stereotypies in female farm mink (*Mustela vison*) may be genetically transmitted and associated with higher fertility due to effects on body weight. *Applied Animal Behaviour Science*, 86(1-2), 137-143. <https://doi.org/10.1016/j.applanim.2003.11.011>

Kelleher, S. R., Silla, A. J., & Byrne, P. G. (2018). Animal personality and behavioral syndromes in amphibians: A review of the evidence, experimental approaches, and implications for conservation. *Behavioral Ecology and Sociobiology* 2018 72:5, 72(5), 1-26. <https://doi.org/10.1007/S00265-018-2493-7>

Koenig, A. M., & Oosterhout, B. H. (2018). Behavioral syndrome persists over metamorphosis in a pond-breeding amphibian. *Behavioral Ecology and*

Sociobiology 2018 72:12, 72(12), 1-12. <https://doi.org/10.1007/S00265-018-2595-2>

Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. W., & Blokhuis, H. J. (1999). Coping styles in animals: Current status in behavior and stress- physiology. *Neuroscience and Biobehavioral Reviews*, 23(7), 925-935. [https://doi.org/10.1016/S0149-7634\(99\)00026-3](https://doi.org/10.1016/S0149-7634(99)00026-3)

Koski, S. E., & Burkart, J. M. (2015). Common marmosets show social plasticity and group-level similarity in personality. *Scientific Reports*, 5. <https://doi.org/10.1038/srep08878>

Krause, J., James, R., & Croft, D. P. (2010). Personality in the context of social networks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 4099-4106. <https://doi.org/10.1098/rstb.2010.0216>

Krause, J., Lusseau, D., & James, R. (2009). Animal social networks: An introduction. *Behavioral Ecology and Sociobiology*, 63(7), 967-973. <https://doi.org/10.1007/s00265-009-0747-0>

Lardies, M. A., & Bozinovic, F. (2008). Genetic variation for plasticity in physiological and life-history traits among populations of an invasive species, the terrestrial isopod *Porcellio laevis*. *Evolutionary Ecology Research*, 10(June 2014), 747-762.

Lardies, M. A., Carter, M. J., & Bozinovic, F. (2004). Dietary effects on life history traits in a terrestrial isopod: The importance of evaluating maternal effects and trade-offs. *Oecologia*, 138(3), 387-395. <https://doi.org/10.1007/s00442-003-1447-5>

Lardies, M. A., Cotoras, I. S., & Bozinovic, F. (2004). The energetics of reproduction and parental care in the terrestrial isopod *Porcellio laevis*. *Journal of Insect Physiology*, 50(12), 1127-1135. <https://doi.org/10.1016/j.jinsphys.2004.10.005>

Laskowski, K. L., & Bell, A. M. (2014). Strong personalities, not social niches, drive individual differences in social behaviours in sticklebacks. *Animal Behaviour*, 90, 287-295. <https://doi.org/10.1016/j.anbehav.2014.02.010>

Magnhagen, C., & Bunnefeld, N. (2009). Express your personality or go along with the group: What determines the behaviour of shoaling perch? *Proceedings of the Royal Society B: Biological Sciences*, 276(1671), 3369-3375. <https://doi.org/10.1098/RSPB.2009.0851>

Marchetti, C., & Drent, P. J. (2000). Individual differences in the use of social information in foraging by captive great tits. *Animal Behaviour*, 60(1), 131-140. <https://doi.org/10.1006/anbe.2000.1443>

Mason, G. J. (1993). Age and Context Affect the Stereotypes of Caged Mink. *Behaviour*, 127(3-4), 191-229. <https://doi.org/10.1163/156853993X00029>

Mather, J., & Logue, D. (2013). The Bold and the Spineless Invertebrate Personalities. En C. Carere & D. Maestripieri (Eds.), *Animal Personalities: Behavior, Physiology, and*

Evolution (pp. 12-35). University of Chicago Press.

<https://doi.org/10.7208/chicago/9780226922065.003.0002>

Matsuno, H., & Moriyama, T. (2012). Behavioral evidence for internal factors affecting duration of conglobation in pill bugs (*Armadillidium vulgare*, Isopoda, Crustacea).

Acta Biologica Hungarica, 63(Supplement 2), 80-82.

<https://doi.org/10.1556/ABiol.63.2012.Supp1.2.9>

McElreath, R., Luttbeg, B., Fogarty, S. P., Brodin, T., & Sih, A. (2007). Evolution of animal personalities. *Nature*, 450(7167), E5-E5. <https://doi.org/10.1038/nature06326>

McNamara, J. M., & Leimar, O. (2010). Variation and the response to variation as a basis for successful cooperation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1553), 2627-2633. <https://doi.org/10.1098/rstb.2010.0159>

McNamara, J. M., Stephens, P. A., Dall, S. R. X., & Houston, A. I. (2009). Evolution of trust and trustworthiness: Social awareness favours personality differences. *Proceedings of the Royal Society B: Biological Sciences*, 276(1657), 605-613. <https://doi.org/10.1098/rspb.2008.1182>

McPherson, M., Smith-Lovin, L., & Cook, J. M. (2001). Birds of a feather: Homophily in social networks. *Annual Review of Sociology*, 27, 415-444. <https://doi.org/10.1146/annurev.soc.27.1.415>

Modlmeier, A. P., Keiser, C. N., Wright, C. M., Lichtenstein, J. L. L., & Pruitt, J. N. (2015). Integrating animal personality into insect population and community ecology.

Current Opinion in Insect Science, 9, 77-85.

<https://doi.org/10.1016/j.cois.2015.03.008>

Montiglio, P. O., Ferrari, C., & Réale, D. (2013). Social niche specialization under constraints: Personality, social interactions and environmental heterogeneity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1618), 20120343. <https://doi.org/10.1098/rstb.2012.0343>

Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews*, 85(4), no-no. <https://doi.org/10.1111/j.1469-185X.2010.00141.x>

Newman, M. E. J. (2003). The Structure and Function of Complex Networks. *SIAM Review*, 45(2), 167-256. <https://doi.org/10.1137/S003614450342480>

Newman, M. E. J. (2004). Fast algorithm for detecting community structure in networks. *Physical Review E - Statistical Physics, Plasmas, Fluids, and Related Interdisciplinary Topics*, 69(6), 5. <https://doi.org/10.1103/PhysRevE.69.066133>

Newman, M. E. J., & Girvan, M. (2004). Finding and evaluating community structure in networks. *Physical Review E - Statistical, Nonlinear, and Soft Matter Physics*, 69(2), 026113. <https://doi.org/10.1103/PhysRevE.69.026113>

Pálková, R. (2013). Space activity and sheltering behaviour of terrestrial isopods. Palacký University in Olomouc.

Pearson, D. L., & Anderson, J. J. (1985). Perching Heights and Nocturnal Communal Roosts of Some Tiger Beetles (Coleoptera: Cicindelidae) in Southeastern Peru. *Biotropica*, 17(2), 126. <https://doi.org/10.2307/2388504>

Pike, T. W., Samanta, M., Lindström, J., & Royle, N. J. (2008). Behavioural phenotype affects social interactions in an animal network. *Proceedings of the Royal Society B: Biological Sciences*, 275(1650), 2515-2520. <https://doi.org/10.1098/rspb.2008.0744>

Quadros, A. F., Bugs, P. S., & Araujo, P. B. (2012). Tonic immobility in terrestrial isopods: Intraspecific and interspecific variability. *ZooKeys*, 176(176), 155. <https://doi.org/10.3897/ZOOKEYS.176.2355>

R Development Core Team. (2012). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. <https://www.r-project.org/>

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2), 291-318. <https://doi.org/10.1111/j.1469-185X.2007.00010.x>

Rojas, J. M., Castillo, S. B., Folguera, G., Abades, S., & Bozinovic, F. (2014). Coping with daily thermal variability: Behavioural performance of an ectotherm model in a warming world. *PLoS ONE*, 9(9), 1-9. <https://doi.org/10.1371/journal.pone.0106897>

Saltz, J. B., Geiger, A. P., Anderson, R., Johnson, B., & Marren, R. (2016). What, if anything, is a social niche? *Evolutionary Ecology*, 30(2), 349-364.
<https://doi.org/10.1007/s10682-015-9792-5>

Schino, G., & Aureli, F. (2017). Reciprocity in group-living animals: Partner control versus partner choice. *Biological Reviews*, 92(2), 665-672.
<https://doi.org/10.1111/brv.12248>

Schmalfuss, H. (2018). EVOLUTIONARY STRATEGIES OF THE ANTENNAE IN TERRESTRIAL ISOPODS. *Journal of Crustacean Biology*, 18(April), 10-24.
<https://doi.org/10.1163/193724098X00025>

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19(7), 372-378.
<https://doi.org/10.1016/j.tree.2004.04.009>

Sih, A., & Bell, A. M. (2008). Insights for Behavioral Ecology from Behavioral Syndromes. Advances in the study of behavior, 38, 227. [https://doi.org/10.1016/S0065-3454\(08\)00005-3](https://doi.org/10.1016/S0065-3454(08)00005-3)

Sih, A., Hanser, S. F., & McHugh, K. A. (2009). Social network theory: New insights and issues for behavioral ecologists. *Behavioral Ecology and Sociobiology*, 63(7), 975-988. <https://doi.org/10.1007/s00265-009-0725-6>

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: A meta-analysis. *Behavioral Ecology*, 19(2), 448-455.
<https://doi.org/10.1093/BHECO/ARM144>

Sokal, R. R., & Rohlf, F. J. (1995). *Biometry: The Principles and Practices of Statistics in Biological Research* (Cop. W. H. Freeman and Company, Ed.).

Stephenson, R., & Lewis, V. (2011). Behavioural evidence for a sleep-like quiescent state in a pulmonate mollusc, *Lymnaea stagnalis* (Linnaeus). *Journal of Experimental Biology*, 214(5), 747-756. <https://doi.org/10.1242/jeb.050591>

Strandburg-Peshkin, A., Twomey, C. R., Bode, N. W. F., Kao, A. B., Katz, Y., Ioannou, C. C., Rosenthal, S. B., Torney, C. J., Wu, H. S., Levin, S. A., & Couzin, I. D. (2013). Visual sensory networks and effective information transfer in animal groups. *Current Biology*, 23(17). <https://doi.org/10.1016/j.cub.2013.07.059>

Sumpter, D. J. T. (2006). The principles of collective animal behaviour. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 361(1465), 5-22. <https://doi.org/10.1098/rstb.2005.1733>

Takeda, N. (1984). The aggregation phenomenon in terrestrial isopods.

Teng, B., Dao, S., Donaldson, Z. R., & Grether, G. F. (2012). New communal roosting tradition established through experimental translocation in a Neotropical harvestman. *Animal Behaviour*, 84(5), 1183-1190. <https://doi.org/10.1016/J.ANBEHAV.2012.08.022>

Theraulaz, G., Gautrais, J., Camazine, S., & Deneubourg, J. L. (2003). The formation of spatial patterns in social insects: From simple behaviours to complex structures. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and*

Engineering Sciences, 361(1807), 1263-1282.

<https://doi.org/10.1098/RSTA.2003.1198>

Tobler, I. (1983). Effect of forced locomotion on the rest-activity cycle of the cockroach.

Behavioural Brain Research, 8(3), 351-360. [https://doi.org/10.1016/0166-4328\(83\)90180-8](https://doi.org/10.1016/0166-4328(83)90180-8)

Tuf, I. H., Drábková, L., & Šipoš, J. (2015). Personality affects defensive behaviour of

Porcellio scaber (Isopoda, Oniscidea). ZooKeys, 2015(515), 159-171.

<https://doi.org/10.3897/zookeys.515.9429>

Van Oers, K., Drent, P. J., De Goede, P., & Van Noordwijk, A. J. (2004). Realized heritability

and repeatability of risk-taking behaviour in relation to avian personalities.

Proceedings of the Royal Society B: Biological Sciences, 271(1534), 65-73.

<https://doi.org/10.1098/rspb.2003.2518>

Van Oers, K., Klunder, M., & Drent, P. J. (2005). Context dependence of personalities: Risk-

taking behavior in a social and a nonsocial situation. Behavioral Ecology, 16(4),

716-723. <https://doi.org/10.1093/beheco/ari045>

Van Oers, K., & Naguib, M. (2013). Avian Personality. En C. Carere & D. Maestripieri

(Eds.), Animal Personalities: Behavior, Physiology and Evolution (pp. 66-95).

University of Chicago Press.

<https://doi.org/10.7208/chicago/9780226922065.003.0004>

Verbeek, M. E. M., Boon, A., & Drent, P. J. (1996). Exploration, Aggressive Behaviour and Dominance in Pair-Wise Confrontations of Juvenile Male Great Tits. *Behaviour*, 133(11/12), 945-963.

Verbeek, M. E. M., Drent, P. J., & Wiepkema, P. R. (1994). Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour*, 48(5), 1113-1121. <https://doi.org/10.1006/anbe.1994.1344>

Warburg, M. R. (1965). The Microclimate in the Habitats of Two Isopod Species in Southern Arizona. *American Midland Naturalist*, 73(2), 363. <https://doi.org/10.2307/2423460>

Waters, R. M., Bowers, B. B., & Burghardt, G. M. (2017). Personality and individuality in reptile behavior. In *Personality in Nonhuman Animals* (pp. 153-184). Springer, Cham. https://doi.org/10.1007/978-3-319-59300-5_8

Watts, D. J., & Strogatz, S. H. (1998). Collective dynamics of ‘small-world’ networks. *Nature*, 393(6684), 440-442. <https://doi.org/10.1038/30918>

Webber, Q. M. R., & Vander Wal, E. (2019). Trends and perspectives on the use of animal social network analysis in behavioural ecology: A bibliometric approach. *Animal Behaviour*, 149, 77-87. <https://doi.org/10.1016/j.anbehav.2019.01.010>

Webster, M. M., & Ward, A. J. W. (2011). Personality and social context. *Biological Reviews*, 86(4), 759-773. <https://doi.org/10.1111/j.1469-185X.2010.00169.x>

Webster, M. M., Ward, A. J. W., & Hart, P. J. B. (2007). Boldness is influenced by social context in threespine sticklebacks (*Gasterosteus aculeatus*). *Behaviour*, 144(3), 351-371. <https://doi.org/10.1163/156853907780425721>

Weinstein, T. A. R., & Capitanio, J. P. (2012). Longitudinal stability of friendships in Rhesus monkeys (*Macaca mulatta*): Individual-and relationship-level effects. *Journal of Comparative Psychology*, 126(1), 97-108. <https://doi.org/10.1037/a0025607>

Whitehead, Hal. (2008). *Analyzing Animal Societies: Quantitative Methods For*. University of Chicago Press.

Wilson, A. D. M., & Krause, J. (2014). Personality and social network analysis in animals. In *Animal Social Networks* (pp. 53-60). Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780199679041.003.0006>

Wolf, M., Doorn, G. S. V., Weissing, F. J., Van Doorn, G. S., & Weissing, F. J. (2011). On the coevolution of social responsiveness and behavioural consistency. *Proceedings of the Royal Society B: Biological Sciences*, 278(1704), 440-448. <https://doi.org/10.1098/rspb.2010.1051>

Wolf, M., & Krause, J. (2014). Why personality differences matter for social functioning and social structure. *Trends in Ecology and Evolution*, 29(6), 306-308. <https://doi.org/10.1016/j.tree.2014.03.008>

Wolf, M., Van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, 447(7144), 581-584. <https://doi.org/10.1038/nature05835>

Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology and Evolution*, 27(8), 452-461. <https://doi.org/10.1016/j.tree.2012.05.001>

Yli-Renko, M., Pettay, J. E., & Vesakoski, O. (2018). Sex and size matters: Selection on personality in natural prey-predator interactions. *Behavioural Processes*, 148(January 2017), 20-26. <https://doi.org/10.1016/j.beproc.2017.12.023>

Zajonc, R. B. (1965). Social Facilitation. *Science*, 149(3681), 269-274. <https://doi.org/10.1126/science.149.3681.269>

Zidar, P., Hribar, M., Žižek, S., & Štrus, J. (2012). Behavioural response of terrestrial isopods (Crustacea: Isopoda) to pyrethrins in soil or food. *European Journal of Soil Biology*, 51, 51-55. <https://doi.org/10.1016/J.EJSOBI.2012.03.010>

TABLES

Table 1. Analysis of behavioral repeatability at the individual level. Animal personality is characterized by repeatable and consistent between-individual behavioral differences across different situations.

| Variables | Repeatability | SE | Confidence Interval | | <i>P</i> |
|-----------------------------|---------------|------|---------------------|-------|----------------|
| | | | 2.5% | 97.5% | |
| Pre-Social Exposure | | | | | |
| Distance | 0.40 | 0.07 | 0.25 | 0.51 | < 0.001 |
| Stops | 0.28 | 0.07 | 0.12 | 0.40 | < 0.001 |
| Immobility | 0.46 | 0.06 | 0.32 | 0.56 | < 0.001 |
| Escape attempts | 0.46 | 0.07 | 0.31 | 0.56 | < 0.001 |
| Mobility interval | 0.11 | 0.06 | 0.00 | 0.23 | 0.04 |
| Escape interval | 0.23 | 0.07 | 0.10 | 0.36 | < 0.001 |
| Speed | 0.32 | 0.07 | 0.17 | 0.44 | < 0.001 |
| Average direction | 0.08 | 0.06 | 0.00 | 0.19 | 0.10 |
| Directional deviation | 0.12 | 0.06 | 0.00 | 0.23 | 0.04 |
| Turns | 0.07 | 0.06 | 0.00 | 0.20 | 0.14 |
| Post-Social Expose | | | | | |
| Distance | 0.59 | 0.06 | 0.42 | 0.67 | < 0.001 |
| Stops | 0.48 | 0.07 | 0.33 | 0.61 | < 0.001 |
| Immobility | 0.64 | 0.06 | 0.48 | 0.71 | < 0.001 |
| Escape attempts | 0.63 | 0.06 | 0.48 | 0.71 | < 0.001 |
| Mobility interval | 0.21 | 0.07 | 0.08 | 0.35 | < 0.001 |
| Escape interval | 0.31 | 0.07 | 0.16 | 0.43 | < 0.001 |
| Speed | 0.60 | 0.06 | 0.45 | 0.69 | < 0.001 |
| Average direction | 0.25 | 0.07 | 0.10 | 0.37 | < 0.001 |
| Directional deviation | 0.02 | 0.04 | 0.00 | 0.14 | 0.39 |
| Turns | 0.47 | 0.07 | 0.32 | 0.58 | < 0.001 |
| Total (Pre and Post) | | | | | |
| Distance | 0.40 | 0.04 | 0.31 | 0.49 | < 0.001 |
| Stops | 0.26 | 0.04 | 0.17 | 0.35 | < 0.001 |
| Immobility | 0.40 | 0.05 | 0.29 | 0.48 | < 0.001 |
| Escape attempts | 0.41 | 0.05 | 0.30 | 0.51 | < 0.001 |
| Mobility interval | 0.14 | 0.04 | 0.05 | 0.22 | < 0.001 |
| Escape interval | 0.18 | 0.04 | 0.09 | 0.26 | < 0.001 |
| Speed | 0.35 | 0.05 | 0.24 | 0.44 | < 0.001 |
| Directional deviation | 0.07 | 0.03 | 0.01 | 0.14 | 0.01 |
| Sd. Direction | 0.02 | 0.03 | 0.00 | 0.08 | 0.21 |
| Turns | 0.16 | 0.04 | 0.07 | 0.23 | < 0.001 |

SE: standard error, *p*: distribution probability. Confidence Interval based two-tailed test.
Significant probability was highlighted in bold.

Table 2. Attributes of association network. Density: proportion of links present in the network relative to the total number of possible links; Average Path Length (APL): average of all the geodesics between nodes; Diameter: length of the shortest path between two nodes in the network; Transitivity: probability that the adjacent vertices of a vertex are connected; Modularity: level of division of a network into clusters; Greedy Optimization Modularity (GOM): hierarchical agglomeration algorithm for detecting community structure.

| Group | Observation | Density | APL | Diameter | Transitivity | Modularity | GOM |
|-------|-------------|---------|------|----------|--------------|------------|------|
| 1 | 1 | 0.96 | 1.04 | 2 | 0.96 | 0.00 | 0.03 |
| | 2 | 0.97 | 1.03 | 2 | 0.97 | 0.03 | 0.06 |
| | 3 | 0.90 | 1.04 | 2 | 0.96 | 0.10 | 0.18 |
| 2 | 1 | 0.93 | 1.07 | 2 | 0.95 | 0.00 | 0.05 |
| | 2 | 0.80 | 1.20 | 2 | 0.86 | 0.00 | 0.14 |
| | 3 | 0.82 | 1.13 | 2 | 0.92 | 0.02 | 0.06 |
| 3 | 1 | 0.54 | 1.33 | 2 | 0.74 | 0.00 | 0.17 |
| | 2 | 0.81 | 1.00 | 1 | 1.00 | 0.00 | 0.00 |
| | 3 | 0.80 | 1.01 | 2 | 0.99 | 0.00 | 0.00 |

APL: Average Path Length, GOM: Greedy Optimization Modularity. Average network attributes were generated from the arithmetic average of the association indexes recorded for each observation. Average network saturates because network averaging confers additive properties to the node linkage.

Table 3. Estimated parameters obtained from models testing the effect of behavioral variables on dyadic associations. The model includes multi-membership grouping at the level of individuals within each group evaluated as a random factor and behaviors representing the personality of individuals before and after the social contest, sex, and place of origin as fixed factors.

| Parameter | Estimate | Est.Error | 95% Credible Interval | Rhat | Bulk_ESS | Tail_ESS | | |
|---|-------------------------|-----------|-----------------------|-------|----------|----------|-------|-------|
| Dyadic associations ($r^2 = 0.57 \pm 0.01$) | | | | | | | | |
| Pre social | Intercept | -1.79 | 0.86 | -3.57 | -0.02 | 1 | 10595 | 12598 |
| | Distance difference | 0.01 | 0.02 | -0.03 | 0.04 | 1 | 33542 | 22297 |
| | Stops difference | 0.09 | 0.03 | 0.03 | 0.14 | 1 | 36429 | 21674 |
| | Escape attempts diff. | -0.01 | 0.03 | -0.06 | 0.04 | 1 | 32489 | 23502 |
| Post social | Average direction diff. | 0 | 0.02 | -0.03 | 0.03 | 1 | 34629 | 21516 |
| | Distance difference | -0.04 | 0.02 | -0.07 | -0.01 | 1 | 36781 | 21907 |
| | Stops difference | 0.04 | 0.03 | -0.03 | 0.11 | 1 | 35780 | 22627 |
| | Escape attempts diff. | 0.13 | 0.03 | 0.08 | 0.18 | 1 | 32422 | 22227 |
| | Average direction diff. | 0.03 | 0.02 | 0 | 0.06 | 1 | 33823 | 22591 |
| | Sex difference | -0.01 | 0.04 | -0.08 | 0.06 | 1 | 34672 | 21965 |
| | Population difference | 0.01 | 0.07 | -0.12 | 0.15 | 1 | 38812 | 23005 |

For each parameter, we present the mean value and 95% credible intervals (95% CI). Rhat is the potential scale reduction factor and indicates the MCMC convergence (at convergence Rhat = 1). Bulk_ESS and Tail_ESS are measures of effective sample size. Diff: Difference.

Table 4. Estimated parameters obtained from models testing the effect of behavioral variables on individual centrality measures. In: (A) Degree centrality; (B) Betweenness centrality; and (C) average association strength.

| Parameter | Estimate | Est.Error | 95% Credible Interval | Rhat | Bulk_ESS | Tail_ESS |
|--|-------------------|-----------|-----------------------|-------|----------|----------|
| (A) Degree centrality ($r^2 = 0.5 \pm 0.02$) | | | | | | |
| Pre social | Intercept | 49.71 | 5.19 | 39.82 | 60.25 | 1 |
| | Distance | -0.39 | 0.22 | -0.83 | 0.03 | 1 |
| | Stops | -0.46 | 0.25 | -0.98 | 0.02 | 1 |
| | Escape attempts | 0.03 | 0.16 | -0.28 | 0.35 | 1 |
| | Average direction | 0.1 | 0.6 | -1.14 | 1.21 | 1 |
| Post social | Distance | 0.21 | 0.23 | -0.25 | 0.67 | 1 |
| | Stops | 0.25 | 0.22 | -0.2 | 0.68 | 1 |
| | Escape attempts | -0.07 | 0.18 | -0.43 | 0.28 | 1 |
| | Average direction | 0.5 | 0.84 | -1.18 | 2.14 | 1 |
| | Sex | 0.07 | 0.23 | -0.38 | 0.55 | 1 |
| (B) Betweenness centrality ($r^2 = 0.51 \pm 0.07$) | | | | | | |
| Pre social | Intercept | 0.53 | 3.33 | -6 | 7.08 | 1 |
| | Distance | -0.2 | 0.12 | -0.44 | 0.03 | 1 |
| | Stops | -0.33 | 0.14 | -0.6 | -0.06 | 1 |
| | Escape attempts | -0.01 | 0.09 | -0.19 | 0.16 | 1 |
| | Average direction | -0.08 | 0.35 | -0.76 | 0.61 | 1 |
| Post social | Distance | 0 | 0.13 | -0.25 | 0.25 | 1 |
| | Stops | 0.15 | 0.12 | -0.08 | 0.39 | 1 |
| | Escape attempts | -0.05 | 0.1 | -0.24 | 0.14 | 1 |
| | Average direction | 0.45 | 0.6 | -0.72 | 1.62 | 1 |
| | Sex | -0.19 | 0.13 | -0.44 | 0.07 | 1 |
| (C) Average association strength ($r^2 = 0.69 \pm 0.02$) | | | | | | |
| Pre social | Intercept | -3.03 | 2.29 | -7.5 | 1.5 | 1 |
| | Distance | -0.14 | 0.08 | -0.3 | 0.01 | 1 |
| | Stops | -0.2 | 0.1 | -0.39 | -0.01 | 1 |
| | Escape attempts | 0.02 | 0.06 | -0.1 | 0.14 | 1 |
| | Average direction | 0.07 | 0.25 | -0.43 | 0.55 | 1 |
| Post social | Distance | -0.12 | 0.09 | -0.29 | 0.05 | 1 |
| | Stops | 0.07 | 0.08 | -0.09 | 0.23 | 1 |
| | Escape attempts | 0.04 | 0.07 | -0.09 | 0.17 | 1 |
| | Average direction | 0.5 | 0.4 | -0.29 | 1.28 | 1 |
| | Sex | -0.02 | 0.09 | -0.19 | 0.15 | 1 |

The models were controlled for random effects at the level of individuals, locality of origin, and observations by experimental group of individuals. For each parameter, we present the mean value and 95% credible intervals (95% CI). Rhat is the potential scale reduction factor and indicates the MCMC convergence (at convergence Rhat = 1). Bulk_ESS and Tail_ESS are measures of effective sample size.

Table 5. Estimated parameters obtained from the models testing the effect of social context on the number of stops.

| Parameter | Estimate | Est.Error | 95% Credible Interval | Rhat | Bulk_ESS | Tail_ESS |
|--|----------|-----------|-----------------------|-------|----------|----------|
| (A) Generalized model of number of stops ($r^2 = 0.35 \pm 0.03$) | | | | | | |
| Intercept | 1.19 | 0.48 | 0.22 | 2.18 | 1 | 9508 |
| Social context | -0.07 | 0.05 | -0.17 | 0.02 | 1 | 46256 |
| (B) Models by groups of number of stops | | | | | | |
| Group 1 ($r^2 = 0.31 \pm 0.05$) | | | | | | |
| Intercept | 0.72 | 0.14 | 0.45 | 0.99 | 1 | 6120 |
| Social context | 0.19 | 0.09 | 0.01 | 0.37 | 1 | 34054 |
| Group 2 ($r^2 = 0.40 \pm 0.04$) | | | | | | |
| Intercept | 1.07 | 0.13 | 0.81 | 1.22 | 1 | 4860 |
| Social context | 0.26 | 0.08 | 0.11 | 0.41 | 1 | 31323 |
| Group 3 ($r^2 = 0.26 \pm 0.05$) | | | | | | |
| Intercept | 1.49 | 0.08 | 1.32 | 1.65 | 1 | 11306 |
| Social context | -0.19 | 0.08 | -0.34 | -0.04 | 1 | 38255 |

The generalized model was controlled for random effects at the level of individuals and experimental assemblages of individuals, while the group model only controlled at the individual level. For each parameter, we present the mean value and 95% credible intervals (95% CI). Rhat is the potential scale reduction factor and indicates the MCMC convergence (at convergence Rhat = 1). Bulk_ESS and Tail_ESS are measures of effective sample size.

Table 6. Estimated parameters obtained from models testing the effect of personality score on social responsiveness as represented by behavioral plasticity. We fit the model to a skew normal distribution.

| Parameter | Estimate | Est.Error | 95% Credible Interval | Rhat | Bulk_ESS | Tail_ESS |
|---|----------|-----------|-----------------------|-------|----------|----------|
| Social responsiveness ($r^2 = 0.27 \pm 0.06$) | | | | | | |
| Intercept | 2.76 | 0.64 | 1.53 | 4.01 | 1 | 17338 |
| Personality score | -0.70 | 0.11 | -0.91 | -0.50 | 1 | 31824 |

The models were controlled for random effects at the level of individuals and experimental assemblages of individuals. For each parameter, we present the mean value and 95% credible intervals (95% CI). Rhat is the potential scale reduction factor and indicates the MCMC convergence (at convergence Rhat = 1). Bulk_ESS and Tail_ESS are measures of effective sample size.

FIGURES

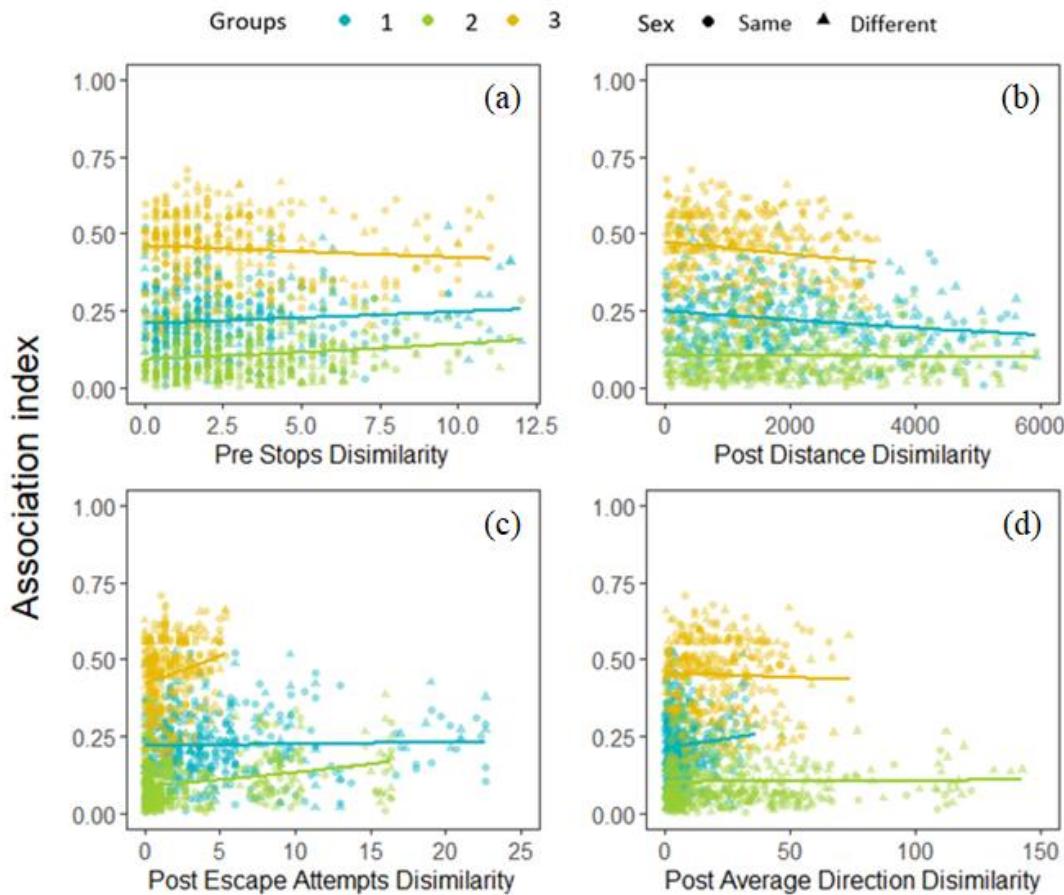


Figure 4. Relationship between dissimilarity in personality and dyadic association in *Porcellio scaber*. Structuring is observed with respect to the assembly of individuals in each group. Sex difference does not influence association intensity. (a) Association index increases with dissimilarity in number of stops pre-social expose, (b) Association index decreases with dissimilarity in distance post-social expose, (c) Association index increases with dissimilarity in escape attempts post-social expose, (d) Association index increases with dissimilarity in average direction post-social expose but present a marginal effect.

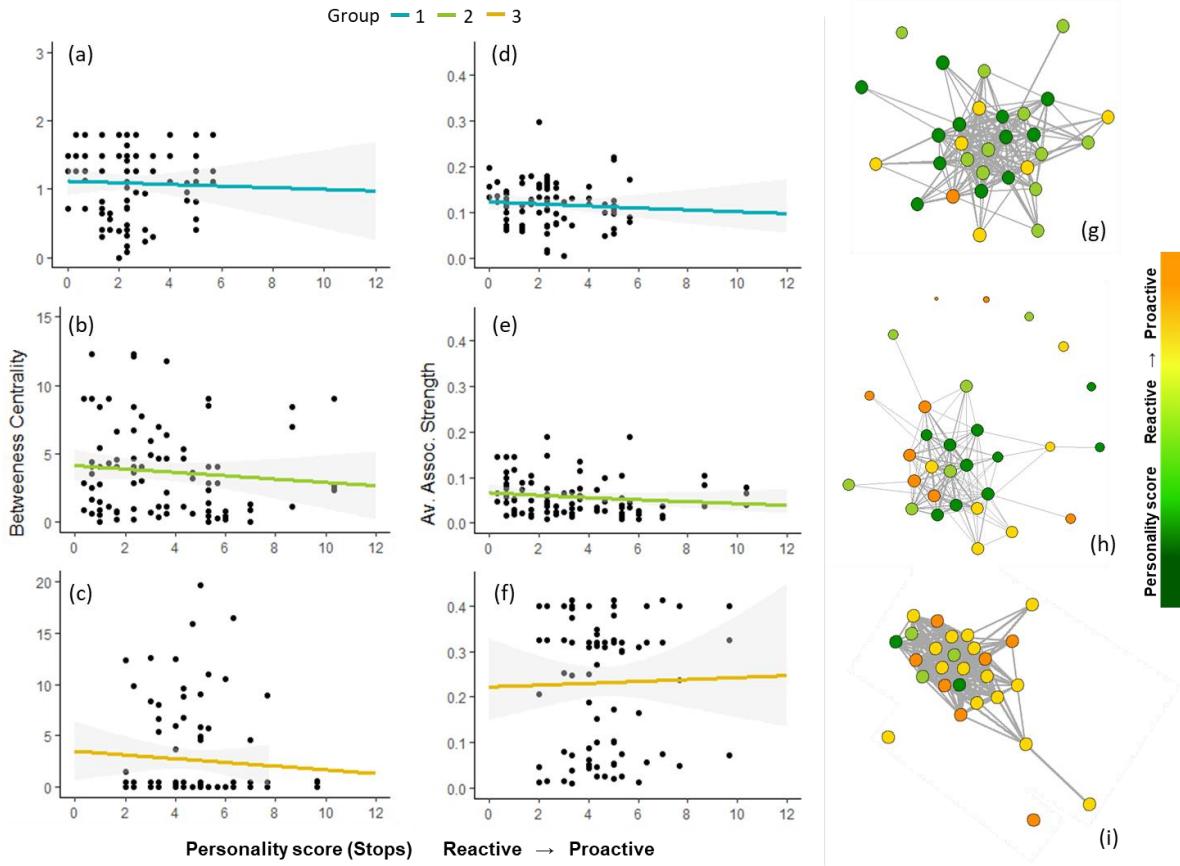


Figure 5. Relationship between personality, centrality measures and association social network in *Porcellio scaber*. (a-c) Betweenness centrality decreases with personality score described as a function of number of stops in group 2 and 3, no definite effect was recorded in group 1; (d-f) Average association strength decreases with personality score described as a function of number of stops in group 1 and 2, no definite effect was recorded in group 3. (g-i) are the network graphical representations of groups 1, 2 and 3, respectively, where values below the mean have been omitted for graphical reasons. The node color represents the personality score, ranging from the most proactive phenotypes, in orange, to the most reactive, in green. Intermediate phenotypes have been colored in yellow and lime green. The size of the nodes represents the degree centrality. The weight of the links has been represented by the thickness of the lines.

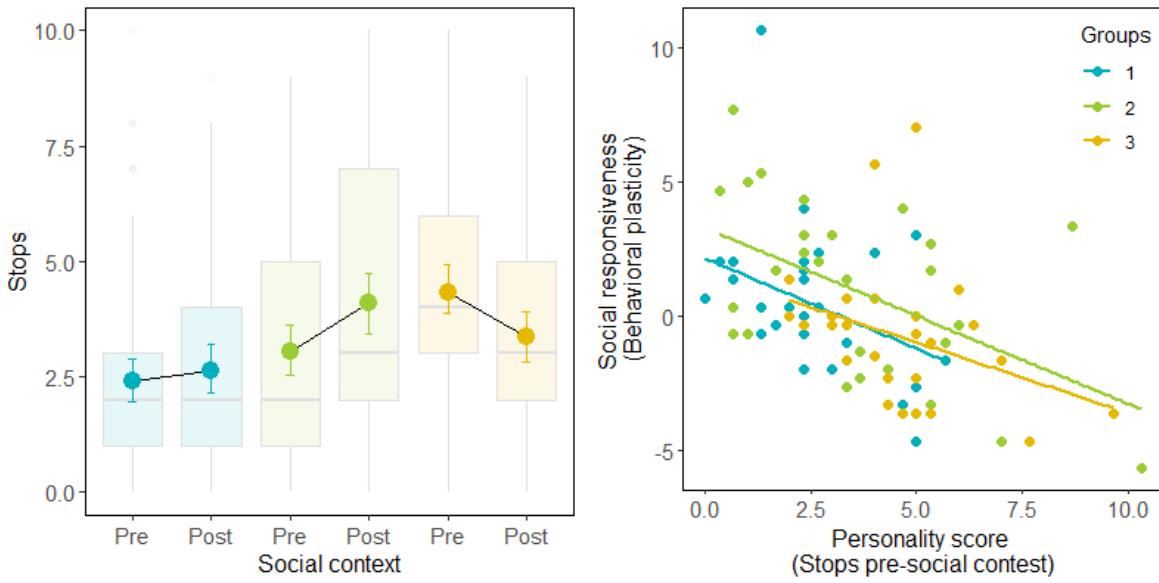


Figure 6. Performance of *P. scaber* individuals expressed in the number of stops across social context. (Left) Behavioral reaction norm of the number of stops across the social context. We found no difference in behavioral performance on this variable in relation to the social context, but it can be observed that there is a tendency to increase behavioral expression in groups 1 and 2, and a decrease in group 3. (Right) Influence of the personality score represented by the number of stops before the social contest on social responsiveness (behavioral plasticity). We found that personality score was negatively related to social responsiveness, i.e., proactive individuals tended to decrease behavioral expression after the social contest and reactive individuals expressed behavior to a greater extent after the contest.

SUPPLEMENTARY MATERIAL 1

Table S1. Kernel correlation between behaviors and body size.

| Behaviors | Length | Width | Dist. | Stops | Immob. | Esc.att | Mob.Int. | Esc.Int. | Speed | Av.direct. | Sd.direct. | Turns |
|------------------------------|--------|-------|---------|---------|---------|---------|----------|----------|--------|------------|------------|-------|
| Length | 1 | | | | | | | | | | | |
| Width | 0.50** | 1 | | | | | | | | | | |
| Distance | 0.24 | 0.21 | 1 | | | | | | | | | |
| Stops | -0.15 | -0.14 | -0.24** | 1 | | | | | | | | |
| Immobility | -0.16 | -0.16 | -0.42** | 0.5*** | 1 | | | | | | | |
| Escape attempts | 0.17 | 0.16 | 0.15 | -0.20* | -0.30* | 1 | | | | | | |
| Mobility interval | -0.06 | -0.05 | -0.06 | 0.25*** | 0.13 | -0.04 | 1 | | | | | |
| Escape interval | 0.11 | 0.10 | 0.15 | -0.16 | -0.25 | 0.55*** | 0.02 | 1 | | | | |
| Speed | 0.24 | 0.21 | 0.84*** | -0.25** | -0.38** | 0.13 | -0.08 | 0.11 | 1 | | | |
| Average direction | 0.13 | 0.12 | 0.36* | -0.22* | -0.32** | 0.12 | -0.11 | 0.12 | 0.34** | 1 | | |
| Directional deviation | 0.09 | 0.09 | 0.23 | -0.07 | -0.14 | 0.07 | 0.04 | 0.06 | 0.23 | 0.08 | 1 | |
| Turns | 0.17 | 0.18 | 0.51** | -0.02 | -0.13 | 0.01 | 0.05 | 0.04 | 0.46* | 0.15 | 0.17 | 1 |

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Table S2. Analysis of behavioral repeatability at the original locality level with original behaviors. Significant probability was highlighted in bold.

| Variables | Original Location | SE | Confidence Interval | | p |
|---|-------------------|------|---------------------|-------|------|
| | | | 2.5% | 97.5% | |
| Pre-Social Exposure | | | | | |
| Distance | 0.00 | 0.02 | 0.00 | 0.07 | 0.50 |
| Stops | 0.00 | 0.02 | 0.00 | 0.06 | 0.50 |
| Immobility | 0.00 | 0.00 | 0.00 | 0.00 | 1.00 |
| Escape attempts | 0.04 | 0.04 | 0.00 | 0.15 | 0.17 |
| Mobility interval | 0.00 | 0.02 | 0.00 | 0.05 | 0.46 |
| Escape interval | 0.06 | 0.05 | 0.00 | 0.17 | 0.05 |
| Speed | 0.00 | 0.02 | 0.00 | 0.06 | 1.00 |
| Average direction | 0.01 | 0.02 | 0.00 | 0.06 | 0.40 |
| Sd. Direction | 0.01 | 0.02 | 0.00 | 0.08 | 0.31 |
| Turns | 0.00 | 0.02 | 0.00 | 0.06 | 0.42 |
| Post-Social Exposure | | | | | |
| Distance | 0.00 | 0.03 | 0.00 | 0.10 | 1.00 |
| Stops | 0.03 | 0.04 | 0.00 | 0.15 | 0.20 |
| Immobility | 0.00 | 0.03 | 0.00 | 0.10 | 1.00 |
| Escape attempts | 0.01 | 0.03 | 0.00 | 0.11 | 0.41 |
| Mobility interval | 0.00 | 0.02 | 0.00 | 0.06 | 1.00 |
| Escape interval | 0.00 | 0.02 | 0.00 | 0.07 | 1.00 |
| Speed | 0.00 | 0.03 | 0.00 | 0.10 | 1.00 |
| Average direction | 0.01 | 0.02 | 0.00 | 0.08 | 0.41 |
| Sd. Direction | 0.00 | 0.01 | 0.00 | 0.05 | 1.00 |
| Turns | 0.00 | 0.03 | 0.00 | 0.09 | 0.46 |
| Average Pre and Post Social Exposure | | | | | |
| Distance | 0.00 | 0.00 | 0.00 | 0.00 | 1.00 |
| Stops | 0.00 | 0.00 | 0.00 | 0.00 | 1.00 |
| Immobility | 0.00 | 0.02 | 0.00 | 0.06 | 0.50 |
| Escape attempts | 0.03 | 0.04 | 0.00 | 0.12 | 0.17 |
| Mobility interval | 0.00 | 0.01 | 0.00 | 0.04 | 1.00 |
| Escape interval | 0.03 | 0.03 | 0.00 | 0.11 | 0.08 |
| Speed | 0.00 | 0.02 | 0.00 | 0.06 | 1.00 |

| | | | | | |
|-------------------|------|------|------|------|------|
| Average direction | 0.00 | 0.01 | 0.00 | 0.03 | 1.00 |
| Sd. Direction | 0.00 | 0.01 | 0.00 | 0.02 | 1.00 |
| Turns | 0.00 | 0.01 | 0.00 | 0.04 | 0.50 |

SE: standard error, p : distribution probability. Confidence Interval based two-tailed test.

Table S3. Probabilities recorded from the distributions of randomizations at the network and node level. The observed test statistic can be larger or smaller than the random one, and two-tailed values are used. The result is significant at $p=0.05$ if less than 2.5% (0.025) of the random values are greater than the observed value, or if more than 97.5% (0.975) of the random values are greater than the observed value. Significant probability was highlighted in bold. “n. v” represents networks whose coefficients do not vary due to the low variability between centrality values.

| Group | Obs. | Degree Centr. | | Betweenness | | Eigen Value | | Av. Assoc. strength | |
|-------|------|---------------|-------|-------------|-------|-------------|-------|---------------------|-------|
| | | Network | Node | Network | Node | Network | Node | Network | Node |
| 1 | 1 | 0.005 | 0.063 | 0 | 0.065 | 0.008 | 0.072 | 0 | 0.067 |
| | 2 | 0.045 | 0.202 | 0 | 0.005 | 0.083 | 0.283 | 0.137 | 0.364 |
| | 3 | 0.297 | 0.435 | 0.221 | 0.24 | 0.295 | 0.446 | 0.582 | 0.538 |
| 2 | 1 | 0 | 0.001 | 0 | 0.029 | 0 | 0.004 | 0 | 0.004 |
| | 2 | 0.168 | 0.456 | 0.071 | 0.42 | 0.226 | 0.508 | 0.001 | 0.112 |
| | 3 | 0.047 | 0.368 | 0 | 0.089 | 0.1 | 0.392 | 0 | 0.138 |
| 3 | 1 | 0.395 | 0.386 | 0.098 | 0.23 | 0.515 | 0.461 | 1 | 0.976 |
| | 2 | 0.719 | 0.523 | 0.65 | n.v | 0.695 | 0.536 | 0.997 | 0.758 |
| | 3 | 0.603 | 0.468 | 0.451 | 0.259 | 0.646 | 0.526 | 0.008 | 0.362 |

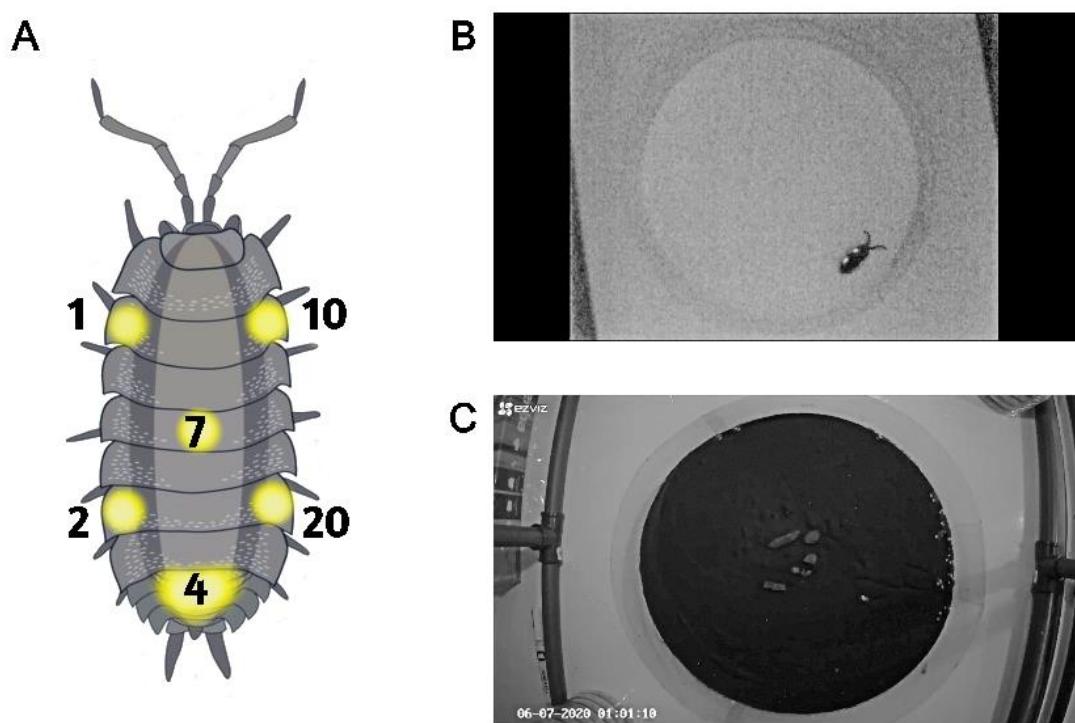


Figure S1. Methodological aspects related to video recordings in isolated and social environments (A) Identification of individuals by marking (B) Recording of behaviors in an isolated and novel environment (C) Recording of social behaviors in a common arena.

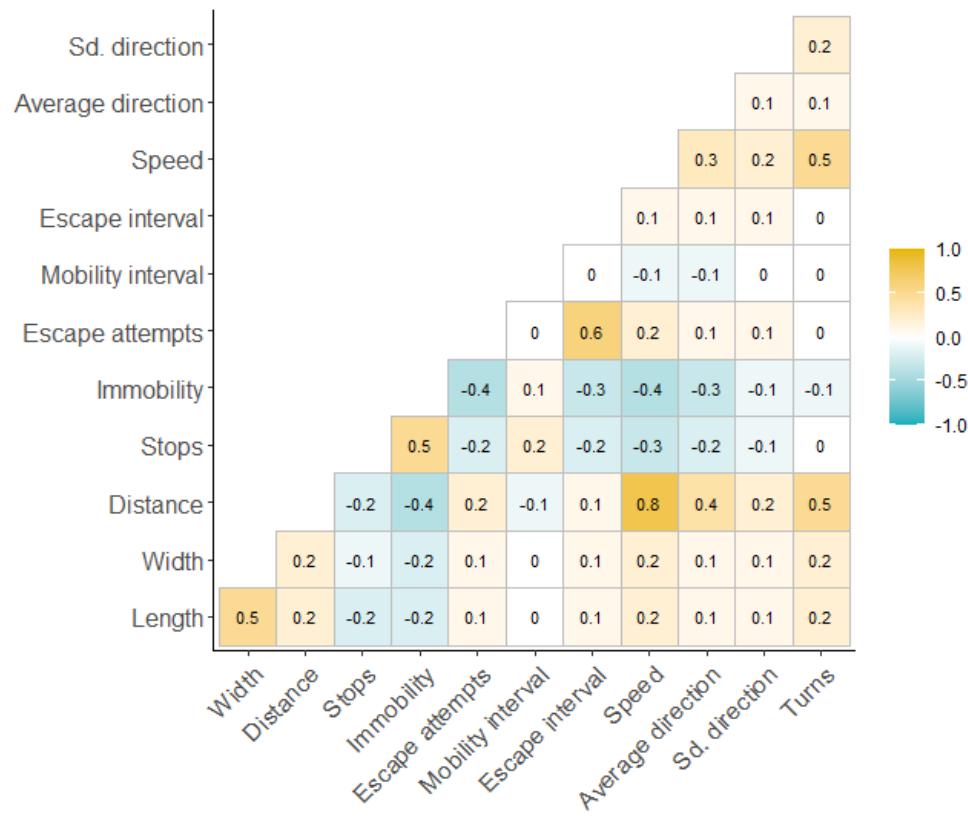


Figure S2. Kernel correlation between original behaviors and body size.

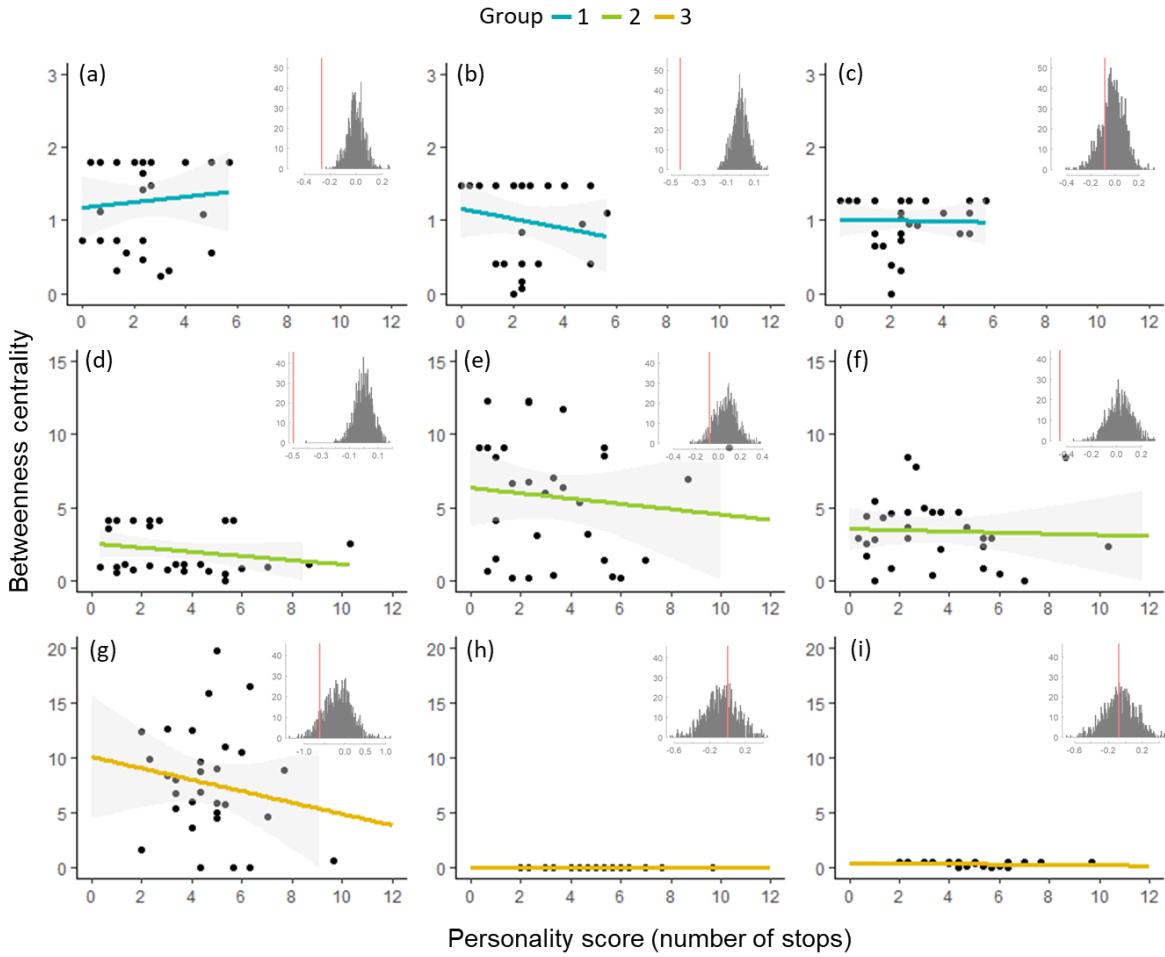


Figure S3. Relationship between personality and betweenness centrality in *Porcellio scaber*. In general terms betweenness centrality decreases with personality score described as a function of number of stops in group 2 and 3, no definite effect was recorded in group 1. (a), (b) and (c) represent the sequence of three daily observations of group 1 respectively. (d), (e) and (f) represent the sequence of three daily observations of group 2 respectively. (g), (h) and (i) represent the sequence of three daily observations of group 3 respectively. The distribution of expected values by permutation of networks is shown in the upper left corner. The observed coefficient value (red vertical line) is significantly different than expected by chance (the black histogram) in group 3.

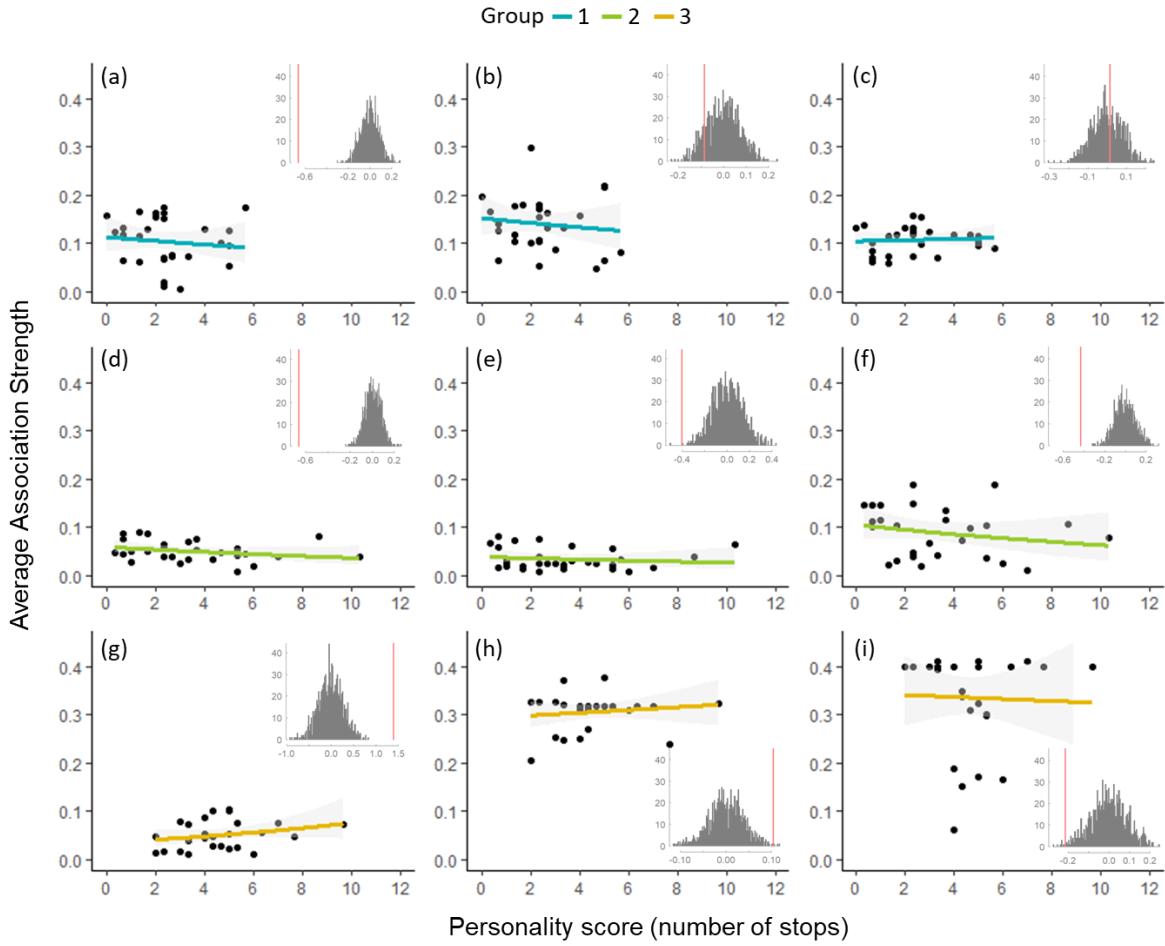


Figure S4. Relationship between personality and average association strength in *Porcellio scaber*. In general terms average association strength decreases with personality score described as a function of number of stops in group 2 and 3, no definite effect was recorded in group 1. (a), (b) and (c) represent the sequence of three daily observations of group 1 respectively. (d), (e) and (f) represent the sequence of three daily observations of group 2 respectively. (g), (h) and (i) represent the sequence of three daily observations of group 3 respectively. The distribution of expected values by permutation of networks is shown in the upper left corner. The observed coefficient value (red vertical line) is significantly different than expected by chance (the black histogram) in group 1.

APPENDIX 1

EFFECTS MODEL IN DYADIC ASSOCIATIONS

```
brm(Formula: log(weight of edges in networks) ~ log(distance.pre.distance)  
+ log(1 + distance.pre.stops) + log(1 + distance.pre.rearing)  
+ log(distance.pre.direction) + log (distance.post.distance) + log (1  
+ distance.post.stops) + log (1 + distance.post.rearing)  
+ log (distance.post.direction) + distance.sex + distance.pop  
+ (1 | mm(id1,id2)|group),  
iter = 10000, warmup = 4000, cores = 5, chains = 5,  
control = list(adapt_delta = 0.999, max_treedepth = 20),  
family = "gaussian")
```

PERSONALITY EFFECTS MODELS IN CENTRALITY MEASURES

```
brm(Formula: Gaussianize(degree) ~ log(pre.distance) + log(1 + pre.n.stops)
     + log(1 + pre.rearing.up) + log(pre.direction.prom) + log(post.distance)
     + log(1 + post.n.stops) + log(1 + post.rearing.up)
     + log(post.direction.prom) + sex + (1 | id) + (1 | population)
     + (1 | observation:group),
prior = c(set_prior("normal(0, 1)", class = "b"),
          set_prior("cauchy(0, 2)", class = "sd")), iter = 10000,
warmup = 4000, chains = 5,
cores = 5, control = list(adapt_delta = 0.999, max_treedepth = 15),
family = "skew_normal")
```

```
brm(Formula: betweenness ~ log(pre.distance) + log(1 + pre.n.stops)
     + log(1 + pre.rearing.up) + log(pre.direction.prom) + log(post.distance)
     + log(1 + post.n.stops) + log(1 + post.rearing.up)
     + log(post.direction.prom) + sex + (1 | id) + (1 | population)
     + (1 | observation:group),
prior = c(set_prior("normal(0, 1)", class = "b"),
          set_prior("cauchy(0, 2)", class = "sd")), iter = 10000,
warmup = 4000, chains = 5, cores = 5,
control = list(adapt_delta = 0.999, max_treedepth = 15),
family = "hurdle_lognormal"))
```

```

brm(Formula: log (Average association strength) ~ log(pre.distance)

+ log(1 + pre.n.stops) + log(1 + pre.rearing.up) + log(pre.direction.prom)

+ log (post.distance) + log (1 + post.n.stops) + log (1 + post.rearing.up)

+ log (post.direction.prom) + sex + (1 | id) + (1 | population)

+ (1 | observation:group),

prior = c(set_prior("normal(0,1)", class = "b"),

set_prior("cauchy(0,2)", class = "sd")), iter = 10000,

warmup = 4000, chains = 5, cores = 5,

control = list(adapt_delta = 0.999, max_treedepth = 15),

family = "Gaussian"))

```

APPENDIX 2

Table A1. Conditional modes of random effects in the degree centrality model. Random effects at the level of individuals, locality of origin and observations per experimental group of individuals were controlled for in the model.

| Individual identity | | | | |
|----------------------------|------------------|-----------------|------------------|-------------|
| | Intercept | Estimate | Est.Error | 2.5% |
| 1.1 | | -0.0013 | 0.1959 | -0.4298 |
| 1.10 | | 0.0094 | 0.1979 | 0.4576 |
| 1.11 | | -0.0194 | 0.2090 | -0.5127 |
| 1.12 | | 0.0002 | 0.1988 | -0.4268 |
| 1.13 | | 0.0103 | 0.1990 | -0.4049 |
| 1.14 | | -0.0076 | 0.2068 | -0.4671 |
| 1.15 | | -0.0226 | 0.2087 | -0.5136 |
| 1.16 | | -0.0082 | 0.1997 | -0.4536 |
| 1.17 | | 0.0056 | 0.1997 | -0.4195 |
| 1.18 | | 0.0153 | 0.1985 | -0.3878 |
| 1.2 | | 0.0232 | 0.1961 | -0.3712 |
| 1.20 | | 0.0185 | 0.1957 | -0.3824 |
| 1.21 | | -0.0030 | 0.1990 | -0.4331 |
| 1.22 | | 0.0347 | 0.2003 | -0.3413 |
| 1.23 | | -0.0305 | 0.2123 | -0.5463 |
| 1.24 | | -0.0107 | 0.2068 | -0.4794 |
| 1.25 | | -0.0272 | 0.2152 | -0.5384 |
| 1.26 | | 0.0098 | 0.1992 | -0.4000 |
| 1.27 | | -0.0034 | 0.2035 | -0.4514 |
| 1.28 | | -0.0423 | 0.2178 | -0.5768 |
| 1.29 | | 0.0426 | 0.2010 | -0.3259 |
| 1.3 | | 0.0209 | 0.1949 | -0.3686 |
| 1.30 | | 0.0067 | 0.2007 | -0.4167 |
| 1.4 | | 0.0169 | 0.2003 | -0.3873 |
| 1.5 | | -0.0049 | 0.2036 | -0.4573 |
| 1.6 | | 0.0018 | 0.2009 | -0.4293 |
| 1.7 | | -0.0182 | 0.2013 | -0.4822 |
| 1.8 | | 0.0221 | 0.2006 | -0.3716 |
| 1.9 | | -0.0082 | 0.2008 | -0.4548 |
| 2.1 | | 0.0177 | 0.1959 | -0.3746 |
| 2.11 | | 0.0238 | 0.1965 | -0.3646 |
| 2.12 | | 0.0099 | 0.1919 | -0.3914 |
| 2.13 | | -0.0069 | 0.1998 | -0.4429 |
| 2.14 | | -0.0457 | 0.2140 | -0.5792 |
| 2.15 | | 0.0726 | 0.2081 | -0.2650 |
| 2.16 | | -0.0750 | 0.2382 | -0.6941 |
| 2.17 | | 0.0034 | 0.2007 | -0.4295 |
| 2.18 | | 0.0219 | 0.1968 | -0.3659 |
| 2.19 | | 0.0026 | 0.1956 | -0.4203 |
| 2.2 | | -0.0534 | 0.2234 | -0.6211 |
| 2.20 | | 0.0470 | 0.2053 | -0.3168 |
| 2.21 | | 0.0363 | 0.2028 | -0.3356 |
| 2.22 | | 0.0147 | 0.1984 | -0.3817 |
| 2.23 | | 0.0626 | 0.2063 | -0.2792 |
| 2.24 | | -0.0189 | 0.2123 | -0.5173 |
| 2.25 | | 0.0774 | 0.2180 | -0.2589 |

| | | | | |
|------|---------|--------|---------|--------|
| 2.26 | 0.0061 | 0.1917 | -0.3984 | 0.4400 |
| 2.27 | -0.0698 | 0.2359 | -0.6886 | 0.3015 |
| 2.28 | 0.0128 | 0.2001 | -0.3969 | 0.4758 |
| 2.29 | -0.0326 | 0.2129 | -0.5544 | 0.3708 |
| 2.3 | -0.0077 | 0.2013 | -0.4512 | 0.4192 |
| 2.30 | 0.0030 | 0.1955 | -0.4190 | 0.4340 |
| 2.4 | -0.0459 | 0.2164 | -0.5860 | 0.3456 |
| 2.5 | -0.0342 | 0.2127 | -0.5479 | 0.3624 |
| 2.6 | -0.0292 | 0.2118 | -0.5327 | 0.3835 |
| 2.7 | 0.0056 | 0.1976 | -0.4162 | 0.4468 |
| 2.8 | -0.0518 | 0.2183 | -0.6049 | 0.3311 |
| 2.9 | 0.0774 | 0.2235 | -0.2679 | 0.6608 |
| 3.1 | -0.0088 | 0.2036 | -0.4661 | 0.4223 |
| 3.10 | -0.0203 | 0.2076 | -0.5047 | 0.4019 |
| 3.11 | -0.0216 | 0.2112 | -0.5156 | 0.4004 |
| 3.12 | -0.0058 | 0.2025 | -0.4615 | 0.4244 |
| 3.14 | 0.0090 | 0.1983 | -0.4037 | 0.4513 |
| 3.15 | 0.0043 | 0.1999 | -0.4252 | 0.4516 |
| 3.16 | 0.0211 | 0.1969 | -0.3743 | 0.4854 |
| 3.17 | -0.0001 | 0.2011 | -0.4375 | 0.4451 |
| 3.18 | -0.0154 | 0.2050 | -0.4945 | 0.4036 |
| 3.19 | -0.0064 | 0.2012 | -0.4502 | 0.4273 |
| 3.20 | -0.0114 | 0.2074 | -0.4826 | 0.4209 |
| 3.22 | 0.0293 | 0.1986 | -0.3525 | 0.5049 |
| 3.23 | -0.0072 | 0.2052 | -0.4689 | 0.4284 |
| 3.24 | -0.0169 | 0.2100 | -0.4938 | 0.4143 |
| 3.25 | -0.0075 | 0.2058 | -0.4675 | 0.4302 |
| 3.26 | -0.0058 | 0.2028 | -0.4583 | 0.4222 |
| 3.27 | -0.0107 | 0.2082 | -0.4847 | 0.4292 |
| 3.28 | -0.0050 | 0.2046 | -0.4484 | 0.4412 |
| 3.29 | -0.0085 | 0.2044 | -0.4704 | 0.4178 |
| 3.3 | 0.0139 | 0.2004 | -0.3957 | 0.4739 |
| 3.30 | -0.0160 | 0.2017 | -0.4803 | 0.3986 |
| 3.4 | -0.0100 | 0.2034 | -0.4624 | 0.4207 |
| 3.5 | 0.1089 | 0.2321 | -0.2096 | 0.7425 |
| 3.6 | -0.0164 | 0.2058 | -0.4847 | 0.4023 |
| 3.7 | 0.0040 | 0.2017 | -0.4224 | 0.4515 |
| 3.8 | -0.0125 | 0.2069 | -0.4890 | 0.4210 |
| 3.9 | -0.0232 | 0.2108 | -0.5246 | 0.3877 |

Locality of origin

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|-------------|----------|-----------|---------|--------|
| Locality 2 | 0.0037 | 0.1335 | -0.2845 | 0.3065 |
| Locality 6 | 0.0000 | 0.1327 | -0.2879 | 0.2890 |
| Locality 7 | -0.0011 | 0.1359 | -0.2957 | 0.3005 |
| Locality 8 | 0.0155 | 0.1408 | -0.2630 | 0.3411 |
| Locality 9 | -0.0039 | 0.1373 | -0.3150 | 0.2940 |
| Locality 10 | 0.0025 | 0.1395 | -0.2967 | 0.3235 |
| Locality 11 | -0.0195 | 0.1401 | -0.3495 | 0.2639 |
| Locality 12 | -0.0379 | 0.1477 | -0.4094 | 0.2288 |
| Locality 13 | 0.0450 | 0.1502 | -0.2097 | 0.4324 |
| Locality 14 | -0.0029 | 0.1375 | -0.3004 | 0.2964 |

Observation by group

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|-----------------------|----------|-----------|----------|---------|
| Group 1 observation 1 | 2.8240 | 1.2344 | 0.3978 | 5.2580 |
| Group 1 observation 2 | 2.1965 | 1.2196 | -0.2177 | 4.5984 |
| Group 1 observation 3 | -8.1322 | 1.2671 | -10.6996 | -5.7068 |

| | | | | |
|-----------------------|---------|--------|---------|--------|
| Group 2 observation 1 | 2.9035 | 1.2354 | 0.4744 | 5.3540 |
| Group 2 observation 2 | 0.4848 | 1.2240 | -1.9620 | 2.8746 |
| Group 2 observation 3 | -1.1327 | 1.2627 | -3.6319 | 1.3452 |
| Group 3 observation 1 | 1.6264 | 1.2288 | -0.8154 | 4.0480 |
| Group 3 observation 2 | 0.0004 | 1.2272 | -2.4513 | 2.3919 |
| Group 3 observation 3 | -1.3569 | 1.2508 | -3.8575 | 1.0847 |

Table A2. Conditional modes of random effects in the betweenness centrality model. Random effects at the level of individuals, locality of origin and observations per experimental group of individuals were controlled for in the model.

| Individual identity | | | | | |
|----------------------------|------------------|-----------------|------------------|-------------|--------------|
| | Intercept | Estimate | Est.Error | 2.5% | 97.5% |
| 1.1 | | -0.0462 | 0.1481 | -0.4118 | 0.2183 |
| 1.10 | | -0.0215 | 0.1425 | -0.3477 | 0.2626 |
| 1.11 | | -0.0472 | 0.1512 | -0.4208 | 0.2209 |
| 1.12 | | 0.0097 | 0.1428 | -0.2913 | 0.3332 |
| 1.13 | | 0.0251 | 0.1446 | -0.2576 | 0.3675 |
| 1.14 | | -0.0246 | 0.1468 | -0.3742 | 0.2668 |
| 1.15 | | -0.0624 | 0.1582 | -0.4650 | 0.1988 |
| 1.16 | | 0.0051 | 0.1441 | -0.3044 | 0.3230 |
| 1.17 | | -0.0036 | 0.1453 | -0.3255 | 0.3096 |
| 1.18 | | 0.0200 | 0.1455 | -0.2760 | 0.3566 |
| 1.2 | | 0.0415 | 0.1490 | -0.2341 | 0.3980 |
| 1.20 | | 0.0221 | 0.1436 | -0.2654 | 0.3566 |
| 1.21 | | 0.0100 | 0.1466 | -0.2958 | 0.3398 |
| 1.22 | | 0.0301 | 0.1466 | -0.2477 | 0.3760 |
| 1.23 | | -0.0142 | 0.1441 | -0.3431 | 0.2851 |
| 1.24 | | -0.0190 | 0.1458 | -0.3553 | 0.2730 |
| 1.25 | | 0.0096 | 0.1441 | -0.2968 | 0.3348 |
| 1.26 | | 0.0133 | 0.1444 | -0.2848 | 0.3439 |
| 1.27 | | 0.0316 | 0.1459 | -0.2454 | 0.3816 |
| 1.28 | | -0.0741 | 0.1628 | -0.4857 | 0.1816 |
| 1.29 | | 0.0373 | 0.1478 | -0.2391 | 0.3988 |
| 1.3 | | 0.0497 | 0.1535 | -0.2195 | 0.4320 |
| 1.30 | | -0.0156 | 0.1440 | -0.3454 | 0.2824 |
| 1.4 | | 0.0369 | 0.1482 | -0.2386 | 0.3983 |
| 1.5 | | -0.0054 | 0.1427 | -0.3204 | 0.2999 |
| 1.6 | | -0.0062 | 0.1412 | -0.3173 | 0.2933 |
| 1.7 | | -0.0400 | 0.1487 | -0.4007 | 0.2326 |
| 1.8 | | 0.0488 | 0.1510 | -0.2175 | 0.4227 |
| 1.9 | | -0.0322 | 0.1466 | -0.3854 | 0.2468 |
| 2.1 | | -0.0154 | 0.1463 | -0.3509 | 0.2854 |
| 2.11 | | 0.0583 | 0.1555 | -0.2005 | 0.4581 |
| 2.12 | | -0.0259 | 0.1454 | -0.3679 | 0.2576 |
| 2.13 | | 0.0071 | 0.1417 | -0.2963 | 0.3229 |
| 2.14 | | -0.0336 | 0.1470 | -0.3881 | 0.2478 |
| 2.15 | | 0.0593 | 0.1541 | -0.1970 | 0.4503 |
| 2.16 | | -0.1416 | 0.2047 | -0.6819 | 0.1047 |
| 2.17 | | -0.0038 | 0.1501 | -0.3369 | 0.3183 |
| 2.18 | | 0.0210 | 0.1477 | -0.2778 | 0.3675 |
| 2.19 | | -0.0174 | 0.1470 | -0.3573 | 0.2853 |
| 2.2 | | -0.0981 | 0.1744 | -0.5532 | 0.1480 |
| 2.20 | | 0.0228 | 0.1507 | -0.2747 | 0.3719 |
| 2.21 | | 0.0450 | 0.1491 | -0.2285 | 0.4125 |
| 2.22 | | -0.0024 | 0.1463 | -0.3161 | 0.3154 |
| 2.23 | | 0.0607 | 0.1568 | -0.2015 | 0.4547 |
| 2.24 | | 0.0413 | 0.1501 | -0.2330 | 0.4091 |
| 2.25 | | 0.0576 | 0.1545 | -0.2045 | 0.4512 |
| 2.26 | | -0.0437 | 0.1490 | -0.4081 | 0.2283 |
| 2.27 | | -0.0536 | 0.1568 | -0.4506 | 0.2141 |
| 2.28 | | 0.0282 | 0.1449 | -0.2539 | 0.3731 |
| 2.29 | | 0.0135 | 0.1430 | -0.2866 | 0.3373 |

| | | | | |
|------|---------|--------|---------|--------|
| 2.3 | 0.0280 | 0.1452 | -0.2502 | 0.3695 |
| 2.30 | 0.0165 | 0.1448 | -0.2736 | 0.3481 |
| 2.4 | -0.0529 | 0.1526 | -0.4346 | 0.2113 |
| 2.5 | 0.0117 | 0.1449 | -0.2918 | 0.3406 |
| 2.6 | -0.0148 | 0.1433 | -0.3418 | 0.2812 |
| 2.7 | 0.0061 | 0.1465 | -0.3083 | 0.3347 |
| 2.8 | -0.0241 | 0.1516 | -0.3820 | 0.2755 |
| 2.9 | 0.0806 | 0.1663 | -0.1677 | 0.5039 |
| 3.1 | -0.0439 | 0.1535 | -0.4259 | 0.2323 |
| 3.10 | -0.0194 | 0.1452 | -0.3530 | 0.2777 |
| 3.11 | -0.0030 | 0.1459 | -0.3255 | 0.3117 |
| 3.12 | -0.0176 | 0.1481 | -0.3556 | 0.2854 |
| 3.14 | 0.0360 | 0.1512 | -0.2457 | 0.3998 |
| 3.15 | 0.0182 | 0.1463 | -0.2742 | 0.3585 |
| 3.16 | 0.0385 | 0.1521 | -0.2420 | 0.4075 |
| 3.17 | 0.0165 | 0.1491 | -0.2879 | 0.3604 |
| 3.18 | -0.0092 | 0.1465 | -0.3412 | 0.2975 |
| 3.19 | 0.0109 | 0.1475 | -0.2992 | 0.3463 |
| 3.20 | -0.0231 | 0.1482 | -0.3745 | 0.2701 |
| 3.22 | 0.0327 | 0.1516 | -0.2589 | 0.3945 |
| 3.23 | -0.0251 | 0.1473 | -0.3736 | 0.2661 |
| 3.24 | 0.0011 | 0.1469 | -0.3151 | 0.3188 |
| 3.25 | 0.0172 | 0.1476 | -0.2795 | 0.3574 |
| 3.26 | -0.0011 | 0.1475 | -0.3252 | 0.3210 |
| 3.27 | 0.0323 | 0.1506 | -0.2522 | 0.3924 |
| 3.28 | -0.0486 | 0.1555 | -0.4396 | 0.2231 |
| 3.29 | 0.0142 | 0.1469 | -0.2844 | 0.3536 |
| 3.3 | 0.0273 | 0.1504 | -0.2699 | 0.3896 |
| 3.30 | -0.0430 | 0.1532 | -0.4195 | 0.2369 |
| 3.4 | 0.0152 | 0.1479 | -0.2884 | 0.3547 |
| 3.5 | 0.0583 | 0.1593 | -0.2124 | 0.4604 |
| 3.6 | -0.0233 | 0.1483 | -0.3739 | 0.2718 |
| 3.7 | -0.0330 | 0.1543 | -0.4072 | 0.2567 |
| 3.8 | 0.0018 | 0.1437 | -0.3098 | 0.3154 |
| 3.9 | -0.0301 | 0.1504 | -0.3920 | 0.2563 |

Locality of origin

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|-------------|----------|-----------|---------|--------|
| Locality 2 | 0.0099 | 0.0894 | -0.1721 | 0.2122 |
| Locality 6 | 0.0270 | 0.0934 | -0.1454 | 0.2499 |
| Locality 7 | -0.0233 | 0.0953 | -0.2477 | 0.1575 |
| Locality 8 | 0.0618 | 0.1096 | -0.0992 | 0.3405 |
| Locality 9 | 0.0054 | 0.0913 | -0.1887 | 0.2093 |
| Locality 10 | -0.0179 | 0.0953 | -0.2422 | 0.1677 |
| Locality 11 | -0.0318 | 0.0957 | -0.2647 | 0.1376 |
| Locality 12 | -0.0716 | 0.1152 | -0.3692 | 0.0856 |
| Locality 13 | 0.0153 | 0.0972 | -0.1792 | 0.2423 |
| Locality 14 | 0.0245 | 0.0945 | -0.1532 | 0.2525 |

Observation by group

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|-----------------------|----------|-----------|---------|--------|
| Group 1 observation 1 | -0.2224 | 0.4173 | -1.0535 | 0.6078 |
| Group 1 observation 2 | -0.0118 | 0.4178 | -0.8383 | 0.8318 |
| Group 1 observation 3 | 1.4294 | 0.4283 | 0.5818 | 2.2987 |
| Group 2 observation 1 | -0.4681 | 0.4175 | -1.3024 | 0.3597 |
| Group 2 observation 2 | 0.6707 | 0.4155 | -0.1444 | 1.5038 |
| Group 2 observation 3 | -0.0043 | 1.1259 | -2.2603 | 2.2825 |
| Group 3 observation 1 | -0.3000 | 0.4194 | -1.1348 | 0.5304 |

| | | | | |
|-----------------------|---------|--------|---------|---------|
| Group 3 observation 2 | 0.5886 | 0.4192 | -0.2348 | 1.4370 |
| Group 3 observation 3 | -1.5908 | 0.4276 | -2.4542 | -0.7477 |

Table A3. Conditional modes of random effects in the average association strength model. Random effects at the level of individuals, locality of origin and observations per experimental group of individuals were controlled for in the model.

| Individual identity | | | | |
|----------------------------|------------------|-----------------|------------------|-------------|
| | Intercept | Estimate | Est.Error | 2.5% |
| 1.1 | | 0.0131 | 0.1261 | -0.2461 |
| 1.10 | | -0.0433 | 0.1339 | -0.3515 |
| 1.11 | | -0.0064 | 0.1272 | -0.2774 |
| 1.12 | | 0.0450 | 0.1327 | -0.2041 |
| 1.13 | | 0.0754 | 0.1401 | -0.1569 |
| 1.14 | | 0.0033 | 0.1278 | -0.2636 |
| 1.15 | | 0.0442 | 0.1318 | -0.2033 |
| 1.16 | | 0.0141 | 0.1280 | -0.2478 |
| 1.17 | | 0.0207 | 0.1294 | -0.2390 |
| 1.18 | | 0.0604 | 0.1373 | -0.1821 |
| 1.2 | | 0.0430 | 0.1306 | -0.2028 |
| 1.20 | | 0.0337 | 0.1315 | -0.2168 |
| 1.21 | | -0.0509 | 0.1351 | -0.3644 |
| 1.22 | | 0.0370 | 0.1314 | -0.2132 |
| 1.23 | | -0.0025 | 0.1290 | -0.2765 |
| 1.24 | | 0.0661 | 0.1397 | -0.1737 |
| 1.25 | | -0.0258 | 0.1304 | -0.3143 |
| 1.26 | | 0.0121 | 0.1280 | -0.2531 |
| 1.27 | | -0.0022 | 0.1270 | -0.2742 |
| 1.28 | | -0.1405 | 0.1683 | -0.5484 |
| 1.29 | | 0.0242 | 0.1291 | -0.2309 |
| 1.3 | | 0.0074 | 0.1265 | -0.2540 |
| 1.30 | | 0.0460 | 0.1333 | -0.2014 |
| 1.4 | | -0.0140 | 0.1305 | -0.3013 |
| 1.5 | | -0.0694 | 0.1377 | -0.3924 |
| 1.6 | | -0.0468 | 0.1342 | -0.3605 |
| 1.7 | | -0.1021 | 0.1509 | -0.4658 |
| 1.8 | | 0.0133 | 0.1305 | -0.2561 |
| 1.9 | | -0.0375 | 0.1300 | -0.3361 |
| 2.1 | | -0.0640 | 0.1403 | -0.3956 |
| 2.11 | | -0.0753 | 0.1398 | -0.4086 |
| 2.12 | | 0.0017 | 0.1286 | -0.2730 |
| 2.13 | | 0.0353 | 0.1327 | -0.2168 |
| 2.14 | | -0.0046 | 0.1280 | -0.2795 |
| 2.15 | | -0.0047 | 0.1269 | -0.2736 |
| 2.16 | | -0.1649 | 0.1786 | -0.5910 |
| 2.17 | | -0.0226 | 0.1381 | -0.3325 |
| 2.18 | | 0.0559 | 0.1368 | -0.1896 |
| 2.19 | | -0.0019 | 0.1319 | -0.2817 |
| 2.2 | | -0.0668 | 0.1362 | -0.3941 |
| 2.20 | | 0.0335 | 0.1366 | -0.2287 |
| 2.21 | | 0.0236 | 0.1289 | -0.2343 |
| 2.22 | | 0.0492 | 0.1356 | -0.1994 |
| 2.23 | | 0.0396 | 0.1316 | -0.2096 |
| 2.24 | | -0.0286 | 0.1308 | -0.3229 |
| 2.25 | | 0.1129 | 0.1543 | -0.1158 |
| 2.26 | | 0.0667 | 0.1373 | -0.1680 |
| 2.27 | | -0.1158 | 0.1564 | -0.4978 |
| 2.28 | | -0.0126 | 0.1282 | -0.2915 |

| | | | | |
|------|---------|--------|---------|--------|
| 2.29 | -0.0526 | 0.1317 | -0.3611 | 0.1818 |
| 2.3 | 0.0892 | 0.1449 | -0.1431 | 0.4383 |
| 2.30 | 0.0096 | 0.1291 | -0.2613 | 0.2887 |
| 2.4 | -0.0029 | 0.1279 | -0.2774 | 0.2694 |
| 2.5 | -0.0047 | 0.1283 | -0.2819 | 0.2609 |
| 2.6 | -0.0077 | 0.1287 | -0.2886 | 0.2547 |
| 2.7 | 0.0572 | 0.1358 | -0.1843 | 0.3787 |
| 2.8 | -0.0874 | 0.1526 | -0.4595 | 0.1586 |
| 2.9 | 0.0825 | 0.1434 | -0.1528 | 0.4231 |
| 3.1 | -0.0060 | 0.1302 | -0.2851 | 0.2659 |
| 3.10 | -0.0540 | 0.1359 | -0.3713 | 0.1905 |
| 3.11 | -0.0108 | 0.1306 | -0.2938 | 0.2580 |
| 3.12 | 0.0056 | 0.1281 | -0.2604 | 0.2773 |
| 3.14 | 0.0137 | 0.1287 | -0.2489 | 0.2974 |
| 3.15 | 0.0198 | 0.1299 | -0.2409 | 0.3094 |
| 3.16 | 0.0449 | 0.1358 | -0.2045 | 0.3596 |
| 3.17 | 0.0494 | 0.1354 | -0.1999 | 0.3659 |
| 3.18 | -0.0535 | 0.1326 | -0.3626 | 0.1852 |
| 3.19 | 0.0747 | 0.1400 | -0.1610 | 0.4066 |
| 3.20 | -0.0234 | 0.1294 | -0.3132 | 0.2319 |
| 3.22 | -0.0230 | 0.1293 | -0.3081 | 0.2357 |
| 3.23 | -0.0515 | 0.1338 | -0.3656 | 0.1923 |
| 3.24 | -0.0213 | 0.1314 | -0.3190 | 0.2396 |
| 3.25 | -0.0410 | 0.1309 | -0.3420 | 0.2017 |
| 3.26 | 0.0076 | 0.1302 | -0.2650 | 0.2909 |
| 3.27 | 0.0069 | 0.1297 | -0.2572 | 0.2886 |
| 3.28 | 0.1014 | 0.1507 | -0.1303 | 0.4628 |
| 3.29 | -0.0369 | 0.1310 | -0.3400 | 0.2136 |
| 3.3 | 0.0215 | 0.1293 | -0.2372 | 0.3108 |
| 3.30 | -0.0562 | 0.1353 | -0.3758 | 0.1855 |
| 3.4 | -0.0181 | 0.1281 | -0.3032 | 0.2402 |
| 3.5 | 0.0375 | 0.1305 | -0.2109 | 0.3384 |
| 3.6 | 0.0222 | 0.1303 | -0.2385 | 0.3109 |
| 3.7 | 0.0247 | 0.1300 | -0.2348 | 0.3162 |
| 3.8 | 0.0059 | 0.1272 | -0.2594 | 0.2794 |
| 3.9 | 0.0044 | 0.1275 | -0.2648 | 0.2780 |

Locality of origin

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|-------------|----------|-----------|---------|--------|
| Locality 2 | -0.1072 | 0.1008 | -0.3381 | 0.0354 |
| Locality 6 | 0.0335 | 0.0823 | -0.1191 | 0.2206 |
| Locality 7 | 0.0113 | 0.0824 | -0.1550 | 0.1892 |
| Locality 8 | 0.0573 | 0.0892 | -0.0892 | 0.2664 |
| Locality 9 | -0.0456 | 0.0844 | -0.2425 | 0.1020 |
| Locality 10 | -0.0127 | 0.0830 | -0.1958 | 0.1544 |
| Locality 11 | 0.0375 | 0.0817 | -0.1088 | 0.2233 |
| Locality 12 | -0.0001 | 0.0825 | -0.1735 | 0.1724 |
| Locality 13 | 0.0690 | 0.0993 | -0.0853 | 0.3051 |
| Locality 14 | -0.0442 | 0.0859 | -0.2411 | 0.1063 |

Observation by group

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|-----------------------|----------|-----------|---------|---------|
| Group 1 observation 1 | -0.0170 | 0.3344 | -0.6910 | 0.6477 |
| Group 1 observation 2 | -0.6414 | 0.3329 | -1.3120 | 0.0240 |
| Group 1 observation 3 | -0.8678 | 0.3364 | -1.5409 | -0.1940 |
| Group 2 observation 1 | 0.3938 | 0.3360 | -0.2783 | 1.0614 |
| Group 2 observation 2 | -1.1060 | 0.3331 | -1.7859 | -0.4441 |
| Group 2 observation 3 | 1.0697 | 0.3371 | 0.3979 | 1.7507 |

| | | | | |
|-----------------------|---------|--------|---------|--------|
| Group 3 observation 1 | 0.2054 | 0.3349 | -0.4542 | 0.8743 |
| Group 3 observation 2 | -0.2073 | 0.3326 | -0.8734 | 0.4535 |
| Group 3 observation 3 | 1.0977 | 0.3369 | 0.4338 | 1.7794 |

Table A4. Conditional modes of random effects in the social responsiveness model. Random effects at the level of individuals and group were controlled for in the model.

| Individual identity | | | | | |
|----------------------------|------------------|-----------------|------------------|-------------|--------------|
| | Intercept | Estimate | Est.Error | 2.5% | 97.5% |
| 1.1 | | 0.0531 | 0.4560 | -0.8426 | 1.1449 |
| 1.10 | | 0.0065 | 0.4364 | -0.9671 | 0.9368 |
| 1.11 | | 0.0454 | 0.4477 | -0.8618 | 1.1001 |
| 1.12 | | 0.0272 | 0.4532 | -0.9245 | 1.0614 |
| 1.13 | | 0.0142 | 0.4325 | -0.9192 | 0.9740 |
| 1.14 | | 0.1742 | 0.5356 | -0.6402 | 1.5632 |
| 1.15 | | -0.0296 | 0.4180 | -1.0171 | 0.8077 |
| 1.16 | | 0.0233 | 0.4396 | -0.9244 | 1.0320 |
| 1.17 | | -0.0371 | 0.4164 | -1.0278 | 0.7897 |
| 1.18 | | 0.0903 | 0.4751 | -0.7741 | 1.2819 |
| 1.2 | | 0.0838 | 0.4686 | -0.7870 | 1.2264 |
| 1.20 | | -0.1675 | 0.4392 | -1.3120 | 0.5120 |
| 1.21 | | -0.1385 | 0.4245 | -1.2221 | 0.5648 |
| 1.22 | | -0.0316 | 0.4172 | -0.9965 | 0.8073 |
| 1.23 | | 0.0029 | 0.4310 | -0.9511 | 0.9290 |
| 1.24 | | -0.3186 | 0.5058 | -1.6610 | 0.3204 |
| 1.25 | | -0.1223 | 0.4263 | -1.2053 | 0.5918 |
| 1.26 | | 0.0342 | 0.4458 | -0.8831 | 1.0558 |
| 1.27 | | 0.0662 | 0.4617 | -0.8232 | 1.1709 |
| 1.28 | | -0.0980 | 0.4204 | -1.1509 | 0.6388 |
| 1.29 | | 0.0316 | 0.4467 | -0.8930 | 1.0812 |
| 1.3 | | 0.0322 | 0.4429 | -0.8968 | 1.0401 |
| 1.30 | | -0.0748 | 0.4208 | -1.1038 | 0.6995 |
| 1.4 | | 0.0988 | 0.4829 | -0.7566 | 1.3026 |
| 1.5 | | 0.0528 | 0.4573 | -0.8340 | 1.1211 |
| 1.6 | | -0.0246 | 0.4191 | -1.0017 | 0.8363 |
| 1.7 | | -0.0169 | 0.4299 | -1.0183 | 0.8858 |
| 1.8 | | 0.0173 | 0.4373 | -0.9221 | 1.0067 |
| 1.9 | | -0.0021 | 0.4229 | -0.9534 | 0.9080 |
| 2.1 | | -0.2134 | 0.4502 | -1.3796 | 0.4273 |
| 2.11 | | 0.0547 | 0.4561 | -0.8431 | 1.1468 |
| 2.12 | | 0.0550 | 0.4585 | -0.8527 | 1.1232 |
| 2.13 | | -0.1504 | 0.4273 | -1.2657 | 0.5249 |
| 2.14 | | 0.0506 | 0.4554 | -0.8761 | 1.1294 |
| 2.15 | | 0.0890 | 0.4796 | -0.7734 | 1.2570 |
| 2.16 | | 0.0490 | 0.4591 | -0.8675 | 1.1366 |
| 2.17 | | 0.0944 | 0.4851 | -0.7790 | 1.2974 |
| 2.18 | | 0.1188 | 0.4927 | -0.7253 | 1.3535 |
| 2.19 | | -0.1887 | 0.4444 | -1.3393 | 0.4804 |
| 2.2 | | 0.0412 | 0.4430 | -0.8611 | 1.0756 |
| 2.20 | | 0.1345 | 0.4976 | -0.6678 | 1.4095 |
| 2.21 | | 0.0898 | 0.4796 | -0.7816 | 1.2605 |
| 2.22 | | 0.0750 | 0.4646 | -0.8049 | 1.1809 |
| 2.23 | | -0.0607 | 0.4227 | -1.0652 | 0.7458 |
| 2.24 | | -0.0166 | 0.4234 | -0.9742 | 0.8559 |
| 2.25 | | 0.0701 | 0.4638 | -0.8276 | 1.1961 |
| 2.26 | | 0.0347 | 0.4521 | -0.9070 | 1.0606 |
| 2.27 | | 0.0784 | 0.4681 | -0.7843 | 1.2087 |

| | | | | |
|------|---------|--------|---------|--------|
| 2.28 | -0.0373 | 0.4224 | -1.0498 | 0.7889 |
| 2.29 | 0.0758 | 0.4627 | -0.7953 | 1.2066 |
| 2.3 | -0.1200 | 0.4260 | -1.2097 | 0.5842 |
| 2.30 | 0.0385 | 0.4472 | -0.9018 | 1.0757 |
| 2.4 | 0.0851 | 0.4789 | -0.8073 | 1.2558 |
| 2.5 | -0.1047 | 0.4298 | -1.2166 | 0.6119 |
| 2.6 | 0.1063 | 0.4864 | -0.7437 | 1.3158 |
| 2.7 | -0.0189 | 0.4245 | -0.9892 | 0.8479 |
| 2.8 | -0.1308 | 0.4378 | -1.2554 | 0.5791 |
| 2.9 | -0.0178 | 0.4325 | -0.9891 | 0.8732 |
| 3.1 | 0.0384 | 0.4444 | -0.8765 | 1.0636 |
| 3.10 | 0.1238 | 0.4924 | -0.7008 | 1.3766 |
| 3.11 | 0.0524 | 0.4584 | -0.8623 | 1.1378 |
| 3.12 | 0.1538 | 0.5139 | -0.6737 | 1.4816 |
| 3.14 | 0.0601 | 0.4585 | -0.8372 | 1.1540 |
| 3.15 | 0.0528 | 0.4488 | -0.8400 | 1.1086 |
| 3.16 | -0.0558 | 0.4231 | -1.0764 | 0.7578 |
| 3.17 | -0.0123 | 0.4219 | -0.9945 | 0.8756 |
| 3.18 | -0.0028 | 0.4259 | -0.9631 | 0.8933 |
| 3.19 | -0.0483 | 0.4215 | -1.0598 | 0.7710 |
| 3.20 | -0.1935 | 0.4397 | -1.3336 | 0.4620 |
| 3.22 | 0.0142 | 0.4346 | -0.9316 | 0.9716 |
| 3.23 | 0.0795 | 0.4713 | -0.7925 | 1.2376 |
| 3.24 | -0.0461 | 0.4091 | -1.0351 | 0.7487 |
| 3.25 | -0.0061 | 0.4260 | -0.9552 | 0.9119 |
| 3.26 | 0.0273 | 0.4420 | -0.9129 | 1.0432 |
| 3.27 | 0.0401 | 0.4527 | -0.8915 | 1.1198 |
| 3.28 | 0.0425 | 0.4540 | -0.8692 | 1.1015 |
| 3.29 | 0.0228 | 0.4349 | -0.9095 | 0.9968 |
| 3.3 | -0.1746 | 0.4321 | -1.2984 | 0.4931 |
| 3.30 | 0.0001 | 0.4292 | -0.9603 | 0.9217 |
| 3.4 | 0.0352 | 0.4537 | -0.9105 | 1.0835 |
| 3.5 | -0.1556 | 0.4252 | -1.2702 | 0.4963 |
| 3.6 | 0.0423 | 0.4589 | -0.8767 | 1.1182 |
| 3.7 | -0.1220 | 0.4231 | -1.1885 | 0.5828 |
| 3.8 | 0.0435 | 0.4553 | -0.8738 | 1.1167 |
| 3.9 | -0.0456 | 0.4109 | -1.0109 | 0.7599 |

| Group | Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|---------|-----------|----------|-----------|---------|--------|
| Group 1 | | -0.1210 | 0.5298 | -1.2295 | 0.9525 |
| Group 2 | | 0.1643 | 0.5373 | -0.7311 | 1.4364 |
| Group 3 | | 0.0385 | 0.5300 | -0.9820 | 1.2224 |

CAPÍTULO III

PERSONALITY DRIVES SOCIAL NICHE SPECIALIZATION IN *Porcellio scaber*.

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Manuscrito sometido a Animal Behaviour

ABSTRACT

Social niche specialization is based on the selection of certain social conditions that allow individuals to reduce costs and conflicts with their conspecifics. This process may be limited by the consistent behavioral responses linked to the personality of individuals to the changing social environments of which they are a part. Here we define social niches by examining the consistency of social roles based on association and agonistic interactions, including dominance status, through social network analysis. Next, we evaluate the relationship of social niche to the personality of individuals using the social niche hypothesis approach. We evidence consistency in social roles at the individual level across different social environments. We also show that both personality and other socially influenced behaviors modulate the social roles and interindividual relationships that define dominance status. We propose that social niche construction exists in *Porcellio scaber* and that personality and behavioral responsiveness influence social performance in agonistic interactions. We suggest that this approach may be repeatable in organisms with social aggregation capacity, such as invertebrates.

INTRODUCTION

In animals living in groups, the social environment is a crucial factor in the maintenance of consistent individual differences in behavioral traits (Bergmüller & Taborsky, 2010). The behavior of animals in a social environment is expected to be plastic in response to environmental stimuli and interaction dynamics with conspecifics (Bergmüller *et al.*, 2010; Sih *et al.*, 2004). However, the social responsiveness of individuals may be limited by personality and individual state-dependent conditions (Biro & Stamps, 2008; Kelleher *et al.*, 2018; Réale *et al.*, 2007). Personality is inter-individual differences in the expression of behaviors that are temporally and contextually consistent (Dall *et al.*, 2004; Dingemanse *et al.*, 2010). Thus, there will be individuals who can change their behavioral tendencies in response to heterogeneities in the environment, while others will maintain their behavioral types regardless of environmental changes (Dall *et al.*, 2012; Réale & Dingemanse, 2010). This behavioral pattern could be especially beneficial for species living in societies, since if the behaviors of group mates are consistent over time and across different contexts, the outcomes of future interactions will be predictable (Dall *et al.*, 2004; Wolf *et al.*, 2011). In this sense, mechanisms that reduce the extent of conflicts among the parties involved should be favored by selection, given that conflicts involve increased interaction costs among the parties involved (Aureli & Waal, 2000; Bergmüller & Taborsky, 2010).

One of the most studied hypotheses describing optimal clustering is the "social niche specialization hypothesis". This hypothesis is derived from the central idea of ecological niche specialization (Hutchinson, 1957), and is based on the ability of individuals to select certain social conditions and avoid others to reduce conflicts within populations (Bergmüller & Taborsky, 2010). Individuals in a population can perform different social roles when they

adopt a social niche or achieve social niche specialization by establishing their behavior according to a particular social role (Bergmüller & Taborsky, 2010; Montiglio *et al.*, 2013). The social role, which could be understood as a complex of behaviors that an individual performs in response to a challenge that occurs in the social environment, may show a certain level of social responsiveness depending on the individual's response capacity. In this sense, it is expected that the way individuals occupy social roles or positions in their social group is related to their personality (Réale & Dingemanse, 2010; Webster & Ward, 2011), either because their personality enables good performance when intraspecific competition occurs (Cote & Clobert, 2007; Dingemanse & Réale, 2005) or because their personality tends to promote agonistic behaviors that shape dominance status (Liker & Barta, 2002; Sapolsky, 2005).

The study of aggregation processes provides an excellent approach evaluate the nature of social niche specialization and its relationship to animal personality. Aggregation of individuals is a process that can occur around a resource or by the attraction between individuals (Camazine *et al.*, 2001). In addition, it is known that animal personality plays a fundamental role in the structuring and social organization of the aggregates since it can modulate collective decision-making (Aplin *et al.*, 2014; Jolles *et al.*, 2017), competition for limited resources (Hall *et al.*, 2017) and reproductive strategies (Miranda-de la Lama *et al.*, 2019; Smith & Blumstein, 2008). In aggregations, social niche specialization may arise as a behavioral strategy to avoid the high energetic costs in fluctuating social environments, associated with multiple types of interactions occurring simultaneously in the group (Bergmüller & Taborsky, 2010; Saltz *et al.*, 2016).

The vertebrates are the group for which the most social behaviors based on niche specialization have been described. For example, non-receptive guppy females (*Poecilia*

reticulata) associate with receptive females in avoid male harassment (Brask *et al.*, 2012), or in pigtailed macaques *Macaca nemestrina* group structure is dependent on policing functions performed by a small group of individuals (Flack *et al.*, 2006), and female capuchins *Cebus capuchinus* establish their social rank based on encounters when the social environment changes (Silk, 2007). In invertebrates, as in vertebrates, socially guided behaviors such as social learning and social influence have been identified (Webster & Fiorito, 2001). In this sense, although niche specialization has been less explored, it is expected to occur in populations. Female cockroaches *Diploptera punctata* are known to be significantly more gregarious than males and form the core of the social group (Stanley *et al.*, 2018). It is also known that individuals of *Drosophila melanogaster* that sustain behaviors that generate a more favorable social environment for their mating strategy are more reproductively successful (Saltz & Foley, 2011). For *Porcellio scaber*, it is known that local aggregations of individuals are directed by individual preferences based on chemical signals and that aggregation dynamics and collective decision-making are controlled by social interactions among conspecifics (Broly *et al.*, 2016; Devigne *et al.*, 2011; Takeda, 1984). In addition, individuals in this species exhibit consistently differentiated behavioral responses to environmental and social stimuli (Anselme, 2013, 2015, 2018; Tuf *et al.*, 2015). Although there are no specific studies on social niche consistency in *P. scaber*, work on another terrestrial isopod species (*Oniscus asellus*) has shown that interindividual variation in behavior plays an important role in the emergent group-level behaviors, but the level of social organization was not sufficiently structured to provide more information (Drinkwater, 2020). We expected that the social roles of individuals, defined by their social behaviors within groups, are consistent across different social assemblages manifesting levels of social specialization. Furthermore, we also suggest that individuals' personalities and coping

abilities influence social roles. Finally, the social environment is a selective force that can shape the way personality types interact with each other, and we expect that the assortment of individuals occurs in a non-random manner and exhibit some level of structure (Krause *et al.*, 2010; Stamps & Groothuis, 2010).

To test these predictions, we assessed the existence of social niches by quantifying the consistency of social roles in different random assemblages of *P. scaber* individuals under laboratory conditions. Additionally, we determined the effect of personality, individual dependent states, and dominance relationships on individuals' social attributes (association and aggression). Finally, we evaluated interindividual association and dominance relationships based on agonistic behaviors at the dyadic scale to understand the nature of the mechanisms that promote group structure and the expression of social roles. We use social network centrality measures based on interindividual association and aggression as a proxy for social roles.

MATERIALS AND METHODS

Collect and housing conditions

We collected ninety woodlice (*P. scaber*) from teen localities in Valdivia, Chile. The individuals were separated by localities and maintained in PVC containers with organic matter in different states of decomposition (barks, roots, and leaves) and wet soil. We maintained the substrate constantly kept humid to avoid the desiccation of the individuals. Similarly, ventilation was allowed through perforations in the upper part of the containers to prevent mold formation. The individuals were acclimatized for ten days under controlled conditions (temperature: $16 \pm 3^\circ\text{C}$ and humidity: $80 \pm 10\% \text{ RH}$). Before group formation,

everyone was sexed and marked with a unique identification code using a white non-toxic acrylic marker and isolated in a 95 mm diameter Petri dish with wet plaster as substrate and provided with decomposing organic matter. All individuals remained isolated for 24 hours before the personality test.

Personality test

We performed the estimation of personality traits under isolation. The personality test consisted of 5 minutes of recording in a 94 mm Petri dish with a homogeneous novel substrate (sterilized paper filter) inside a dark chamber. The behavioral variables we quantified from the video recordings were: (a) distance traveled, as the linear distance covered; (b) the number of stops, the number of times the individual stopped; (c) immobility time, a sum of all time intervals that the individual remains immobile or with the low sensory activity of the antennae; (d) Escape attempts, the number of escape attempts on the arena side walls; (e) mobility intervals, the average duration of mobility intervals; f) Escape interval, the average time interval between two events of escape attempt; g) speed, the average speed of displacement; h) average direction angle, the average direction of displacement based on the sexagesimal system; i) directional deviation, the angle of deviation of displacement; and j) a number of turns, indicates the number of times the individual changed direction by more than 45° (modified from Anselme, 2015, 2018). This process was repeated at the end of each random assembly of individuals to include possible personality changes influenced by the social environment (see below). We used the free software BORIS (Friard & Gamba, 2016) and the R packages "pathtrackR" (Harmer & Thomas, 2019) to extract the information on the behaviors from the video recordings.

To assess the correlated behavioral traits defining personality, we conducted Kendall's correlation analysis between all behavior displays and body size. We found significative correlations between some behavioral variables and non-correlation with body size (Table S1). Thus, we performed a repeatability test to evaluate the consistency of behavioral responses across different assemblies, controlling the locality of origin, sex, and pregnancy in females. Here we used the individual behavioral variables to determine the expression of personality. The traditional measure of repeatability can be defined as the proportion of the total variance accounted for by differences among groups (Sokal & Rohlf, 1995). Finally, we took the behavioral variables that showed significant repeatability and reduced them by eliminating those correlated with defining the variables representing personality in the subsequent analyses (Table S2). These variables were: distance, the number of stops, escape attempts and escape interval. Additionally, we decided to include directional deviance to include behaviors representing social responsiveness in different social environments. All analyses were realized in R software (R Development Core Team, 2012), and in a particular "rptR" package to quantify the repeatability of behaviors (Nakagawa & Schielzeth, 2010). For more details about the repeatability test see Supplementary Material 1-A.

Social assembly

To evaluate the consistency of social roles and their relationship with personality, we randomly established twenty assemblies of up to fifteen individuals each at the beginning of the experiment, where some were part of the assemblies up to five times. However, in some cases, the final number of individuals was reduced by mortality associated with aggression between individuals. Then, each of these assemblages was placed in a circular arena of 40 cm diameter, with a black painted plaster substrate and flexible PVC walls, for two

consecutive days. We propose the establishment phase during the first day, and from the second day onwards, we recorded the associations and agonistic behaviors. We consider an association when individuals are no more than one body length apart (approximately 10 mm) or when they are part of an aggregate and an agonistic behavior when an individual performs aggressive behavior to cause potential injury to another. Records were realized in darkness and consisted of 5-minute video recordings every two hours, from 00:00 to 04:00 hours, amounting to a total of three video samples per assemblage (modified from Drahokoupilová & Tuf, 2012). All records were realized using EZVIZ network video recorder (model EZWIRELESS X5C) and EZVIZ cameras (model C3W). From the video recordings, we constructed dyadic association matrices based on the time individuals spent together in each observation and dyadic aggression matrices based on the number of recorded agonistic behaviors.

Consistency of social roles

From the association matrices, we calculate the social attributes of individuals for both social components based on three network centrality metrics: degree centrality, betweenness centrality, and average association strength (Croft *et al.*, 2008). The degree represents an individual's direct connections (Freeman & Gosling, 2010). The betweenness reflects the number of shortest paths that pass through an individual to connect with other partners, meaning that individuals with higher values of betweenness play a critical role in connecting or transmitting information to other individuals that did not interact (Kulahci *et al.*, 2018; Lusseau & Newman, 2004). The average association strength is based on weighted networks and represents the average proportion of time everyone spends in association with others.

This metric is calculated by dividing the strength of the association by the degree (Aplin *et al.*, 2013; Croft *et al.*, 2008).

In the case of agonistic behavior-based centrality measures, we calculate degree centrality, in-degree centrality, out-degree centrality, betweenness centrality, and average aggression strength for further resolution. The degree represents the number of group members with whom an individual had conflicts, in-degree indicates the number of group members who assaulted a particular individual, and out-degree represents the number of group members whom a particular individual aggressed against (Kulahci *et al.*, 2018). Aggressivity betweenness represents the capacity of individuals to engage in aggressive events, either by attacking or being attacked. Average aggression strength refers to the number of times an individual assaults another. This value is calculated by dividing the aggression strength by the degree (Croft *et al.*, 2008).

To build the network and obtain the metrics, we will use the R packages called "sna" (Butts, 2015) and "igraph" (Csardi & Nepusz, 2005). Additionally, we calculate the dominance status of the individuals called "David's score" from the aggression matrices (David, 1988). The dyadic association ratio was estimated from the association matrices through the simple index ratio (Whitehead, 2008). Then, we assessed consistency in social roles, including dominance and the dyadic association index, by quantifying the repeatability of the social attributes expressed by everyone in each of the assemblages of which it was a part. We use the "rptR" package in R to quantify the repeatability (Nakagawa & Schielzeth, 2010). This approach allowed us to estimate niche specialization by approximating it as a function of the consistency of social behaviors.

Influence of personality on social roles

We assessed the effect of personality on individual social roles across different sets to induce variation in the social environment. For this purpose, we ran multilevel Bayesian models that included the personality of the individuals, based on individual behaviors consistent across variables, as fixed factors. Individual identity, sex-linked to reproductive status, locality of origin, and assembly were set as random factors. In addition, the models included an autoregressive term that considered observations of the same individual and was controlled for group size and the time sequence of each observation. The analysis of the models was carried out using R software (R Development Core Team, 2012) through the package "brms" (Bürkner, 2017). Convergence and stability of the Bayesian sampling have been assessed using R-hat, which should be below 1.01 (Vehtari *et al.*, 2021), and Effective Sample Size (ESS), which should be greater than 1000 (Bürkner, 2017). For details of the models used, see Supplementary Material 1-B.

Relationships at the dyad level

We evaluated the effect of personality, social responsiveness, and dominance status dissimilarity between individuals (Euclidean distance) on the dyadic associations' index (proportion of total time per observation that each pair of individuals spends in association). We also evaluated the effect of dyadic dissimilarity in personality and social responsiveness on dissimilarity in dominance status. We performed Bayesian multilevel models that included multi-membership and the nature of their interactions at the level of sex, pregnancy, and location of origin as random factors (modified from Hart *et al.*, 2021). In these models, we include dyadic dissimilarity in the distance, the number of stops, immobility, escape attempts, escape intervals, directional deviation, and body size. We also included group size

as a fixed factor to control the density-dependent effect. We calculated Euclidean distances using R software (R Development Core Team, 2012), and models were performed using R packages: "brms" (Bürkner, 2017) and "mm" (Altham & Hankin, 2012). The convergence and stability criteria were the same as in the previous analysis. For details of the models used, see Supplementary Material 1-C.

RESULTS

Consistency of social roles

Concerning social roles based on association behaviors, we found repeatability in the associative betweenness ($R = 0.11 \pm 0.07$, 95% CI [0.00 - 0.26], $p = 0.03$). We did not find repeatability in the weighted associative degree ($R = 0.01 \pm 0.02$, 95% CI [0.00 - 0.06], $p = 0.34$) nor in the mean association strength ($R = 0.03 \pm 0.03$, 95% CI [0.00 - 0.10], $p = 0.08$). Regarding agonistic behaviors, we found a significant effect at the individual level on the aggressiveness weighted degree ($R = 0.33 \pm 0.12$, 95% CI [0.13 - 0.59], $p < 0.01$), aggressiveness weighted in-degree ($R = 0.36 \pm 0.11$, 95% CI [0.12 - 0.55], $p = 0.02$), aggressiveness weighted out-degree ($R = 0.57 \pm 0.15$, 95% CI [0.23 - 0.79], $p < 0.01$) and aggressiveness betweenness ($R = 0.49 \pm 0.11$, 95% CI [0.19 - 0.60], $p = 0.03$). We did not find repeatability in average aggression strength ($R = 0.15 \pm 0.08$, 95% CI [0.02 - 0.32], $p = 0.33$). Complementarily, we found that the repeatability of the dominance status (David's score) was significant ($R = 0.15 \pm 0.07$, 95% CI [0.2 - 0.28], $p < 0.01$). Finally, we did not find repeatability in the dyadic-level association index between different sets of individuals ($R = 0.4 \pm 0.04$, 95% CI [0.0 - 0.14], $p = 0.25$). Thus, the intensity of the dyadic association

between pairs of individuals was dependent on the social environment given by the different assemblages of individuals.

Influence of personality on social roles

We found no evidence of an effect of personality on the social roles defined in terms of association (Table 1). When social role defined in terms of agonistic behaviors was assessed, we found a positive effect of directional deviation on weighted degree, weighted in-degree, and weighted out-degree (Table 2A-C and Figure 1). To aggressiveness betweenness, we found a non-significant effect of personality or intrinsic attributes of the individuals (Table 2D). Instead, we noted a positive effect of the number of stops on average aggression strength and a marginally positive effect of corporal size. Since the number of stops was consistent at the individual level, it is possible to confirm that personality influenced the intensity of agonistic behaviors at the individual level in general aspects (Table 2-E and Figure 2). We also found that the period in which individuals were subjected or group size, had a non-significant effect on the association and agonistic attributes. In addition, we found no influence of personality or group characteristics on the dominance status of everyone (Table 3). Furthermore, we found no effect of dominance status on the social roles linked to the associative capacity of individuals across assemblages in any of the centrality metrics evaluated (Table S3).

Relationships at the dyad level

Individuals with low dissimilarity in dominance status presented a more stable association, whereas individuals with an elevated level of dissimilarity (i.e., one dominated and one dominant individual) had less stable associations or were not associated (Table 3-A and Figure 3-A). In addition, we also detected a positive effect between dissimilarity and the

escape interval on the dyadic association index. This result presented a low power effect close to the marginal values (Table 3-B and Figure 3-B). Regarding dissimilarity in dominance status, we observed that dissimilarity in the number of stops, immobility time, number of escape attempts, and directional deviation had a marginal effect (Figure 4). We found no non-significant effect of either body size difference or group size on the dyadic association index or dissimilarity in dominance status. The relationship between sex level and reproductive status also had no effect on the dyadic association index and dissimilarity in dominance status (Table S4).

DISCUSSION

The social niche hypothesis describes how interindividual variation in behavior can lead to the specialization of different social roles that reduce conflict in populations (Bergmüller & Taborsky, 2010). Here we use centrality measures based on social network analyses of association and agonistic behaviors to define the social roles that individuals perform within a group, assess their consistency as a proxy for social niche across different social environments, and determine the influence of personality and intrinsic attributes of individuals on the expression of these social roles in *P. scaber*. We showed that certain behavioral patterns may be related to individuals' ability to engage in conflict, however, we do not find consistency in these behaviors. Furthermore, we observed that social roles can be described primarily by agonistic interaction-based sociability attributes rather than by association-based attributes.

We found that the betweenness based on association and agonistic interaction networks was consistent across the different social environments. However, we did not observe any effect of personality or individual intrinsic attributes on betweenness based on association and agonistic behaviors across changing social environments. We propose that betweenness in *P. scaber* is a consistent social attribute not related to exploratory or stereotypic behaviors performed in novel environments, whereby some individuals occupy a critical social role in transmitting information and consistently limit access to resources, referring to a particular social niche. This behavior has been observed in organisms with complex social systems, as in the case of *Macaca nemestrina*, where a few individuals can reduce conflicts and maintain stability in the group structure with their presents (Flack *et al.*, 2006). Gregarious animals depend on the transmission of information to improve habitat use, resource search, predator avoidance, and in an integrated way with the rest of the members, group decision-making (Conradt & Roper, 2003), so the role played by individuals with high intermediate values is fundamental in a group cohesion (Brent, 2015; Kanngiesser *et al.*, 2011; Manno, 2008).

On the other hand, we also found consistency in the three centrality measures based on the centrality degree of aggression. This result means that individuals who usually participated in agonistic events, either as aggressors or as aggrieved, were the same even when the social environment changed. Similarly, we found that the dominance status based on David's score was consistent across the different assemblages, but it had a lower magnitude of repeatability than the metrics describing the degree of aggression. In inter-individual aggression scenarios, it was common to observe that aggressors expelled from aggregates or kept aggrieved individuals on the periphery. This behavior may be explained by the fact that socially dominant individuals tend to improve and defend their access to limited resources, such as reproductive mates, which may result in increased reproductive success linked to social status

(Ellis, 1995; Pizzari & Birkhead, 2000). The literature argues that agonistic behavior-based dominance relationships can be driven by differences in individual characteristics among group members through repeated encounters that tend to favor one of the participants or a particular behavioral type (Chase, 1980). Positive correlations between aggressiveness behaviors, boldness attributes, and exploratory ability have been commonly reported at the individual level. This has made it possible to describe a spectrum of proactivity that helps to understand the relationship between social and isolation behaviors (Coppens *et al.*, 2010; Koolhaas *et al.*, 1999).

In our case, we found that directional deviance is positively related to the degree of centrality of individuals based on interindividual agonistic interaction. This result is particularly interesting because directional deviance did not show consistency at the individual level across different social environments, so it is not part of the complex of behaviors representing personality but represents the social responsiveness reflecting the impact of conflicts during the establishment of aggregates in changing social environments. It is known that movement can be influenced by the agonistic encounter, activity patterns, audacity of individuals, and by aspects of sociability and tolerance to the behavior of their group mates, so it is expected that the capacity for aggression and the effect of being aggrieved affect the performance of individuals and sensitivity level of the interactions (Shaw, 2020; Spiegel *et al.*, 2017).

In addition, we observed that the number of stops the animal performs when isolated in a novel environment is positively related to average aggression strength. In our case, the number of stops was consistent at the individual level, while average aggression strength was not repeatable at the individual level. Concerning dominance status, we found no effect of any behavior performed in a novel asocial environment or intrinsic attributes of individuals.

Therefore, we have support to suggest that aggression strength in *P. scaber* is an individual attribute related to stereotyped behaviors that define the personality of individuals.

The relationship between personality and the agonistic capacity that defines social status is variable and species-dependent (Favati *et al.*, 2013). For example, in individuals of three-spined sticklebacks (*Gasterosteus aculeatus*), those with higher levels of boldness tended to be more aggressive than shy individuals (Huntingford, 1976). Similarly, in great tits (*Parus major*), it was found that individuals with greater exploratory ability tended to be more successful in confrontations compared to less exploratory individuals. (Verbeek *et al.*, 1996).

In contrast, in mountain chickadees (*Poecile gambeli*), individuals with lower exploratory ability in familiar environments were more likely to be dominant than more exploratory individuals (Fox *et al.*, 2009). In the case of aquatic isopods, in the Socorro isopod (*Thermosphaeroma thermophilum*) the probability and latency of aggression are dependent on body size, the sex of the individual, and the sex of the target individual (Bleakley *et al.*, 2013). Our results found a marginal positive influence of body size on average aggression strength, but no difference between sexes or reproductive states. This difference in the sexual specificity of conflicts is likely because terrestrial isopods lack prolonged female guarding and tend to perform multiple copulations (Zimmer, 2001).

Concerning dominance based on agonistic interactions across changing social environments, we found that it did not influence the social roles of individuals as a function of their ability to associate. However, we observed that dyads composed of individuals with similar dominance status tend to be highly variable in the time they remain associated. As the dissimilarity in dominance status in the dyad increases, the time spent in association decreases considerably. This relationship suggests that dominance status in *P. scaber* has an inference on its affiliative behaviors at the relational level has an inference on its affiliative

behaviors at the relational level as an intrinsic attribute of the individual that conspecifics can recognize. The main groups of crustaceans are capable of emitting mechanical, visual, and chemical signals that transmit information about their physical and physiological conditions when they are in the presence of other individuals (Moore, 2007). In addition, terrestrial isopods present adaptations in their antennae that have allowed them to develop chemoreceptive functions that help in the search for potential reproductive mates and in the recognition of the status of conspecifics to reduce agonistic conflicts (Cardé & Millar, 2004; Lefebvre *et al.*, 2000).

In crustaceans, the behaviors that define social dominance are strongly influenced by the concentration of neuromodulatory substances that vary between individuals as an intrinsic trait (Yeh *et al.*, 1997). Furthermore, it is proposed that dominance relationships in this group are maintained by the capacity for individual recognition and status recognition, which reduces the number and intensity of continuous interactions between two individuals (Lord *et al.*, 2021; Zulandt Schneider *et al.*, 2001). In our dyad-level tests, we found that dissimilarity in personality and plastic behaviors were related to the dominance relationship. This relationship between dominance and personality was found only at the dyad level, and not when we performed the analyses at the individual level. So, we can reinforce the idea that dominance status depends on the recognition and how an individual can perceive the other. Our results support the idea that the expression of social roles arises from interindividual recognition and perception in dyadic interactions. In this sense, individual decision-making that defines group structure could be subject to conflict assessment based on sensory cues, particularly in cases of direct aggression events.

In conclusion, we found supporting evidence for the social niche hypothesis in *P. scaber*. First, we found that certain social roles at an individual level, defined by centrality attributes

based on association and agonistic behaviors, were consistent across different social environments. These social roles have been proposed as crucial in transmitting information and limiting access to resources, as well as being fundamental in the stability of social groups. Second, we found that individuals' personalities and behavioral responsiveness influence social role performance, primarily through agonistic interactions. Finally, we observed that the nature of the dominance status relationship between individuals and interindividual differences in personality influences the intensity of dyadic associations. This relationship is related to the similarity in their personalities and social responsiveness. Thus, the conflict assessment based on perceived dominance and behavioral types, or aggression *per se*, are the drivers of social stability and consistent expression of certain social roles in *P. scaber*.

REFERENCES

- Altham, P. M. E., & Hankin, R. K. S. (2012). Multivariate generalizations of the multiplicative binomial distribution: Introducing the MM package. *Journal of Statistical Software*, 46(12), 1–23. <https://doi.org/10.18637/jss.v046.i12>
- Anselme, P. (2013). Sensitivity to tactile novelty in the terrestrial isopod, *Porcellio scaber*. *Behavioural Processes*, 92, 52–59. <https://doi.org/10.1016/j.beproc.2012.10.007>
- Anselme, P. (2015). Enhanced exploratory activity in woodlice exposed to random visuo-tactile patterns. *Learning and Motivation*, 50, 48–58. <https://doi.org/10.1016/j.lmot.2014.09.002>

Anselme, P. (2018). Rotational stress influences sensitized, but not habituated, exploratory behaviors in the woodlouse, *Porcellio scaber*. *Learning & Behavior* 2018 46:3, 46(3), 294–305. <https://doi.org/10.3758/S13420-018-0315-4>

Aplin, L. M., Farine, D. R., Mann, R. P., & Sheldon, B. C. (2014). Individual-level personality influences social foraging and collective behaviour in wild birds. *Proceedings of the Royal Society B: Biological Sciences*, 281(1789), 20141016–20141016. <https://doi.org/10.1098/rspb.2014.1016>

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cole, E. F., Cockburn, A., & Sheldon, B. C. (2013). Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). *Ecology Letters*, 16(11), 1365–1372. <https://doi.org/10.1111/ele.12181>

Aureli, F., & Waal, F. B. M. (2000). Why natural conflict resolution? In F. Aureli & F. B. M. Waal (Eds.), *Natural conflict resolution* (pp. 3–10). University of California Press.

Bergmüller, R., Schürch, R., & Hamilton, I. M. (2010). Evolutionary causes and consequences of consistent individual variation in cooperative behaviour. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1553), 2751–2764. <https://doi.org/10.1098/rstb.2010.0124>

Bergmüller, R., & Taborsky, M. (2010). Animal personality due to social niche specialisation. *Trends in Ecology and Evolution*, 25(9), 504–511. <https://doi.org/10.1016/j.tree.2010.06.012>

Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology and Evolution*, 23(7), 361–368.
<https://doi.org/10.1016/j.tree.2008.04.003>

Bleakley, B. H., Welter, S. M., McCauley-Cole, K., Shuster, S. M., & Moore, A. J. (2013). Cannibalism as an interacting phenotype: Precannibalistic aggression is influenced by social partners in the endangered Socorro Isopod (*Thermosphaeroma thermophilum*). *Journal of Evolutionary Biology*, 26(4), 832–842.
<https://doi.org/10.1111/jeb.12098>

Brask, J. B., Croft, D. P., Thompson, K., Dabelsteen, T., & Darden, S. K. (2012). Social preferences based on sexual attractiveness: A female strategy to reduce male sexual attention. *Proceedings of the Royal Society B: Biological Sciences*, 279(1734), 1748–1753. <https://doi.org/10.1098/rspb.2011.2212>

Brent, L. J. N. (2015). Friends of friends: Are indirect connections in social networks important to animal behaviour? *Animal Behaviour*, 103, 211–222.
<https://doi.org/10.1016/j.anbehav.2015.01.020>

Broly, P., Mullier, R., Devigne, C., & Deneubourg, J.-L. (2016). Evidence of self-organization in a gregarious land-dwelling crustacean (Isopoda: Oniscidea). *Animal Cognition*, 19(1), 181–192. <https://doi.org/10.1007/s10071-015-0925-6>

Bürkner, P. C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, 80(1), 1–28. <https://doi.org/10.18637/jss.v080.i01>

Butts, C. T. (2015). Social Network Analysis with sna. *Journal of Statistical Software*, 24(6).

<https://doi.org/10.18637/jss.v024.i06>

Camazine, S., Deneubourg, J.-L., Franks, N. R., Sneyd, J., Theraula, G., & Bonabeau, E. (2001). *Self-Organization in Biological Systems*. Princeton University Press.

<https://doi.org/10.1515/9780691212920>

Cardé, R. T., & Millar, J. G. (Eds.). (2004). *Advances in Insect Chemical Ecology* (1st ed.).

Cambridge University Press. <https://doi.org/10.1017/CBO9780511542664>

Chase, I. D. (1980). Social Process and Hierarchy Formation in Small Groups: A Comparative Perspective. *American Sociological Review*, 45(6), 905–924.

<https://doi.org/10.2307/2094909>

Conradt, L., & Roper, T. J. (2003). Group decision-making in animals. *Nature*, 421(6919), Article 6919. <https://doi.org/10.1038/nature01294>

Coppens, C. M., de Boer, S. F., & Koolhaas, J. M. (2010). Coping styles and behavioural flexibility: Towards underlying mechanisms. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 4021–4028.

<https://doi.org/10.1098/rstb.2010.0217>

Cote, J., & Clobert, J. (2007). Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society B: Biological Sciences*, 274(1608), 383–390. <https://doi.org/10.1098/rspb.2006.3734>

Croft, D. P., James, R., & Krause, J. (2008). Exploring animal social networks. Princeton University Press. <https://www.jstor.org/stable/j.ctt7sfqv>

Csardi, G., & Nepusz, T. (2005). The Igraph Software Package for Complex Network Research. *InterJournal, Complex Systems*, 1695.

Dall, S. R. X., Bell, A. M., Bolnick, D. I., & Ratnieks, F. L. W. (2012). An evolutionary ecology of individual differences. *Ecology Letters*, 15(10), 1189–1198. <https://doi.org/10.1111/j.1461-0248.2012.01846.x>

Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters*, 7(8), 734–739. <https://doi.org/10.1111/j.1461-0248.2004.00618.x>

David, H. A. (1988). *The method of paired comparisons* (2nd ed., rev). C. Griffin ; Oxford University Press.

Devigne, C., Broly, P., & Deneubourg, J. L. (2011). Individual preferences and social interactions determine the aggregation of woodlice. *PLoS ONE*, 6(2), e17389. <https://doi.org/10.1371/journal.pone.0017389>

Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: Animal personality meets individual plasticity. *Trends in Ecology and Evolution*, 25(2), 81–89. <https://doi.org/10.1016/j.tree.2009.07.013>

Dingemanse, N. J., & Réale, D. (2005). Natural selection and animal personality. *Behaviour*, 142(9), 1159–1184. <https://doi.org/10.1163/156853905774539445>

Drahokoupilová, T., & Tuf, I. H. (2012). The effect of external marking on the behaviour of the common pill woodlouse *Armadillidium vulgare*. *ZooKeys*, 176(SPECIAL ISSUE), 145–154. <https://doi.org/10.3897/zookeys.176.2375>

Drinkwater, E. (2020). How does inter-individual variation affect group level behaviour? [PhD, University of York]. <https://etheses.whiterose.ac.uk/29012/>

Ellis, L. (1995). Dominance and reproductive success among nonhuman animals: A cross-species comparison. *Ethology and Sociobiology*, 16(4), 257–333. [https://doi.org/10.1016/0162-3095\(95\)00050-U](https://doi.org/10.1016/0162-3095(95)00050-U)

Favati, A., Leimar, O., Radesäter, T., & Løvlie, H. (2013). Social status and personality: Stability in social state can promote consistency of behavioural responses. *Proceedings of the Royal Society B: Biological Sciences*, 281(1774). <https://doi.org/10.1098/rspb.2013.2531>

Flack, J. C., Girvan, M., de Waal, F. B. M., & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature*, 439(7075), 426–429. <https://doi.org/10.1038/nature04326>

Fox, R. A., Ladage, L. D., Roth, T. C., & Pravosudov, V. V. (2009). Behavioural profile predicts dominance status in mountain chickadees, *Poecile gambeli*. *Animal Behaviour*, 77(6), 1441–1448. <https://doi.org/10.1016/j.anbehav.2009.02.022>

Freeman, H. D., & Gosling, S. D. (2010). Personality in nonhuman primates: A review and evaluation of past research. *American Journal of Primatology*, 72(8), 653–671. <https://doi.org/10.1002/ajp.20833>

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, 7(11), 1325–1330. <https://doi.org/10.1111/2041-210X.12584>

Hadrián Tuf, I., Drábková, L., & Šipoš, J. (2015). Personality affects defensive behaviour of *Porcellio scaber* (Isopoda, Oniscidea). ZooKeys, 2015(515), 159–171.
<https://doi.org/10.3897/zookeys.515.9429>

Hall, M. L., Parson, T., Riebel, K., & Mulder, R. A. (2017). Personality, plasticity, and resource defense. Behavioral Ecology, 28(1), 138–144.
<https://doi.org/10.1093/beheco/arw104>

Harmer, A. M. T., & Thomas, D. B. (2019). pathtrackr: An r package for video tracking and analysing animal movement. Methods in Ecology and Evolution, 2041-210X.13200.
<https://doi.org/10.1111/2041-210X.13200>

Hart, J. D. A., Weiss, M. N., Brent, L. J. N., & Franks, D. W. (2021). Common Permutation Methods in Animal Social Network Analysis Do Not Control for Non-independence. BioRxiv, 2021.06.04.447124. <https://doi.org/10.1101/2021.06.04.447124>

Huntingford, F. A. (1976). The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. Animal Behaviour, 24(2), 245–260. [https://doi.org/10.1016/S0003-3472\(76\)80034-6](https://doi.org/10.1016/S0003-3472(76)80034-6)

Hutchinson, G. E. (1957). Concluding Remarks. Cold Spring Harbor Symposia on Quantitative Biology, 22(0), 415–427. <https://doi.org/10.1101/SQB.1957.022.01.039>

Jolles, J. W., Boogert, N. J., Sridhar, V. H., Couzin, I. D., & Manica, A. (2017). Consistent Individual Differences Drive Collective Behavior and Group Functioning of Schooling Fish. Current Biology, 27(18), 2862-2868.e7.
<https://doi.org/10.1016/J.CUB.2017.08.004>

Kanngiesser, P., Sueur, C., Riedl, K., Grossmann, J., & Call, J. (2011). Grooming network cohesion and the role of individuals in a captive chimpanzee group. *American Journal of Primatology*, 73(8), 758–767. <https://doi.org/10.1002/ajp.20914>

Kelleher, S. R., Silla, A. J., & Byrne, P. G. (2018). Animal personality and behavioral syndromes in amphibians: A review of the evidence, experimental approaches, and implications for conservation. *Behavioral Ecology and Sociobiology* 2018 72:5, 72(5), 1–26. <https://doi.org/10.1007/S00265-018-2493-7>

Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. W., & Blokhuis, H. J. (1999). Coping styles in animals: Current status in behavior and stress- physiology. *Neuroscience and Biobehavioral Reviews*, 23(7), 925–935. [https://doi.org/10.1016/S0149-7634\(99\)00026-3](https://doi.org/10.1016/S0149-7634(99)00026-3)

Krause, J., James, R., & Croft, D. P. (2010). Personality in the context of social networks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 4099–4106. <https://doi.org/10.1098/rstb.2010.0216>

Kulahci, I. G., Ghazanfar, A. A., & Rubenstein, D. I. (2018). Consistent individual variation across interaction networks indicates social personalities in lemurs. *Animal Behaviour*, 136, 217–226. <https://doi.org/10.1016/j.anbehav.2017.11.012>

Lefebvre, F., Limousin, M., & Caubet, Y. (2000). Sexual dimorphism in the antennae of terrestrial isopods: A result of male contests or scramble competition? *Canadian Journal of Zoology*, 78(11), 1987–1993. <https://doi.org/10.1139/z00-128>

Liker, A., & Barta, Z. (2002). The effects of dominance on social foraging tactic use in House Sparrows. *Behaviour*, 139(8), 1061–1076.
<https://doi.org/10.1163/15685390260337903>

Lord, J. P., Moser, R. M., Buonocore, E. M., Sylvester, E. E., Morales, M. J., Granitz, A. P., Disipio, A., Blakely, E., O'Sullivan-Evangelista, S. L., Mateo, T. F., Chlebove, G. J., Carey, C. M., & Lucas, O. (2021). Dominance Hierarchies in Marine Invertebrates. *The Biological Bulletin*, 240(1), 2–15. <https://doi.org/10.1086/712973>

Lusseau, D., & Newman, M. E. J. (2004). Identifying the role that animals play in their social networks. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271(suppl_6), S477-81. <https://doi.org/10.1098/rsbl.2004.0225>

Manno, T. G. (2008). Social networking in the Columbian ground squirrel, *Spermophilus columbianus*. *Animal Behaviour*, 75(4), 1221–1228.
<https://doi.org/10.1016/j.anbehav.2007.09.025>

Miranda-de la Lama, G. C., Pascual-Alonso, M., Aguayo-Ulloa, L., Sepúlveda, W. S., Villarroel, M., & María, G. A. (2019). Social personality in sheep: Can social strategies predict individual differences in cognitive abilities, morphology features and reproductive success? *Journal of Veterinary Behavior*, 31, 82–91.
<https://doi.org/10.1016/j.jveb.2019.03.005>

Montiglio, P. O., Ferrari, C., & Réale, D. (2013). Social niche specialization under constraints: Personality, social interactions and environmental heterogeneity.

Philosophical Transactions of the Royal Society B: Biological Sciences, 368(1618), 20120343. <https://doi.org/10.1098/rstb.2012.0343>

Moore, P. A. (2007). Agonistic Behavior in Freshwater Crayfish: The Influence of Intrinsic and Extrinsic Factors on Aggressive Encounters and Dominance. In J. E. Duffy & M. Thiel (Eds.), *Evolutionary Ecology of Social and Sexual Systems* (1st ed., pp. 90–114). Oxford University PressNew York. <https://doi.org/10.1093/acprof:oso/9780195179927.003.0005>

Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews*, 85(4), no-no. <https://doi.org/10.1111/j.1469-185X.2010.00141.x>

Pizzari, T., & Birkhead, T. R. (2000). Female feral fowl eject sperm of subdominant males. *Nature*, 405(6788), Article 6788. <https://doi.org/10.1038/35015558>

R Development Core Team. (2012). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. <https://www.r-project.org/>

Réale, D., & Dingemanse, N. J. (2010). Personality and individual social specialisation. In T. Székely, A. J. Moore, & J. Komdeur (Eds.), *Social Behaviour* (pp. 417–441). Cambridge University Press. <https://doi.org/10.1017/CBO9780511781360.033>

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2), 291–318. <https://doi.org/10.1111/j.1469-185X.2007.00010.x>

Saltz, J. B., & Foley, B. R. (2011). Natural Genetic Variation in Social Niche Construction: Social Effects of Aggression Drive Disruptive Sexual Selection in *Drosophila melanogaster*. The American Naturalist, 177(5), 645–654.

<https://doi.org/10.1086/659631>

Saltz, J. B., Geiger, A. P., Anderson, R., Johnson, B., & Marren, R. (2016). What, if anything, is a social niche? Evolutionary Ecology, 30(2), 349–364.

<https://doi.org/10.1007/s10682-015-9792-5>

Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. Science (New York, N.Y.), 308(5722), 648–652. <https://doi.org/10.1126/science.1106477>

Shaw, A. K. (2020). Causes and consequences of individual variation in animal movement. Movement Ecology, 8(1), 12. <https://doi.org/10.1186/s40462-020-0197-x>

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. Trends in Ecology & Evolution, 19(7), 372–378. <https://doi.org/10.1016/j.tree.2004.04.009>

Silk, J. B. (2007). Social Components of Fitness in Primate Groups. Science, 317(5843), 1347–1351. <https://doi.org/10.1126/science.1140734>

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: A meta-analysis. Behavioral Ecology, 19(2), 448–455. <https://doi.org/10.1093/BHECO/ARM144>

Sokal, R. R., & Rohlf, F. J. (1995). Biometry: The Principles and Practices of Statistics in Biological Research (Cop. W. H. Freeman and Company, Ed.).

Spiegel, O., Leu, S. T., Bull, C. M., & Sih, A. (2017). What's your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecology Letters*, 20(1), 3–18. <https://doi.org/10.1111/ele.12708>

Stamps, J., & Groothuis, T. G. G. (2010). The development of animal personality: Relevance, concepts and perspectives. *Biological Reviews*, 85(2), 301–325. <https://doi.org/10.1111/j.1469-185X.2009.00103.x>

Stanley, C. R., Liddiard Williams, H., & Preziosi, R. F. (2018). Female clustering in cockroach aggregations—A case of social niche construction? *Ethology*, 124(10), 706–718. <https://doi.org/10.1111/eth.12799>

Takeda, N. (1984). The aggregation phenomenon in terrestrial isopods.

Vehtari, A., Gelman, A., Simpson, D., Carpenter, B., & Bürkner, P.-C. (2021). Rank-Normalization, Folding, and Localization: An Improved R^* for Assessing Convergence of MCMC (with Discussion). *Bayesian Analysis*, 16(2), 667–718. <https://doi.org/10.1214/20-BA1221>

Verbeek, M. E. M., Boon, A., & Drent, P. J. (1996). Exploration, Aggressive Behaviour and Dominance in Pair-Wise Confrontations of Juvenile Male Great Tits. *Behaviour*, 133(11/12), 945–963.

Webster, M. M., & Ward, A. J. W. (2011). Personality and social context. *Biological Reviews*, 86(4), 759–773. <https://doi.org/10.1111/j.1469-185X.2010.00169.x>

Webster, S., & Fiorito, G. (2001). Socially guided behaviour in non-insect invertebrates. *Animal Cognition*, 4(2), 69–79. <https://doi.org/10.1007/s100710100108>

Whitehead, Hal. (2008). *Analyzing Animal Societies: Quantitative Methods For*. University of Chicago Press.

Wolf, M., Van Doorn, G. S., & Weissing, F. J. (2011). On the coevolution of social responsiveness and behavioural consistency. *Proceedings of the Royal Society B: Biological Sciences*, 278(1704), 440–448. <https://doi.org/10.1098/rspb.2010.1051>

Yeh, S.-R., Musolf, B. E., & Edwards, D. H. (1997). Neuronal Adaptations to Changes in the Social Dominance Status of Crayfish. *The Journal of Neuroscience*, 17(2), 697–708. <https://doi.org/10.1523/JNEUROSCI.17-02-00697.1997>

Zimmer, M. (2001). Why do male terrestrial isopods (Isopoda: Oniscidea) not guard females? *Animal Behaviour*, 62, 815–821. <https://doi.org/10.1006/anbe.2001.1845>

Zulandt Schneider, R. A. Z., Huber, R., & Moore, P. A. (2001). Individual and Status Recognition in the Crayfish, *Orconectes rusticus*: The Effects of Urine Release on Fight Dynamics. *Behaviour*, 138(2), 137–153.

TABLES

Table 1. Estimated parameters obtained from models testing the effect of personality on individual social roles based on association.

| Parameter | Estimate | Est.Error | 95% Credible Interval | Rhat | Bulk_ESS | Tail_ESS |
|--|----------|-----------|-----------------------|-------------|----------|----------|
| (A) Associative degree ($r^2 = 0.40 \pm 0.014$) | | | | | | |
| Intercept | 0.21 | 7.32 | -12.64 | 16.19 | 1.00 | 9125 |
| Distance | 0.09 | 0.23 | -0.38 | 0.53 | 1.00 | 25814 |
| Stops | 0.22 | 0.24 | -0.24 | 0.69 | 1.00 | 30795 |
| Escape attempts | 0.10 | 0.27 | -0.40 | 0.68 | 1.00 | 19925 |
| Escape interval | 0.38 | 0.25 | -0.10 | 0.89 | 1.00 | 19742 |
| Directional deviation | -0.67 | 0.83 | -2.41 | 0.87 | 1.00 | 18806 |
| Body size (Area) | -0.00 | 0.02 | -0.03 | 0.03 | 1.00 | 35402 |
| Temporal sequence | -0.98 | 0.80 | -2.76 | 0.40 | 1.00 | 8161 |
| Group size | 1.75 | 0.43 | 0.78 | 2.50 | 1.00 | 8180 |
| (B) Associative betweenness ($r^2 = 0.29 \pm 0.02$) | | | | | | |
| Intercept | -1.86 | 1.62 | -5.15 | 1.22 | 1.00 | 1287 |
| Distance | -0.09 | 0.06 | -0.20 | 0.02 | 1.00 | 3005 |
| Stops | 0.04 | 0.06 | -0.08 | 0.16 | 1.00 | 4445 |
| Escape attempts | 0.07 | 0.07 | -0.07 | 0.21 | 1.00 | 2681 |
| Escape interval | 0.08 | 0.06 | -0.04 | 0.21 | 1.00 | 2507 |
| Directional deviation | 0.03 | 0.19 | -0.34 | 0.41 | 1.00 | 2696 |
| Body size (Area) | 0.00 | 0.00 | -0.01 | 0.01 | 1.00 | 4227 |
| Temporal sequence | -0.26 | 0.18 | -0.60 | 0.09 | 1.01 | 1089 |
| Group size | -0.00 | 0.09 | -0.18 | 0.19 | 1.00 | 1192 |
| (C) Average association strength ($r^2 = 0.26 \pm 0.14$) | | | | | | |
| Intercept | 0.90 | 5.30 | -9.44 | 11.30 | 1.00 | 24996 |
| Distance | -0.07 | 0.10 | -0.26 | 0.12 | 1.00 | 23710 |
| Stops | -0.03 | 0.10 | -0.24 | 0.17 | 1.00 | 25271 |
| Escape attempts | 0.03 | 0.12 | -0.21 | 0.26 | 1.00 | 20119 |
| Escape interval | 0.12 | 0.11 | -0.09 | 0.34 | 1.00 | 21244 |
| Directional deviation | -0.11 | 1.11 | -2.29 | 2.08 | 1.00 | 26455 |
| Body size (Area) | -0.00 | 0.01 | -0.02 | 0.01 | 1.00 | 25601 |
| Temporal sequence | 0.24 | 0.20 | -0.15 | 0.64 | 1.00 | 12158 |
| Group size | -0.03 | 0.11 | -0.24 | 0.19 | 1.00 | 12613 |

The models were controlled for random effects at the level of individuals, sex-pregnant interaction, locality of origin, and experimental assemblages of individuals. For each parameter, we present the mean value and 95% credible intervals (95% CI). Rhat is the potential scale reduction factor and indicates the MCMC convergence (at convergence Rhat = 1). Bulk_ESS and Tail_ESS are measures of effective sample size.

Table 2. Estimated parameters obtained from models testing the effect of personality on individual social roles based on interindividual aggression.

| Parameter | Estimate | Est.Error | 95% Credible Interval | Rhat | Bulk_ESS | Tail_ESS |
|---|----------|-----------|-----------------------|-------------|----------|----------|
| (A) Aggressiveness degree ($r^2 = 0.58 \pm 0.04$) | | | | | | |
| Intercept | -9.09 | 3.76 | -18.32 | -4.01 | 1.00 | 18759 |
| Distance | 0.06 | 0.12 | -0.17 | 0.31 | 1.00 | 34294 |
| Stops | 0.14 | 0.13 | -0.11 | 0.39 | 1.00 | 33427 |
| Escape attempts | 0.17 | 0.21 | -0.23 | 0.57 | 1.00 | 25914 |
| Escape interval | 0.20 | 0.16 | -0.11 | 0.51 | 1.00 | 25798 |
| Directional deviation | 1.77 | 0.84 | 0.44 | 3.74 | 1.00 | 17241 |
| Body size (Area) | -0.00 | 0.01 | -0.02 | 0.01 | 1.00 | 45108 |
| Temporal sequence | -0.01 | 0.07 | -0.15 | 0.14 | 1.00 | 24993 |
| Group size | -0.18 | 0.14 | -0.46 | 0.10 | 1.00 | 26922 |
| (B) Aggressiveness indegree ($r^2 = 0.40 \pm 0.06$) | | | | | | |
| Intercept | -9.70 | 4.52 | -20.75 | -3.69 | 1.00 | 14464 |
| Distance | -0.01 | 0.17 | -0.33 | 0.33 | 1.00 | 25527 |
| Stops | 0.08 | 0.18 | -0.28 | 0.44 | 1.00 | 24679 |
| Escape attempts | 0.19 | 0.30 | -0.40 | 0.78 | 1.00 | 18340 |
| Escape interval | 0.21 | 0.23 | -0.24 | 0.67 | 1.00 | 19038 |
| Directional deviation | 1.80 | 1.06 | 0.07 | 4.21 | 1.00 | 13635 |
| Body size (Area) | -0.01 | 0.01 | -0.03 | 0.01 | 1.00 | 31204 |
| Temporal sequence | 0.04 | 0.10 | -0.16 | 0.24 | 1.00 | 18721 |
| Group size | -0.17 | 0.19 | -0.55 | 0.20 | 1.00 | 20248 |
| (C) Aggressiveness outdegree ($r^2 = 0.46 \pm 0.09$) | | | | | | |
| Intercept | -15.12 | 7.82 | -33.75 | -4.66 | 1 | 17421 |
| Distance | 0.14 | 0.22 | -0.29 | 0.59 | 1 | 29595 |
| Stops | 0.21 | 0.21 | -0.21 | 0.63 | 1 | 29816 |
| Escape attempts | 0.22 | 0.36 | -0.49 | 0.93 | 1 | 20284 |
| Escape interval | 0.24 | 0.28 | -0.3 | 0.8 | 1 | 19580 |
| Directional deviation | 2.74 | 1.72 | 0.11 | 6.72 | 1 | 17401 |
| Body size (Area) | 0.01 | 0.01 | -0.02 | 0.04 | 1 | 28135 |
| Temporal sequence | -0.04 | 0.12 | -0.28 | 0.19 | 1 | 22651 |
| Group size | -0.21 | 0.21 | -0.63 | 0.21 | 1 | 24937 |
| (D) Aggressiveness betweenness ($r^2 = 0.47 \pm 0.07$) | | | | | | |
| Intercept | -0.03 | 0.63 | -1.23 | 1.14 | 1.00 | 9173 |
| Distance | -0.03 | 0.06 | -0.14 | 0.08 | 1.00 | 18919 |
| Stops | -0.07 | 0.07 | -0.22 | 0.06 | 1.00 | 12629 |
| Escape attempts | -0.02 | 0.11 | -0.24 | 0.19 | 1.00 | 9403 |
| Escape interval | -0.05 | 0.08 | -0.21 | 0.11 | 1.00 | 10394 |
| Directional deviation | 0.12 | 0.24 | -0.34 | 0.60 | 1.00 | 8447 |
| Body size (Area) | 0.00 | 0.01 | -0.01 | 0.01 | 1.00 | 10233 |
| Temporal sequence | 0.03 | 0.05 | -0.07 | 0.12 | 1.00 | 10348 |
| Group size | -0.06 | 0.07 | -0.21 | 0.09 | 1.00 | 13829 |
| (E) Average aggression strength ($r^2 = 0.65 \pm 0.03$) | | | | | | |
| Intercept | 0.54 | 1.10 | -0.49 | 3.95 | 1.01 | 3707 |
| Distance | 0.04 | 0.03 | -0.02 | 0.10 | 1.00 | 18431 |
| Stops | 0.13 | 0.04 | 0.06 | 0.21 | 1.00 | 13122 |
| Escape attempts | -0.01 | 0.05 | -0.12 | 0.09 | 1.00 | 11967 |
| Escape interval | -0.03 | 0.04 | -0.11 | 0.05 | 1.00 | 11688 |
| Directional deviation | -0.13 | 0.30 | -0.97 | 0.28 | 1.00 | 3113 |
| Body size (Area) | 0.00 | 0.00 | -0.00 | 0.01 | 1.00 | 12229 |
| Temporal sequence | 0.01 | 0.04 | -0.06 | 0.11 | 1.00 | 6708 |
| Group size | 0.04 | 0.08 | -0.11 | 0.21 | 1.00 | 6232 |

The models were controlled for random effects at the level of individuals, sex-pregnant interaction, and experimental assemblages of individuals. For each parameter, we present the mean value and 95% credible intervals (95% CI). Rhat is the potential scale reduction factor and indicates the MCMC convergence (at convergence Rhat = 1). Bulk_ESS and Tail_ESS are measures of effective sample size.

Table 3. Estimated parameters obtained from models testing the effect of personality on individual social roles based on dominance status.

| Dominance status ($r^2 = 0.17 \pm 0.09$) | | | | | | | |
|--|----------|-----------|-----------------------|------|----------|----------|--|
| Parameter | Estimate | Est.Error | 95% Credible Interval | Rhat | Bulk_ESS | Tail_ESS | |
| Intercept | -5.58 | 14.89 | -36.45 22.45 | 1.00 | 21326 | 18722 | |
| Distance | 0.20 | 0.24 | -0.25 0.68 | 1.00 | 18756 | 20938 | |
| Stops | 0.19 | 0.33 | -0.42 0.83 | 1.00 | 10212 | 18445 | |
| Escape attempts | 0.17 | 0.36 | -0.53 0.88 | 1.00 | 14576 | 18176 | |
| Escape interval | 0.25 | 0.27 | -0.29 0.78 | 1.00 | 13265 | 16225 | |
| Directional deviation | 0.44 | 3.16 | -5.49 7.04 | 1.00 | 22331 | 19523 | |
| Body size (Area) | 0.01 | 0.01 | -0.02 0.04 | 1.00 | 21449 | 17295 | |
| Temporal sequence | 0.06 | 0.25 | -0.44 0.53 | 1.00 | 14945 | 15906 | |
| Group size | -0.02 | 0.13 | -0.27 0.24 | 1.00 | 16741 | 17242 | |

The models were controlled for random effects at the level individuals, experimental assemblages of individuals and sex-pregnant interaction. For each parameter, we present the mean value and 95% credible intervals (95% CI). Rhat is the potential scale reduction factor and indicates the MCMC convergence (at convergence Rhat=1). Bulk_ESS and Tail_ESS are measures of effective sample size.

Table 4. Estimated parameters obtained from models testing: (A) Personality - and dominance status dissimilarity on dyadic associations, and (B) Personality dissimilarity on dominance status dissimilarity.

| Parameter | Estimate | Est.Error | 95% Credible Interval | Rhat | Bulk_ESS | Tail_ESS |
|---|----------|-----------|-----------------------|--------------|----------|----------|
| (A) Dyadic associations ($r^2 = 0.38 \pm 0.02$) | | | | | | |
| Intercept | -1.42 | 1.85 | -5.03 | 2.26 | 1 | 6313 |
| Distance dissimilarity | -0.01 | 0.03 | -0.06 | 0.05 | 1 | 33330 |
| Stops dissimilarity | -0.04 | 0.06 | -0.16 | 0.07 | 1 | 26322 |
| Immobility dissimilarity | -0.01 | 0.03 | -0.07 | 0.04 | 1 | 20494 |
| Escape attempts diss. | -0.03 | 0.05 | -0.14 | 0.07 | 1 | 20411 |
| Escape interval dissimilarity | 0.04 | 0.02 | 0.01 | 0.07 | 1 | 23974 |
| Directional deviation diss. | -0.01 | 0.04 | -0.09 | 0.07 | 1 | 30094 |
| Dominance status diss. | -0.13 | 0.04 | -0.21 | -0.06 | 1 | 31959 |
| Body size dissimilarity | 0.05 | 0.04 | -0.04 | 0.13 | 1 | 32208 |
| Group size | 0.06 | 0.13 | -0.2 | 0.31 | 1 | 5790 |
| (B) Dissimilarity in Dominance status ($r^2 = 0.37 \pm 0.02$) | | | | | | |
| Intercept | -0.09 | 0.94 | -1.94 | 1.77 | 1 | 6683 |
| Distance dissimilarity | -0.01 | 0.01 | -0.04 | 0.02 | 1 | 27721 |
| Stops dissimilarity | 0.06 | 0.03 | 0.00 | 0.12 | 1 | 26495 |
| Immobility dissimilarity | -0.02 | 0.01 | -0.05 | 0.00 | 1 | 24247 |
| Escape attempts diss. | -0.06 | 0.03 | -0.11 | 0.00 | 1 | 20380 |
| Escape interval dissimilarity | 0.00 | 0.01 | -0.02 | 0.02 | 1 | 21655 |
| Directional deviation diss. | -0.04 | 0.02 | -0.08 | 0.00 | 1 | 29610 |
| Body size dissimilarity | 0.02 | 0.02 | -0.03 | 0.06 | 1 | 32066 |
| Group size | 0.04 | 0.07 | -0.10 | 0.18 | 1 | 6276 |

The models include multi-membership grouping at the level of individuals within each assemble, interindividual sex-pregnant relationship and dissimilarity in original locality were included as random factors. For each parameter, we present the mean value and 95% credible intervals (95% CI). Rhat is the potential scale reduction factor and indicates the MCMC convergence (at convergence Rhat = 1). Bulk_ESS and Tail_ESS are measures of effective sample size. Dissimilarity calculated by Euclidean distance.

Table S1. Correlation between body size and individual behaviors performed in an asocial environment.

| Behaviors | Length | Width | Dist. | Stops | Immob. | Esc.att | Mob.Int. | Esc.Int. | Speed | Av.direct. | Direc. Dev. | Turns | |
|------------------------------|--------|---------|-------|---------|----------|----------|----------|----------|-------|------------|-------------|-------|---|
| Length | 1 | | | | | | | | | | | | |
| Width | | 0.68*** | 1 | | | | | | | | | | |
| Distance | | 0.16 | 0.25 | 1 | | | | | | | | | |
| Stops | | -0.03 | -0.11 | -0.22 | 1 | | | | | | | | |
| Immobility | | -0.11 | -0.18 | -0.46** | 0.75*** | 1 | | | | | | | |
| Escape attempts | | 0.21 | 0.25 | 0.29 | -0.19 | -0.37 | 1 | | | | | | |
| Mobility interval | | 0.01 | 0.06 | 0.19 | -0.87*** | -0.68*** | 0.20 | 1 | | | | | |
| Escape interval | | -0.15 | -0.23 | -0.22 | 0.14 | 0.27 | -0.88*** | -0.13 | 1 | | | | |
| Speed | | 0.16 | 0.23 | 0.94*** | -0.20 | -0.39* | 0.26 | 0.15 | -0.18 | 1 | | | |
| Average direction | | 0.12 | 0.13 | 0.42* | -0.14 | -0.34* | 0.15 | 0.13 | -0.08 | 0.40* | 1 | | |
| Directional deviation | | 0.04 | 0.13 | 0.28 | -0.09 | -0.15 | 0.08 | 0.08 | -0.07 | 0.26 | 0.11 | 1 | |
| Turns | | 0.10 | 0.13 | 0.71*** | 0.08 | -0.10 | 0.18 | -0.06 | -0.14 | 0.70*** | 0.10 | 0.17 | 1 |

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Table S2. Repeatability of individual behaviors in an asocial environment.

| Variables | Repeatability | SE | Confidence Interval | | <i>p</i> |
|-----------------------|---------------|------|---------------------|-------|----------------|
| | | | 2.5% | 97.5% | |
| Distance | 0.27 | 0.06 | 0.13 | 0.38 | < 0.001 |
| Stops | 0.24 | 0.06 | 0.11 | 0.35 | < 0.001 |
| Immobility | 0.40 | 0.06 | 0.25 | 0.51 | < 0.001 |
| Escape attempts | 0.32 | 0.06 | 0.18 | 0.43 | < 0.001 |
| Mobility interval | 0.22 | 0.06 | 0.09 | 0.34 | < 0.001 |
| Escape interval | 0.33 | 0.06 | 0.20 | 0.45 | < 0.001 |
| Speed | 0.14 | 0.06 | 0.02 | 0.24 | 0.002 |
| Average direction | 0.06 | 0.05 | 0.00 | 0.17 | 0.210 |
| Directional deviation | 0.08 | 0.05 | 0.00 | 0.18 | 0.193 |
| Turns | 0.02 | 0.04 | 0.00 | 0.12 | 0.304 |

SE: standard error, *p*: distribution probability. Confidence Interval based two-tailed test. Significant probability was highlighted in bold.

Table S3. Estimated parameters obtained from models testing the effect of dominance status on individual social roles based on association.

| Parameter | Estimate | Est.Error | 95% Credible Interval | Rhat | Bulk_ESS | Tail_ESS |
|--|----------|-----------|-----------------------|-------------|----------|----------|
| (A) Associative degree ($r^2 = 0.68 \pm 0.02$) | | | | | | |
| Intercept | 1.00 | 6.14 | -9.89 | 14.20 | 1.00 | 16007 |
| Dominance status | 0.17 | 0.16 | -0.14 | 0.48 | 1.00 | 55516 |
| Group size | 1.42 | 0.48 | 0.40 | 2.27 | 1.00 | 15874 |
| (B) Associative betweenness ($r^2 = 0.17 \pm 0.07$) | | | | | | |
| Intercept | 2.43 | 1.23 | -0.03 | 4.91 | 1.01 | 658 |
| Dominance status | 0.06 | 0.06 | -0.06 | 0.18 | 1.00 | 3686 |
| Group size | -0.15 | 0.09 | -0.34 | 0.03 | 1.01 | 582 |
| (C) Average association strength ($r^2 = 0.59 \pm 0.04$) | | | | | | |
| Intercept | -3.40 | 1.11 | -5.64 | -1.21 | 1.00 | 6741 |
| Dominance status | -0.01 | 0.04 | -0.08 | 0.07 | 1.00 | 35309 |
| Group size | 0.09 | 0.08 | -0.08 | 0.26 | 1.00 | 6623 |

The models were controlled for random effects at the level of individuals, sex-pregnant interaction, and experimental assemblages of individuals. For each parameter, we present the mean value and 95% credible intervals (95% CI). Rhat is the potential scale reduction factor and indicates the MCMC convergence (at convergence Rhat = 1). Bulk_ESS and Tail_ESS are measures of effective sample size.

Table S4. Estimated parameters obtained from models testing the effect dissimilarity in individual attributes.

| Parameter | Estimate | Est.Error | 95% Credible Interval |
|--|----------|-----------|-----------------------|
| Dyadic association index | | | |
| Male: Male | -0.03 | 0.07 | -0.17 0.09 |
| Male: No pregnant female | 0.01 | 0.06 | -0.12 0.11 |
| Male: Pregnant female | 0.06 | 0.07 | -0.05 0.20 |
| No pregnant female: No pregnant female | -0.10 | 0.06 | -0.24 0.01 |
| Pregnant female: No pregnant female | -0.01 | 0.06 | -0.14 0.11 |
| Pregnant female: Pregnant female | 0.08 | 0.08 | -0.05 0.26 |
| Dissimilarity in dominance status | | | |
| Male: Male | -0.01 | 0.02 | -0.04 0.02 |
| Male: No pregnant female | -0.01 | 0.01 | -0.04 0.01 |
| Male: Pregnant female | -0.01 | 0.01 | -0.04 0.02 |
| No pregnant female: No pregnant female | 0.01 | 0.01 | -0.02 0.04 |
| Pregnant female: No pregnant female | 0.01 | 0.01 | -0.02 0.03 |
| Pregnant female: Pregnant female | 0.01 | 0.02 | -0.02 0.05 |

FIGURES

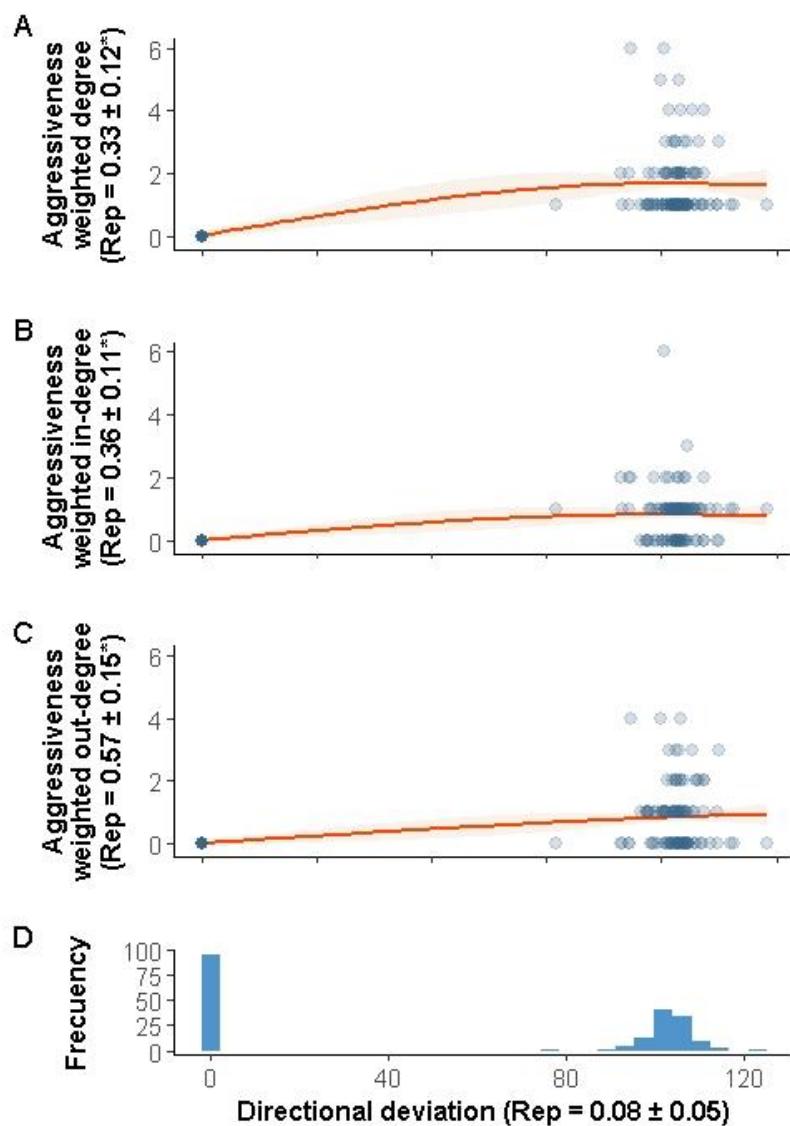


Figure 1. Effect of individual behaviors on social roles in a changing social environment. (A) Aggressiveness degree, (B) aggressiveness in-degree and (C) aggressiveness out-degree increases with individual directional deviation. (D) The histogram of the directional deviation showed observations with zero-inflated distribution. Directional deviation was not consistent in repeatability at the level of individuals but showed plasticity across social assemblies. This behavior represents the chaotic movement in the displacement of individuals. * Represents consistent repeatability measures across social assemblages.

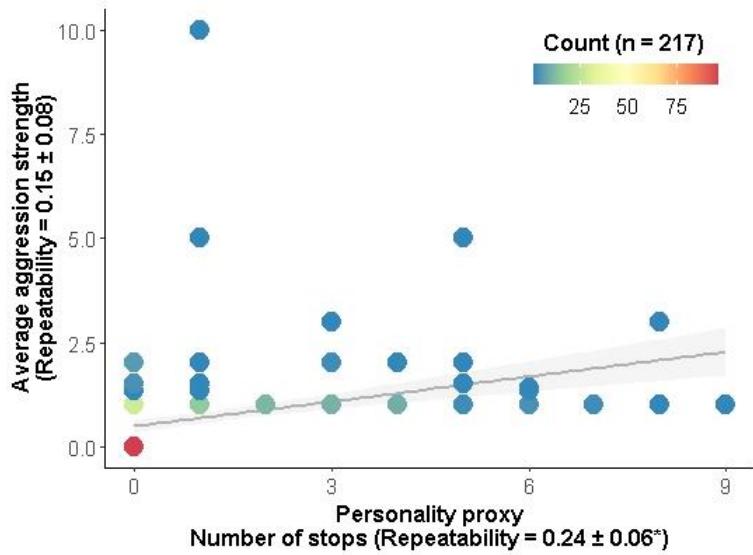


Figure 2. Positive relationship between personality and average aggression strength in changing social settings. Personality was approximated from the number of stops, as this behavior had a consistent repeatability at the individual level of 0.24 ± 0.06 (95% CI [0.11,0.35]).

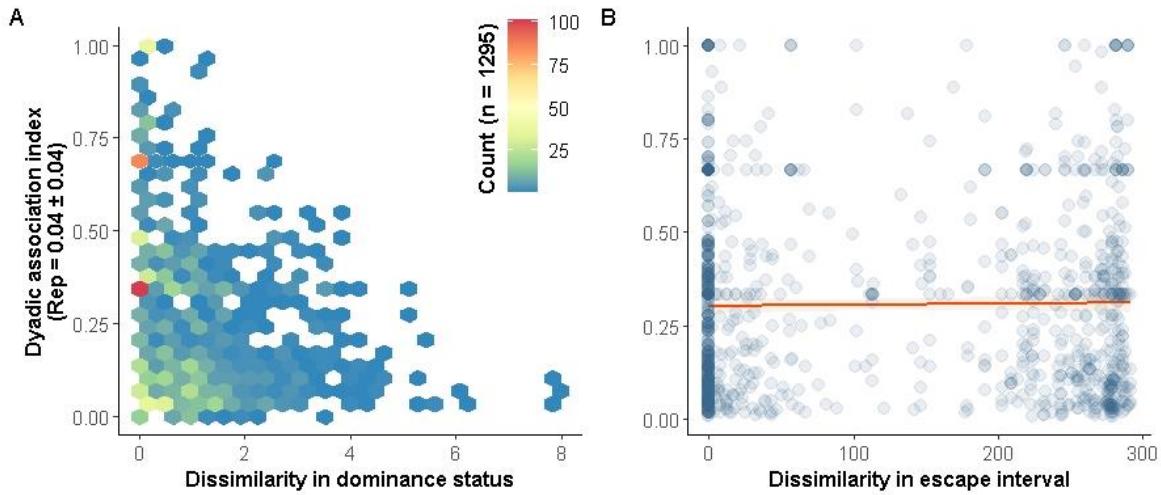


Figure 3. Relationship between personality dissimilarity, dominance status dissimilarity and dyadic association index in changing social environment. (A) The dyadic association index has a trade-off with dissimilarity in dominance status, where the highest incidence of observations occurs when individuals present greater similarity in dominance status. (B) Dyadic association index increases with dissimilarity in escape interval as proxy of personality. At individual level, dominance status had a repeatability at the individual level of 0.15 ± 0.07 (95%CI [0.02,0.28]) and escape interval of 0.33 ± 0.06 (95%CI [0.20,0.45]). Both individual attributes were consistent across different social environments.

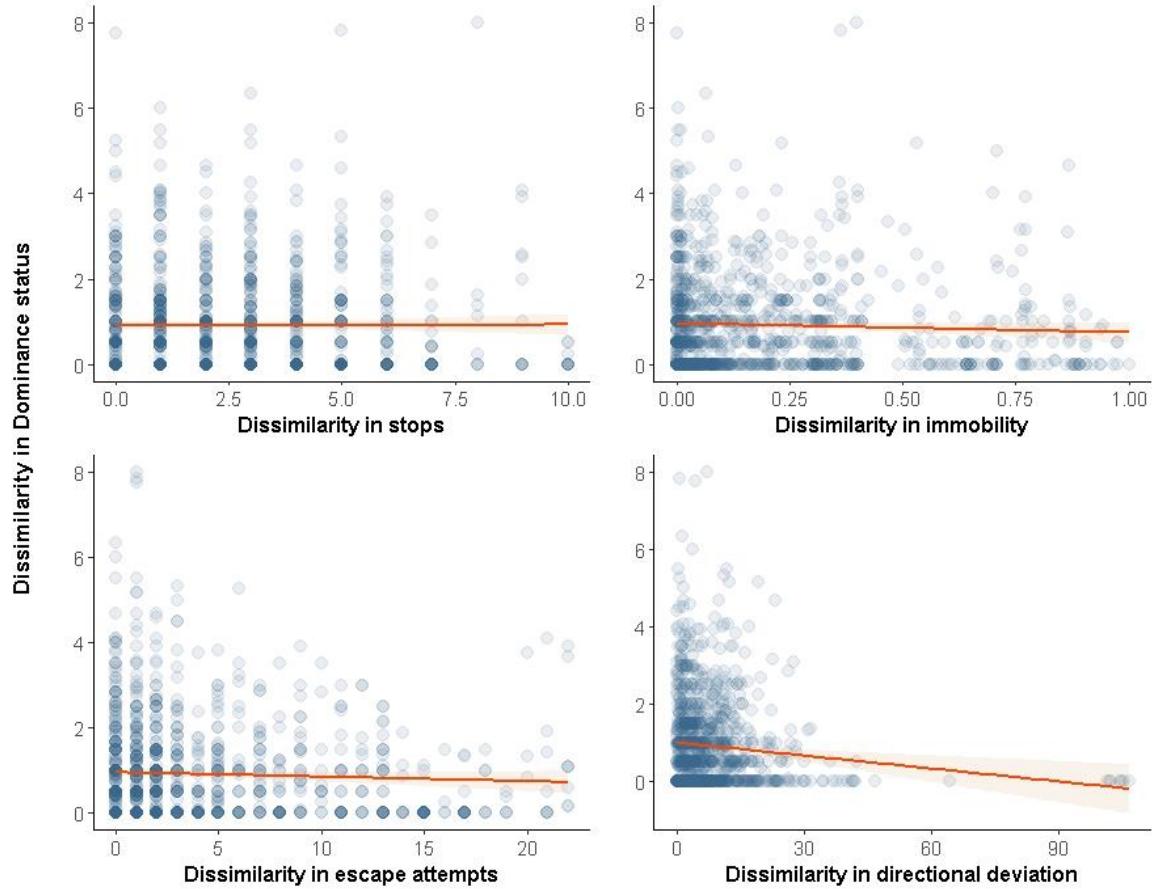


Figure 4. Behaviors marginally influencing dyadic difference in dominance status. At the individual level, number of stop, immobility and escape attempts showed consistency across the social environments, while directional deviation was more plastic behaviors whose performance changed with the social environment.

APPENDIX 1

A) REPEATABILITY OF INDIVIDUAL BEHAVIOURS

The repeatability of individual behaviors performed in an asocial environment and the measures of centrality based on association and aggression were evaluated using the following formula:

Library(rptR)

rptGaussian(Behaviour/centrality measure
= distance + n.stops + escape attempts + escape.interval
+ directional deviation + area corporal + temporal sequency
+ group.size + (1|Sex: Pregnant) + (1|Assamble) + (1|ID)
+ (1|Locality), nboot = 10000, npermut = 1000, adjusted
= FALSE))

B) DETAILS OF THE MODELS USED IN THE ANALYSES

Library("brms")

Influence of personality on social roles based on Association:

*Associative Degree Model = brm(Gaussianize(degree) ~ ar(gr
= ID) + log(1 + distance) + log(1 + stops) + log(1
+ escape.att.) + log(1 + escape.int.) + log(1
+ directional.dev.) + corporal area + time + group size
+ (1|Sex: Pregnant) + (1|ID assemble) + (1|ID) + (1|Locality),
prior = c(set_prior("normal(0, 10)", class = "b"),
set_prior("cauchy(0, 2)", class = "sd")), iter = 10000,
warmup = 4000, chains = 5,
control = list(adapt_delta = 0.999, max_treedepth = 20), family
= "skew_normal")*

Associative betweenness Model = $\text{brm}(\text{Betweenness} \sim \text{ar}(\text{gr}$

$$= \text{ID}) + \log(1 + \text{distance}) + \log(1 + \text{stops}) + \log(1$$

$$+ \text{escape.att.}) + \log(1 + \text{escape.int.}) + \log(1$$

$$+ \text{directional.dev.}) + \text{corporal area} + \text{time} + \text{group size}$$

$$+ (1|\text{Sex: Pregnant}) + (1|\text{ID assemble}) + (1|\text{ID}) + (1|\text{Locality}),$$

$$\text{prior} = c(\text{set_prior}("normal(0, 10)", \text{class} = "b"),$$

$$\text{set_prior}("cauchy(0, 2)", \text{class} = "sd")), \text{iter} = 10000,$$

$$\text{warmup} = 4000, \text{chains} = 5,$$

$$\text{control} = \text{list}(\text{adapt_delta} = 0.999, \text{max_treedepth} = 20), \text{family}$$

$$= "hurdle_lognormal")$$

Average Association Strength Model = $\text{brm}(\log(\text{AAS}) \sim \text{ar}(\text{gr}$

$$= \text{ID}) + \log(1 + \text{distance}) + \log(1 + \text{stops}) + \log(1$$

$$+ \text{escape.att.}) + \log(1 + \text{escape.int.}) + \log(1$$

$$+ \text{directional.dev.}) + \text{corporal area} + \text{time} + \text{group size}$$

$$+ (1|\text{Sex: Pregnant}) + (1|\text{ID assemble}) + (1|\text{ID}) + (1|\text{Locality}),$$

$$\text{prior} = c(\text{set_prior}("normal(0, 10)", \text{class} = "b"),$$

$$\text{set_prior}("cauchy(0, 2)", \text{class} = "sd")), \text{iter} = 10000,$$

$$\text{warmup} = 4000, \text{chains} = 5,$$

$$\text{control} = \text{list}(\text{adapt_delta} = 0.999, \text{max_treedepth} = 20), \text{family}$$

$$= "gaussian")$$

Influence of personality on social roles based on Aggression:

Aggressiveness weighted Degrees Model

```
= brm(c(degree,indegree,outdegree) ~ ar(gr  
= ID) + log(1 + distance) + log(1 + stops) + log(1  
+ escape.att.) + log(1 + escape.int.) + log(1  
+ directional.dev.) + corporal area + time + group size  
+ (1|Sex:Pregnant) + (1|ID assemble) + (1|ID) + (1|Locality),  
prior = c(set_prior("normal(0,10)",  
class = "b")), iter = 10000, warmup = 4000, chains = 5,  
control = list(adapt_delta = 0.999, max_treedepth = 20), family  
= "zero_inflated_poisson")
```

Aggressiveness betweenness Model = $\text{brm}(\text{Betweenness} + 1 \sim \text{ar}(gr$

```
= ID) + log(1 + distance) + log(1 + stops) + log(1  
+ escape.att.) + log(1 + escape.int.) + log(1  
+ directional.dev.) + corporal area + time + group size  
+ (1|Sex:Pregnant) + (1|ID assemble) + (1|ID) + (1|Locality),  
prior = c(set_prior("normal(0,10)",  
class = "b")), iter = 10000, warmup = 4000, chains = 5,  
control = list(adapt_delta = 0.999, max_treedepth = 20), family  
= "Gamma")
```

Average Aggression strength Model = $\text{brm}(AAS + 1 \sim ar(gr$
 $= ID) + \log(1 + distance) + \log(1 + stops) + \log(1$
 $+ escape.att.) + \log(1 + escape.int.) + \log(1$
 $+ directional.dev.) + corporal area + time + group size$
 $+ (1|Sex: Pregnant) + (1|ID assemble) + (1|ID) + (1|Locality),$
 $prior = c(\text{set_prior}("normal(0, 10)",$
 $class = "b")), iter = 10000, \quad warmup = 4000, \quad chains = 5,$
 $control = list(\text{adapt_delta} = 0.999, \text{max_treedepth} = 20), family$
 $= "Gamma")$

Domimance ranking Model = $\text{brm}(Dominance\ Ranking} \sim ar(gr$
 $= ID) + \log(1 + distance) + \log(1 + stops) + \log(1$
 $+ escape.att.) + \log(1 + escape.int.) + \log(1$
 $+ directional.dev.) + corporal area + time + group size$
 $+ (1|Sex: Pregnant) + (1|ID assemble) + (1|ID) + (1|Locality),$
 $prior = c(\text{set_prior}("normal(0,4)", class$
 $= "Intercept"), \text{set_prior}("normal(0,15)", class$
 $= "sd"), \text{set_prior}("normal(10,1)", class$
 $= "quantile"), \text{set_prior}("normal(10,1)", class = "sigma")), iter$
 $= 10000, \quad warmup = 4000,$
 $chains = 5, family = "zero_inflated_asym_laplace")$

Influence of dominance status on Association-based centrality measures:

Associative Degree Model

```
= brm(Gaussianize(degree) ~ Dominance ranking + group size  
+ (1|Sex: Pregnant) + (1|ID assemble) + (1|ID) + (1|Locality),  
prior = c(set_prior("normal(0,10)", class = "b"),  
set_prior("cauchy(0,2)", class = "sd")), iter = 10000,  
warmup = 4000, chains = 5,  
control = list(adapt_delta = 0.999, max_treedepth = 20), family  
= "skew_normal")
```

Associative betweenness Model

```
= brm(Betweenness ~ Dominance ranking + group size  
+ (1|Sex: Pregnant) + (1|ID assemble) + (1|ID) + (1|Locality),  
prior = c(set_prior("normal(0,10)", class = "b"),  
set_prior("cauchy(0,2)", class = "sd")), iter = 10000,  
warmup = 4000, chains = 5,  
control = list(adapt_delta = 0.999, max_treedepth = 20), family  
= "hurdle_lognormal")
```

Average Association Strength Model

```
= brm(log(AAS) ~ Dominance ranking + group size  
+ (1|Sex:Pregnant) + (1|ID assemble) + (1|ID) + (1|Locality),  
prior = c(set_prior("normal(0, 10)", class = "b"),  
set_prior("cauchy(0, 2)", class = "sd")), iter = 10000,  
warmup = 4000, chains = 5,  
control = list(adapt_delta = 0.999, max_treedepth = 20), family  
= "gaussian")
```

C) DETAILS OF THE MODELS USED IN THE DYADIC ANALYSES

Library("brms")

Library("MM")

Influence of dissimilarity in personality and dominance status on dyadic association strength:

Dyadic association index Model

```
= brm(sqrt(DAI) ~ log(1 + diss.distance) + log(1 + diss.stops)
+ log(1 + diss.inmobility) + log(1 + diss.escape.att.)
+ log(1 + diss.escape.int.) + log(1 + diss.directional.dev.)
+ dist.Dominance ranking + corporal size difference + group size
+ (1|mm(ID1, ID2)|assamble)
+ (1|interindividual sex relationship)
+ (1|interindividual sex: pregnant relationship)
+ (1|dissimilarity in location of origin), iter = 10000,
warmup = 4000, chains = 5,
control = list(adapt_delta = 0.999, max_treedepth = 20), family
= "gaussian")
```

Influence of dissimilarity in personality on dissimilarity in dominance status:

Dissimilarity in dominance ranking Model

```
= brm(diss.in dominance ranking + 1 ~ log(1 + diss.distance)  
+ log(1 + diss.stops) + log(1 + diss.inmobility)  
+ log(1 + diss.escape.att.) + log(1 + diss.escape.int.)  
+ log(1 + diss.directional.dev.) + corporal size difference  
+ group size + (1|mm(ID1, ID2)|assamble)  
+ (1|interindividual sex relationship)  
+ (1|interindividual sex: pregnant relationship)  
+ (1|dissimilarity in location of origin), iter = 10000,  
warmup = 4000, chains = 5,  
control = list(adapt_delta = 0.999, max_treedepth = 20), family  
= "Gamma")
```

APPENDIX 2

Table A1. Conditional modes of random effects in the associative degree centrality model. Random effects at the level of individuals, sex-pregnant interaction, locality of origin, and experimental assemblages of individuals were controlled for in the model.

| Individual identity | | | | |
|----------------------------|------------------|-----------------|------------------|-------------|
| | Intercept | Estimate | Est.Error | 2.5% |
| a.1 | | 0.0313 | 0.3442 | -0.6764 |
| a.10 | | 0.1637 | 0.3564 | -0.4071 |
| a.11 | | 0.0277 | 0.3477 | -0.6851 |
| a.12 | | -0.0661 | 0.3487 | -0.8931 |
| a.13 | | -0.0133 | 0.3545 | -0.7899 |
| a.14 | | -0.0835 | 0.3725 | -0.9856 |
| a.15 | | -0.0472 | 0.3630 | -0.8854 |
| a.16 | | 0.0303 | 0.3334 | -0.6596 |
| a.17 | | -0.0802 | 0.3539 | -0.9506 |
| a.18 | | -0.0363 | 0.3440 | -0.8150 |
| a.19 | | 0.0977 | 0.3492 | -0.5344 |
| a.2 | | -0.0321 | 0.3472 | -0.8158 |
| a.20 | | -0.0350 | 0.3490 | -0.8323 |
| a.21 | | 0.2056 | 0.3833 | -0.3696 |
| a.23 | | -0.0266 | 0.3370 | -0.7751 |
| a.24 | | -0.0032 | 0.3316 | -0.7246 |
| a.25 | | 0.0315 | 0.3354 | -0.6583 |
| a.26 | | -0.0020 | 0.3470 | -0.7586 |
| a.27 | | 0.0393 | 0.3408 | -0.6451 |
| a.28 | | -0.0509 | 0.3532 | -0.8780 |
| a.29 | | 0.0249 | 0.3402 | -0.6646 |
| a.3 | | -0.0459 | 0.3603 | -0.8805 |
| a.30 | | -0.0488 | 0.3630 | -0.8963 |
| a.4 | | -0.0231 | 0.3393 | -0.7820 |
| a.5 | | 0.0143 | 0.3428 | -0.6990 |
| a.6 | | -0.0216 | 0.3552 | -0.8194 |
| a.7 | | -0.1360 | 0.3900 | -1.1218 |
| a.8 | | -0.0576 | 0.3561 | -0.8951 |
| a.9 | | -0.0134 | 0.3453 | -0.7686 |
| b.1 | | -0.0227 | 0.3526 | -0.8168 |
| b.10 | | -0.0495 | 0.3721 | -0.9287 |
| b.11 | | -0.0421 | 0.3663 | -0.9066 |
| b.12 | | 0.1494 | 0.3653 | -0.4435 |
| b.13 | | -0.0180 | 0.3501 | -0.7972 |
| b.14 | | -0.0113 | 0.3471 | -0.7723 |
| b.15 | | 0.0181 | 0.3458 | -0.7083 |
| b.16 | | -0.1543 | 0.3911 | -1.1480 |
| b.17 | | -0.0932 | 0.3818 | -1.0471 |
| b.18 | | -0.0544 | 0.3615 | -0.9217 |
| b.19 | | 0.1001 | 0.3434 | -0.5168 |
| b.2 | | 0.0767 | 0.3409 | -0.5631 |
| b.20 | | 0.0022 | 0.3429 | -0.7406 |
| b.21 | | -0.0406 | 0.3556 | -0.8552 |
| b.22 | | 0.0173 | 0.3401 | -0.6930 |
| b.23 | | 0.0120 | 0.3485 | -0.7355 |
| b.24 | | 0.0787 | 0.3520 | -0.5766 |

| | | | | |
|------|---------|--------|---------|--------|
| b.25 | -0.0531 | 0.3677 | -0.9135 | 0.6789 |
| b.26 | 0.0139 | 0.3338 | -0.6861 | 0.7717 |
| b.27 | -0.0114 | 0.3452 | -0.7594 | 0.7290 |
| b.28 | 0.1480 | 0.3611 | -0.4408 | 1.0487 |
| b.29 | 0.1358 | 0.3563 | -0.4606 | 1.0353 |
| b.3 | -0.0119 | 0.3547 | -0.7928 | 0.7415 |
| b.30 | 0.0508 | 0.3318 | -0.6006 | 0.8381 |
| b.5 | -0.0987 | 0.3581 | -0.9847 | 0.5628 |
| b.6 | 0.0179 | 0.3515 | -0.7070 | 0.8120 |
| b.7 | -0.0244 | 0.3566 | -0.8258 | 0.7294 |
| b.8 | 0.0266 | 0.3384 | -0.6749 | 0.7974 |
| b.9 | -0.0042 | 0.3470 | -0.7556 | 0.7581 |
| c.1 | -0.1257 | 0.3728 | -1.0616 | 0.5140 |
| c.10 | -0.0074 | 0.3617 | -0.8015 | 0.7732 |
| c.11 | -0.0081 | 0.3608 | -0.7931 | 0.7599 |
| c.12 | -0.0020 | 0.3515 | -0.7676 | 0.7757 |
| c.14 | -0.0203 | 0.3536 | -0.8091 | 0.7293 |
| c.15 | -0.0460 | 0.3438 | -0.8363 | 0.6519 |
| c.16 | -0.0139 | 0.3361 | -0.7415 | 0.7193 |
| c.18 | 0.0561 | 0.3342 | -0.6075 | 0.8428 |
| c.19 | -0.0810 | 0.3496 | -0.9113 | 0.5914 |
| c.2 | -0.0756 | 0.3541 | -0.9242 | 0.6069 |
| c.21 | 0.0055 | 0.3416 | -0.7163 | 0.7571 |
| c.22 | 0.0152 | 0.3309 | -0.6757 | 0.7721 |
| c.23 | 0.0412 | 0.3378 | -0.6393 | 0.8205 |
| c.24 | 0.3404 | 0.4464 | -0.2017 | 1.4741 |
| c.25 | -0.0734 | 0.3457 | -0.8961 | 0.5971 |
| c.26 | -0.0669 | 0.3576 | -0.9205 | 0.6255 |
| c.27 | 0.0902 | 0.3446 | -0.5463 | 0.9309 |
| c.28 | -0.0889 | 0.3646 | -0.9866 | 0.5814 |
| c.29 | 0.0432 | 0.3330 | -0.6228 | 0.8052 |
| c.3 | 0.0003 | 0.3597 | -0.7872 | 0.7771 |
| c.30 | -0.0860 | 0.3614 | -0.9619 | 0.5918 |
| c.4 | -0.1496 | 0.3846 | -1.1251 | 0.4878 |
| c.5 | 0.0325 | 0.3382 | -0.6556 | 0.8072 |
| c.6 | -0.0025 | 0.3589 | -0.7827 | 0.7800 |
| c.7 | 0.1617 | 0.3516 | -0.4024 | 1.0442 |
| c.8 | 0.0027 | 0.3359 | -0.7183 | 0.7489 |

Locality of origin

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|-------------|----------|-----------|---------|--------|
| Locality 2 | 0.0779 | 0.2308 | -0.3293 | 0.6482 |
| Locality 6 | 0.0228 | 0.2260 | -0.4309 | 0.5538 |
| Locality 7 | -0.0547 | 0.2361 | -0.6211 | 0.3948 |
| Locality 8 | 0.0122 | 0.2287 | -0.4599 | 0.5459 |
| Locality 9 | -0.1215 | 0.2633 | -0.8035 | 0.2877 |
| Locality 10 | 0.0531 | 0.2344 | -0.3874 | 0.6201 |
| Locality 11 | -0.0915 | 0.2648 | -0.7695 | 0.3519 |
| Locality 12 | -0.0954 | 0.2525 | -0.7425 | 0.3217 |
| Locality 13 | 0.0690 | 0.2439 | -0.3831 | 0.6626 |
| Locality 14 | 0.0925 | 0.2409 | -0.3090 | 0.7082 |

Experimental assemble

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|------------|----------|-----------|---------|--------|
| Assemble 1 | 0.5146 | 1.0731 | -1.5812 | 2.6735 |
| Assemble 2 | 0.6099 | 1.0612 | -1.4907 | 2.7107 |
| Assemble 3 | 0.5815 | 1.0866 | -1.5094 | 2.8134 |
| Assemble 4 | -1.3730 | 1.0657 | -3.5940 | 0.6425 |

| Assemble 5 | 1.7694 | 0.9016 | 0.1444 | 3.7149 |
|-----------------------------------|----------|-----------|----------|---------|
| Assemble 6 | 0.3487 | 0.7869 | -1.1693 | 1.9494 |
| Assemble 7 | -3.2211 | 1.0862 | -5.2525 | -0.9246 |
| Assemble 8 | 1.0548 | 0.8736 | -0.5512 | 2.8991 |
| Assemble 9 | -5.7740 | 2.8104 | -11.8706 | -1.0308 |
| Assemble 10 | 2.7274 | 1.3253 | 0.4109 | 5.6908 |
| Assemble 11 | 1.1884 | 1.3645 | -1.2099 | 4.1777 |
| Assemble 12 | 2.1746 | 1.4200 | -0.2885 | 5.3047 |
| Assemble 13 | 0.8825 | 1.1840 | -1.5884 | 3.1518 |
| Assemble 14 | -0.6325 | 1.0788 | -2.8178 | 1.4784 |
| Assemble 15 | -0.2905 | 1.4937 | -3.5482 | 2.3848 |
| Assemble 16 | -1.6321 | 1.2342 | -4.3114 | 0.5699 |
| Assemble 17 | -3.2682 | 1.3319 | -6.1135 | -0.8443 |
| Assemble 18 | 0.5697 | 1.0248 | -1.4696 | 2.6148 |
| Assemble 19 | 1.3805 | 1.3812 | -1.2794 | 4.1947 |
| Assemble 20 | 0.0731 | 1.3913 | -2.6263 | 2.8882 |
| Sex and reproductive state | | | | |
| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
| Pregnant female | -0.0350 | 0.4818 | -1.1096 | 0.8117 |
| No pregnant female | -0.1242 | 0.4755 | -1.2337 | 0.6058 |
| Male | -0.0011 | 0.4665 | -1.0283 | 0.8426 |

Table A2. Conditional modes of random effects in the associative betweenness centrality model. Random effects at the level of individuals, sex-pregnant interaction, locality of origin, and experimental assemblages of individuals were controlled for in the model.

| Individual identity | | | | |
|----------------------------|------------------|-----------------|------------------|-------------|
| | Intercept | Estimate | Est.Error | 2.5% |
| a.1 | | 0.0151 | 0.1667 | -0.3342 |
| a.10 | | 0.0613 | 0.1725 | -0.2385 |
| a.11 | | 0.0248 | 0.1675 | -0.3087 |
| a.12 | | 0.0312 | 0.1623 | -0.2888 |
| a.13 | | -0.0191 | 0.1666 | -0.4032 |
| a.14 | | 0.0008 | 0.1794 | -0.3912 |
| a.15 | | 0.0359 | 0.1691 | -0.2851 |
| a.16 | | 0.0180 | 0.1660 | -0.3268 |
| a.17 | | -0.0181 | 0.1650 | -0.3993 |
| a.18 | | -0.0070 | 0.1668 | -0.3777 |
| a.19 | | -0.0001 | 0.1642 | -0.3590 |
| a.2 | | 0.0048 | 0.1713 | -0.3642 |
| a.20 | | -0.0065 | 0.1655 | -0.3766 |
| a.21 | | 0.0215 | 0.1629 | -0.3094 |
| a.23 | | 0.0095 | 0.1607 | -0.3341 |
| a.24 | | -0.0093 | 0.1590 | -0.3671 |
| a.25 | | -0.0010 | 0.1625 | -0.3595 |
| a.26 | | 0.0038 | 0.1607 | -0.3408 |
| a.27 | | 0.0286 | 0.1659 | -0.2980 |
| a.28 | | -0.0578 | 0.1748 | -0.4977 |
| a.29 | | 0.0213 | 0.1741 | -0.3322 |
| a.3 | | -0.0180 | 0.1636 | -0.3916 |
| a.30 | | -0.0058 | 0.1716 | -0.3913 |
| a.4 | | 0.0179 | 0.1653 | -0.3247 |
| a.5 | | -0.0407 | 0.1723 | -0.4543 |
| a.6 | | -0.0491 | 0.1711 | -0.4728 |
| a.7 | | -0.0274 | 0.1635 | -0.4088 |
| a.8 | | -0.0174 | 0.1627 | -0.3839 |
| a.9 | | -0.0014 | 0.1672 | -0.3629 |
| b.1 | | 0.1065 | 0.2073 | -0.1862 |
| b.10 | | -0.0548 | 0.1816 | -0.5111 |
| b.11 | | -0.0278 | 0.1753 | -0.4383 |
| b.12 | | 0.0820 | 0.1855 | -0.2138 |
| b.13 | | -0.0083 | 0.1647 | -0.3780 |
| b.14 | | 0.0052 | 0.1702 | -0.3613 |
| b.15 | | 0.0027 | 0.1652 | -0.3563 |
| b.16 | | -0.0035 | 0.1664 | -0.3690 |
| b.17 | | -0.0529 | 0.1773 | -0.4925 |
| b.18 | | -0.0568 | 0.1798 | -0.5119 |
| b.19 | | 0.0335 | 0.1712 | -0.3006 |
| b.2 | | -0.0240 | 0.1664 | -0.4112 |
| b.20 | | 0.0298 | 0.1771 | -0.3106 |
| b.21 | | -0.0105 | 0.1643 | -0.3794 |
| b.22 | | 0.0283 | 0.1670 | -0.3025 |
| b.23 | | 0.0064 | 0.1736 | -0.3653 |
| b.24 | | -0.0154 | 0.1657 | -0.3954 |
| b.25 | | -0.0082 | 0.1641 | -0.3747 |
| b.26 | | -0.0018 | 0.1596 | -0.3516 |
| b.27 | | -0.0545 | 0.1700 | -0.4808 |

| | | | | |
|------|---------|--------|---------|--------|
| b.28 | 0.0528 | 0.1698 | -0.2535 | 0.4712 |
| b.29 | 0.0171 | 0.1633 | -0.3168 | 0.3912 |
| b.3 | -0.0451 | 0.1728 | -0.4679 | 0.2671 |
| b.30 | 0.0337 | 0.1690 | -0.2917 | 0.4332 |
| b.5 | 0.0344 | 0.1679 | -0.2913 | 0.4312 |
| b.6 | 0.0071 | 0.1710 | -0.3578 | 0.3874 |
| b.7 | -0.0037 | 0.1697 | -0.3833 | 0.3634 |
| b.8 | 0.0032 | 0.1668 | -0.3468 | 0.3702 |
| b.9 | -0.0674 | 0.1795 | -0.5157 | 0.2404 |
| c.1 | 0.0014 | 0.1813 | -0.3943 | 0.3996 |
| c.10 | 0.0001 | 0.1803 | -0.3975 | 0.3991 |
| c.11 | -0.0011 | 0.1800 | -0.3964 | 0.3936 |
| c.12 | 0.0013 | 0.1798 | -0.3889 | 0.4021 |
| c.14 | 0.0313 | 0.1762 | -0.3168 | 0.4505 |
| c.15 | -0.0196 | 0.1634 | -0.3969 | 0.3173 |
| c.16 | -0.0435 | 0.1657 | -0.4475 | 0.2671 |
| c.18 | -0.0079 | 0.1563 | -0.3593 | 0.3260 |
| c.19 | -0.0952 | 0.1864 | -0.5708 | 0.1877 |
| c.2 | -0.0033 | 0.1676 | -0.3761 | 0.3609 |
| c.21 | -0.0427 | 0.1684 | -0.4563 | 0.2713 |
| c.22 | 0.0914 | 0.1876 | -0.1881 | 0.5797 |
| c.23 | 0.1261 | 0.2036 | -0.1467 | 0.6587 |
| c.24 | 0.1584 | 0.2257 | -0.1189 | 0.7476 |
| c.25 | -0.0557 | 0.1690 | -0.4754 | 0.2442 |
| c.26 | -0.0402 | 0.1677 | -0.4396 | 0.2724 |
| c.27 | 0.0164 | 0.1581 | -0.3174 | 0.3755 |
| c.28 | -0.0995 | 0.1897 | -0.5925 | 0.1788 |
| c.29 | -0.0191 | 0.1611 | -0.3846 | 0.3205 |
| c.3 | 0.0009 | 0.1821 | -0.3941 | 0.4016 |
| c.30 | -0.0226 | 0.1621 | -0.3953 | 0.3082 |
| c.4 | -0.0003 | 0.1806 | -0.3906 | 0.4008 |
| c.5 | 0.0311 | 0.1625 | -0.2868 | 0.4082 |
| c.6 | 0.0001 | 0.1813 | -0.4023 | 0.3955 |
| c.7 | 0.0316 | 0.1664 | -0.2971 | 0.4192 |
| c.8 | -0.0564 | 0.1789 | -0.5026 | 0.2577 |

Locality of origin

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|-------------|----------|-----------|---------|--------|
| Locality 2 | 0.3805 | 0.2064 | 0.0050 | 0.8071 |
| Locality 6 | -0.1423 | 0.1783 | -0.5191 | 0.1872 |
| Locality 7 | 0.0666 | 0.1872 | -0.2957 | 0.4562 |
| Locality 8 | -0.1062 | 0.1809 | -0.4853 | 0.2369 |
| Locality 9 | 0.0055 | 0.1942 | -0.3878 | 0.3985 |
| Locality 10 | -0.0352 | 0.1796 | -0.4073 | 0.3222 |
| Locality 11 | 0.0276 | 0.2015 | -0.3719 | 0.4459 |
| Locality 12 | -0.2533 | 0.2037 | -0.6922 | 0.0971 |
| Locality 13 | -0.0687 | 0.1897 | -0.4654 | 0.2976 |
| Locality 14 | 0.1314 | 0.1879 | -0.2136 | 0.5337 |

Experimental assemble

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|------------|----------|-----------|---------|--------|
| Assemble 1 | 0.0911 | 0.2962 | -0.4898 | 0.6775 |
| Assemble 2 | -0.1576 | 0.3146 | -0.7934 | 0.4566 |
| Assemble 3 | -0.5570 | 0.3045 | -1.1736 | 0.0285 |
| Assemble 4 | 0.2848 | 0.3109 | -0.3150 | 0.9070 |
| Assemble 5 | -0.2814 | 0.2882 | -0.8632 | 0.2671 |
| Assemble 6 | 0.1567 | 0.2699 | -0.3736 | 0.6886 |
| Assemble 7 | 0.8455 | 0.3024 | 0.2775 | 1.4617 |

| Assemble 8 | -0.1529 | 0.2620 | -0.6748 | 0.3562 |
|-----------------------------------|----------|-----------|---------|---------|
| Assemble 9 | 0.5297 | 0.4995 | -0.3797 | 1.5903 |
| Assemble 10 | -0.8356 | 0.3465 | -1.5497 | -0.1880 |
| Assemble 11 | 0.2665 | 0.3724 | -0.4476 | 1.0102 |
| Assemble 12 | 0.0419 | 0.3955 | -0.7393 | 0.8199 |
| Assemble 13 | 0.0032 | 0.5809 | -1.1582 | 1.1529 |
| Assemble 14 | -0.1935 | 0.3032 | -0.8006 | 0.3985 |
| Assemble 15 | -0.1759 | 0.3905 | -0.9679 | 0.5907 |
| Assemble 16 | -0.0968 | 0.3310 | -0.7595 | 0.5563 |
| Assemble 17 | 0.5040 | 0.3544 | -0.1777 | 1.2283 |
| Assemble 18 | 0.5309 | 0.3679 | -0.1656 | 1.2792 |
| Assemble 19 | -0.3972 | 0.3807 | -1.1698 | 0.3273 |
| Assemble 20 | -0.3690 | 0.3695 | -1.1207 | 0.3400 |
| Sex and reproductive state | | | | |
| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
| Pregnant female | -0.0288 | 0.3115 | -0.6595 | 0.6187 |
| No pregnant female | -0.0576 | 0.3052 | -0.6789 | 0.5815 |
| Male | 0.1195 | 0.3130 | -0.4214 | 0.8486 |

Table A3. Conditional modes of random effects in the average association strength model. Random effects at the level of individuals, sex-pregnant interaction, locality of origin, and experimental assemblages of individuals were controlled for in the model.

| Individual identity | | | | |
|----------------------------|------------------|-----------------|------------------|-------------|
| | Intercept | Estimate | Est.Error | 2.5% |
| a.1 | | 0.0474 | 0.1528 | -0.2177 |
| a.10 | | -0.0360 | 0.1444 | -0.3862 |
| a.11 | | 0.0194 | 0.1469 | -0.2859 |
| a.12 | | -0.0325 | 0.1438 | -0.3692 |
| a.13 | | 0.0622 | 0.1576 | -0.2042 |
| a.14 | | -0.0591 | 0.1595 | -0.4495 |
| a.15 | | 0.0393 | 0.1509 | -0.2485 |
| a.16 | | 0.0615 | 0.1554 | -0.1974 |
| a.17 | | -0.1963 | 0.2583 | -0.8640 |
| a.18 | | -0.0216 | 0.1404 | -0.3523 |
| a.19 | | 0.0274 | 0.1386 | -0.2501 |
| a.2 | | 0.0224 | 0.1452 | -0.2777 |
| a.20 | | 0.0029 | 0.1381 | -0.2921 |
| a.21 | | -0.0588 | 0.1530 | -0.4347 |
| a.23 | | -0.0283 | 0.1400 | -0.3533 |
| a.24 | | -0.0146 | 0.1460 | -0.3536 |
| a.25 | | 0.0470 | 0.1470 | -0.2078 |
| a.26 | | -0.0592 | 0.1469 | -0.4247 |
| a.27 | | -0.0299 | 0.1511 | -0.3805 |
| a.28 | | -0.0256 | 0.1485 | -0.3829 |
| a.29 | | 0.0149 | 0.1486 | -0.2904 |
| a.3 | | -0.0051 | 0.1416 | -0.3068 |
| a.30 | | -0.0057 | 0.1443 | -0.3290 |
| a.4 | | -0.0013 | 0.1426 | -0.3170 |
| a.5 | | 0.0053 | 0.1400 | -0.2953 |
| a.6 | | -0.0169 | 0.1459 | -0.3640 |
| a.7 | | 0.0023 | 0.1383 | -0.2870 |
| a.8 | | -0.0299 | 0.1415 | -0.3444 |
| a.9 | | 0.0696 | 0.1542 | -0.1898 |
| b.1 | | -0.0735 | 0.1588 | -0.4733 |
| b.10 | | 0.0229 | 0.1442 | -0.2634 |
| b.11 | | -0.0092 | 0.1516 | -0.3518 |
| b.12 | | 0.0339 | 0.1495 | -0.2537 |
| b.13 | | -0.0737 | 0.1641 | -0.4770 |
| b.14 | | -0.0231 | 0.1455 | -0.3790 |
| b.15 | | 0.0042 | 0.1468 | -0.3006 |
| b.16 | | -0.1628 | 0.2101 | -0.6847 |
| b.17 | | -0.0642 | 0.1567 | -0.4595 |
| b.18 | | 0.0488 | 0.1576 | -0.2333 |
| b.19 | | 0.0828 | 0.1752 | -0.2071 |
| b.2 | | -0.0123 | 0.1493 | -0.3460 |
| b.20 | | 0.0109 | 0.1426 | -0.3121 |
| b.21 | | 0.0573 | 0.1558 | -0.2083 |
| b.22 | | 0.0074 | 0.1438 | -0.3204 |
| b.23 | | 0.0203 | 0.1629 | -0.2970 |
| b.24 | | 0.0524 | 0.1655 | -0.2551 |
| b.25 | | 0.0160 | 0.1479 | -0.2909 |
| b.26 | | 0.0419 | 0.1489 | -0.2523 |
| b.27 | | 0.0798 | 0.1634 | -0.1750 |

| | | | | |
|------|---------|--------|---------|--------|
| b.28 | -0.0908 | 0.1669 | -0.5087 | 0.1549 |
| b.29 | 0.0476 | 0.1455 | -0.2238 | 0.3937 |
| b.3 | 0.0342 | 0.1421 | -0.2342 | 0.3763 |
| b.30 | 0.0359 | 0.1384 | -0.2229 | 0.3727 |
| b.5 | 0.0445 | 0.1458 | -0.2134 | 0.4190 |
| b.6 | -0.0056 | 0.1511 | -0.3512 | 0.3270 |
| b.7 | -0.0203 | 0.1484 | -0.3693 | 0.2801 |
| b.8 | 0.0651 | 0.1656 | -0.2033 | 0.4715 |
| b.9 | 0.0120 | 0.1380 | -0.2752 | 0.3320 |
| c.1 | 0.0107 | 0.1354 | -0.2783 | 0.3096 |
| c.10 | -0.0019 | 0.1573 | -0.3532 | 0.3339 |
| c.11 | -0.0013 | 0.1482 | -0.3276 | 0.3249 |
| c.12 | 0.0023 | 0.1463 | -0.3173 | 0.3222 |
| c.14 | -0.0049 | 0.1408 | -0.3209 | 0.2924 |
| c.15 | -0.1275 | 0.1859 | -0.6012 | 0.1166 |
| c.16 | 0.0621 | 0.1478 | -0.1873 | 0.4151 |
| c.18 | 0.0710 | 0.1514 | -0.1770 | 0.4330 |
| c.19 | -0.0545 | 0.1450 | -0.3975 | 0.1963 |
| c.2 | 0.0144 | 0.1447 | -0.2923 | 0.3327 |
| c.21 | 0.0467 | 0.1510 | -0.2272 | 0.4122 |
| c.22 | -0.0045 | 0.1357 | -0.3039 | 0.2914 |
| c.23 | -0.0777 | 0.1555 | -0.4659 | 0.1769 |
| c.24 | 0.0253 | 0.1386 | -0.2463 | 0.3613 |
| c.25 | -0.0315 | 0.1418 | -0.3595 | 0.2497 |
| c.26 | 0.0430 | 0.1488 | -0.2290 | 0.4133 |
| c.27 | 0.0741 | 0.1632 | -0.1910 | 0.4888 |
| c.28 | 0.0289 | 0.1353 | -0.2387 | 0.3460 |
| c.29 | -0.0640 | 0.1463 | -0.4250 | 0.1791 |
| c.3 | -0.0086 | 0.1554 | -0.3736 | 0.3213 |
| c.30 | -0.0489 | 0.1393 | -0.3659 | 0.2037 |
| c.4 | -0.1617 | 0.2156 | -0.6918 | 0.0941 |
| c.5 | 0.0217 | 0.1346 | -0.2386 | 0.3457 |
| c.6 | 0.0145 | 0.1544 | -0.3069 | 0.3567 |
| c.7 | 0.1036 | 0.1671 | -0.1358 | 0.5188 |
| c.8 | 0.1146 | 0.1784 | -0.1349 | 0.5704 |

Locality of origin

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|-------------|----------|-----------|---------|--------|
| Locality 2 | -0.0204 | 0.0774 | -0.2028 | 0.1296 |
| Locality 6 | 0.0640 | 0.0965 | -0.0694 | 0.3081 |
| Locality 7 | 0.0165 | 0.0769 | -0.1319 | 0.2027 |
| Locality 8 | 0.0333 | 0.0853 | -0.1154 | 0.2374 |
| Locality 9 | -0.0275 | 0.0831 | -0.2186 | 0.1307 |
| Locality 10 | -0.0048 | 0.0810 | -0.1765 | 0.1717 |
| Locality 11 | -0.0120 | 0.0800 | -0.1935 | 0.1514 |
| Locality 12 | -0.0334 | 0.0871 | -0.2479 | 0.1172 |
| Locality 13 | 0.0355 | 0.0866 | -0.1079 | 0.2481 |
| Locality 14 | -0.0426 | 0.0868 | -0.2581 | 0.0997 |

Experimental assemble

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|------------|----------|-----------|---------|---------|
| Assemble 1 | -0.4483 | 0.2539 | -0.9596 | 0.0299 |
| Assemble 2 | 0.6102 | 0.2551 | 0.1008 | 1.1118 |
| Assemble 3 | -0.5251 | 0.2546 | -1.0392 | -0.0376 |
| Assemble 4 | -0.2459 | 0.2501 | -0.7354 | 0.2310 |
| Assemble 5 | 0.4595 | 0.2198 | 0.0142 | 0.8858 |
| Assemble 6 | 0.0960 | 0.2090 | -0.3076 | 0.5203 |
| Assemble 7 | -0.1326 | 0.2525 | -0.6432 | 0.3687 |

| Assemble 8 | 0.1548 | 0.2124 | -0.2665 | 0.5787 |
|-----------------------------------|----------|-----------|---------|---------|
| Assemble 9 | -1.0903 | 0.3941 | -1.9046 | -0.3860 |
| Assemble 10 | 0.2362 | 0.2925 | -0.3400 | 0.8268 |
| Assemble 11 | -0.2103 | 0.3282 | -0.8518 | 0.4351 |
| Assemble 12 | 0.8318 | 0.3264 | 0.1889 | 1.5001 |
| Assemble 13 | 0.8713 | 0.2810 | 0.3336 | 1.4398 |
| Assemble 14 | -0.4260 | 0.2511 | -0.9364 | 0.0533 |
| Assemble 15 | 0.0787 | 0.3340 | -0.5498 | 0.7540 |
| Assemble 16 | -0.3575 | 0.2730 | -0.8828 | 0.1983 |
| Assemble 17 | -0.1183 | 0.2813 | -0.6498 | 0.4604 |
| Assemble 18 | 0.3633 | 0.2520 | -0.1144 | 0.8719 |
| Assemble 19 | -0.1564 | 0.3297 | -0.7947 | 0.5240 |
| Assemble 20 | -0.4483 | 0.2539 | -0.9596 | 0.0299 |
| Sex and reproductive state | | | | |
| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
| Pregnant female | 0.0296 | 0.1879 | -0.3198 | 0.4595 |
| No pregnant female | -0.0024 | 0.1825 | -0.3702 | 0.3617 |
| Male | -0.0021 | 0.1828 | -0.3666 | 0.3455 |

Table A4. Conditional modes of random effects in the Aggressiveness degree centrality model. Random effects at the level of individuals, sex-pregnant interaction and experimental assemblages of individuals were controlled for in the model.

| Individual identity | | | | |
|----------------------------|------------------|-----------------|------------------|-------------|
| | Intercept | Estimate | Est.Error | 2.5% |
| a.1 | | -0.0003 | 0.1452 | -0.3206 |
| a.11 | | 0.0519 | 0.1617 | -0.2227 |
| a.12 | | 0.0092 | 0.1516 | -0.3075 |
| a.13 | | -0.0285 | 0.1541 | -0.3985 |
| a.15 | | 0.0104 | 0.1492 | -0.3059 |
| a.17 | | -0.0007 | 0.1506 | -0.3285 |
| a.18 | | -0.0136 | 0.1521 | -0.3664 |
| a.19 | | 0.0229 | 0.1467 | -0.2706 |
| a.21 | | 0.0321 | 0.1496 | -0.2480 |
| a.23 | | -0.0193 | 0.1464 | -0.3613 |
| a.27 | | -0.0087 | 0.1465 | -0.3440 |
| a.29 | | -0.0200 | 0.1526 | -0.3821 |
| a.3 | | 0.0448 | 0.1607 | -0.2441 |
| a.4 | | -0.0048 | 0.1451 | -0.3281 |
| a.5 | | 0.0339 | 0.1535 | -0.2546 |
| a.6 | | -0.0116 | 0.1508 | -0.3516 |
| a.7 | | 0.0009 | 0.1490 | -0.3279 |
| a.8 | | -0.0049 | 0.1471 | -0.3322 |
| a.9 | | -0.0256 | 0.1504 | -0.3841 |
| b.1 | | 0.0465 | 0.1568 | -0.2313 |
| b.10 | | 0.0024 | 0.1470 | -0.3206 |
| b.11 | | -0.0060 | 0.1518 | -0.3452 |
| b.12 | | -0.0190 | 0.1553 | -0.3835 |
| b.13 | | 0.0628 | 0.1586 | -0.1930 |
| b.14 | | -0.0102 | 0.1524 | -0.3543 |
| b.15 | | 0.1017 | 0.1839 | -0.1450 |
| b.16 | | -0.0279 | 0.1503 | -0.3895 |
| b.17 | | -0.0186 | 0.1548 | -0.3781 |
| b.19 | | -0.0182 | 0.1537 | -0.3725 |
| b.2 | | -0.0130 | 0.1536 | -0.3663 |
| b.20 | | -0.0154 | 0.1531 | -0.3703 |
| b.21 | | -0.0174 | 0.1551 | -0.3784 |
| b.23 | | -0.0057 | 0.1518 | -0.3432 |
| b.24 | | -0.0325 | 0.1536 | -0.4090 |
| b.26 | | -0.0152 | 0.1524 | -0.3676 |
| b.27 | | -0.0291 | 0.1527 | -0.3978 |
| b.28 | | 0.0294 | 0.1481 | -0.2565 |
| b.29 | | -0.0248 | 0.1520 | -0.3868 |
| b.3 | | -0.0364 | 0.1515 | -0.4121 |
| b.30 | | -0.0054 | 0.1533 | -0.3491 |
| b.5 | | -0.0217 | 0.1477 | -0.3744 |
| b.7 | | 0.0647 | 0.1603 | -0.1927 |
| b.8 | | -0.0142 | 0.1508 | -0.3620 |
| b.9 | | -0.0146 | 0.1463 | -0.3518 |
| c.1 | | 0.0142 | 0.1537 | -0.3013 |
| c.14 | | 0.0121 | 0.1519 | -0.3092 |
| c.15 | | 0.0368 | 0.1529 | -0.2424 |
| c.16 | | -0.0147 | 0.1482 | -0.3510 |
| c.18 | | -0.0034 | 0.1460 | -0.3240 |

| | | | | |
|------|---------|--------|---------|--------|
| c.19 | -0.0310 | 0.1531 | -0.4030 | 0.2550 |
| c.21 | -0.0122 | 0.1491 | -0.3560 | 0.3005 |
| c.22 | -0.0318 | 0.1503 | -0.3999 | 0.2522 |
| c.23 | 0.0056 | 0.1413 | -0.2980 | 0.3207 |
| c.24 | -0.0195 | 0.1456 | -0.3578 | 0.2736 |
| c.25 | -0.0061 | 0.1493 | -0.3408 | 0.3149 |
| c.27 | 0.0372 | 0.1572 | -0.2500 | 0.4266 |
| c.28 | -0.0274 | 0.1518 | -0.3960 | 0.2630 |
| c.29 | 0.0755 | 0.1573 | -0.1644 | 0.4861 |
| c.30 | -0.0317 | 0.1482 | -0.3926 | 0.2471 |
| c.4 | -0.0076 | 0.1548 | -0.3578 | 0.3192 |
| c.5 | -0.0061 | 0.1537 | -0.3518 | 0.3134 |
| c.7 | -0.0088 | 0.1501 | -0.3496 | 0.3041 |

Experimental assemble

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|-------------|----------|-----------|---------|--------|
| Assemble 1 | 0.0582 | 0.1526 | -0.2110 | 0.4283 |
| Assemble 3 | 0.1357 | 0.1806 | -0.1119 | 0.5835 |
| Assemble 4 | -0.0771 | 0.1675 | -0.4856 | 0.2060 |
| Assemble 5 | 0.0201 | 0.1556 | -0.2961 | 0.3721 |
| Assemble 6 | -0.0820 | 0.1832 | -0.5435 | 0.2081 |
| Assemble 7 | 0.0054 | 0.1507 | -0.3088 | 0.3364 |
| Assemble 8 | -0.0077 | 0.1550 | -0.3484 | 0.3201 |
| Assemble 9 | -0.0155 | 0.1867 | -0.4389 | 0.3690 |
| Assemble 10 | 0.0173 | 0.1695 | -0.3212 | 0.4083 |
| Assemble 11 | -0.0438 | 0.1823 | -0.4826 | 0.2928 |
| Assemble 14 | -0.0871 | 0.1662 | -0.4983 | 0.1845 |
| Assemble 15 | 0.0771 | 0.1817 | -0.2285 | 0.5304 |
| Assemble 16 | -0.0188 | 0.1676 | -0.4004 | 0.3236 |
| Assemble 17 | -0.0312 | 0.1712 | -0.4370 | 0.3006 |
| Assemble 18 | 0.0172 | 0.1664 | -0.3275 | 0.3942 |
| Assemble 19 | 0.0247 | 0.1784 | -0.3287 | 0.4423 |
| Assemble 20 | 0.0140 | 0.1733 | -0.3446 | 0.4002 |

Sex and reproductive state

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|--------------------|----------|-----------|---------|--------|
| Pregnant female | 0.0485 | 0.3704 | -0.5128 | 0.7749 |
| No pregnant female | 0.0142 | 0.3644 | -0.5682 | 0.7003 |
| Male | -0.0204 | 0.3653 | -0.6519 | 0.6495 |

Table A5. Conditional modes of random effects in the Aggressiveness in-degree centrality model. Random effects at the level of individuals, sex-pregnant interaction and experimental assemblages of individuals were controlled for in the model.

| Individual identity | | | | |
|----------------------------|------------------|-----------------|------------------|-------------|
| | Intercept | Estimate | Est.Error | 2.5% |
| a.1 | | 0.0720 | 0.2079 | -0.2700 |
| a.11 | | -0.0229 | 0.2060 | -0.5021 |
| a.12 | | 0.0051 | 0.2014 | -0.4280 |
| a.13 | | -0.0398 | 0.2071 | -0.5542 |
| a.15 | | 0.0435 | 0.2060 | -0.3430 |
| a.17 | | 0.0201 | 0.1967 | -0.3778 |
| a.18 | | -0.0237 | 0.2046 | -0.5054 |
| a.19 | | 0.0356 | 0.1939 | -0.3389 |
| a.21 | | 0.0368 | 0.1953 | -0.3338 |
| a.23 | | -0.0029 | 0.1951 | -0.4411 |
| a.27 | | 0.0270 | 0.1994 | -0.3707 |
| a.29 | | -0.0018 | 0.1990 | -0.4390 |
| a.3 | | 0.0053 | 0.2012 | -0.4214 |
| a.4 | | 0.0065 | 0.1926 | -0.4045 |
| a.5 | | -0.0181 | 0.1958 | -0.4702 |
| a.6 | | 0.0051 | 0.1995 | -0.4199 |
| a.7 | | 0.0216 | 0.1969 | -0.3826 |
| a.8 | | -0.0047 | 0.1974 | -0.4425 |
| a.9 | | -0.0250 | 0.1990 | -0.4818 |
| b.1 | | -0.0052 | 0.1980 | -0.4472 |
| b.10 | | 0.0064 | 0.1931 | -0.4066 |
| b.11 | | -0.0449 | 0.2092 | -0.5591 |
| b.12 | | 0.0054 | 0.2004 | -0.4155 |
| b.13 | | 0.1451 | 0.2465 | -0.1650 |
| b.14 | | -0.0262 | 0.2042 | -0.5100 |
| b.15 | | 0.0047 | 0.1940 | -0.4112 |
| b.16 | | 0.0190 | 0.1940 | -0.3791 |
| b.17 | | -0.0305 | 0.2072 | -0.5271 |
| b.19 | | -0.0067 | 0.2005 | -0.4539 |
| b.2 | | 0.0044 | 0.1994 | -0.4242 |
| b.20 | | -0.0333 | 0.2051 | -0.5250 |
| b.21 | | 0.0081 | 0.2007 | -0.4252 |
| b.23 | | 0.0070 | 0.2030 | -0.4153 |
| b.24 | | -0.0199 | 0.1998 | -0.4852 |
| b.26 | | -0.0045 | 0.1987 | -0.4511 |
| b.27 | | -0.0463 | 0.2084 | -0.5554 |
| b.28 | | -0.0252 | 0.1997 | -0.4848 |
| b.29 | | 0.0204 | 0.1963 | -0.3805 |
| b.3 | | -0.0090 | 0.1929 | -0.4314 |
| b.30 | | -0.0265 | 0.2044 | -0.5008 |
| b.5 | | -0.0298 | 0.1995 | -0.5022 |
| b.7 | | -0.0003 | 0.1958 | -0.4274 |
| b.8 | | 0.0011 | 0.2016 | -0.4368 |
| b.9 | | -0.0163 | 0.1953 | -0.4589 |
| c.1 | | 0.0091 | 0.2026 | -0.4245 |
| c.14 | | 0.0564 | 0.2164 | -0.3196 |
| c.15 | | 0.0430 | 0.2026 | -0.3339 |
| c.16 | | -0.0185 | 0.1982 | -0.4832 |
| c.18 | | 0.0048 | 0.1915 | -0.3984 |

| | | | | |
|------|---------|--------|---------|--------|
| c.19 | 0.0054 | 0.1959 | -0.4147 | 0.4329 |
| c.21 | 0.0572 | 0.2073 | -0.3106 | 0.5808 |
| c.22 | -0.0108 | 0.1905 | -0.4351 | 0.3956 |
| c.23 | -0.0649 | 0.2041 | -0.5808 | 0.2844 |
| c.24 | -0.0548 | 0.2113 | -0.5857 | 0.3122 |
| c.25 | 0.0261 | 0.1981 | -0.3702 | 0.4918 |
| c.27 | 0.0080 | 0.1983 | -0.4209 | 0.4529 |
| c.28 | -0.0205 | 0.1988 | -0.4919 | 0.3839 |
| c.29 | -0.0030 | 0.1851 | -0.4078 | 0.4029 |
| c.30 | -0.0471 | 0.1990 | -0.5381 | 0.3150 |
| c.4 | -0.0274 | 0.2062 | -0.5210 | 0.3789 |
| c.5 | -0.0219 | 0.2074 | -0.4988 | 0.3913 |
| c.7 | 0.0255 | 0.1967 | -0.3670 | 0.4959 |

Experimental assemble

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|-------------|----------|-----------|---------|--------|
| Assemble 1 | 0.0500 | 0.1714 | -0.2585 | 0.4734 |
| Assemble 3 | 0.0743 | 0.1792 | -0.2212 | 0.5319 |
| Assemble 4 | -0.0403 | 0.1783 | -0.4691 | 0.3002 |
| Assemble 5 | -0.0048 | 0.1721 | -0.3878 | 0.3696 |
| Assemble 6 | -0.0332 | 0.1877 | -0.4875 | 0.3257 |
| Assemble 7 | 0.0044 | 0.1683 | -0.3601 | 0.3825 |
| Assemble 8 | -0.0083 | 0.1702 | -0.3961 | 0.3551 |
| Assemble 9 | -0.0301 | 0.2053 | -0.5163 | 0.3607 |
| Assemble 10 | 0.0106 | 0.1840 | -0.3705 | 0.4277 |
| Assemble 11 | 0.0029 | 0.1891 | -0.4026 | 0.4184 |
| Assemble 14 | -0.0755 | 0.1859 | -0.5522 | 0.2197 |
| Assemble 15 | 0.0536 | 0.1911 | -0.2864 | 0.5346 |
| Assemble 16 | 0.0085 | 0.1852 | -0.3828 | 0.4278 |
| Assemble 17 | -0.0234 | 0.1863 | -0.4623 | 0.3469 |
| Assemble 18 | -0.0070 | 0.1807 | -0.4150 | 0.3727 |
| Assemble 19 | 0.0094 | 0.1953 | -0.4031 | 0.4421 |
| Assemble 20 | 0.0129 | 0.1885 | -0.3772 | 0.4420 |

Sex and reproductive state

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|--------------------|----------|-----------|---------|--------|
| Pregnant female | 0.0678 | 0.5979 | -0.9647 | 1.3392 |
| No pregnant female | 0.2203 | 0.5978 | -0.7539 | 1.5385 |
| Male | -0.1886 | 0.5957 | -1.3296 | 0.9674 |

Table A6. Conditional modes of random effects in the Aggressiveness out-degree centrality model. Random effects at the level of individuals, sex-pregnant interaction and experimental assemblages of individuals were controlled for in the model.

| Individual identity | | | | |
|----------------------------|------------------|-----------------|------------------|-------------|
| | Intercept | Estimate | Est.Error | 2.5% |
| a.1 | | -0.3601 | 0.5643 | -1.6323 |
| a.11 | | 0.6025 | 0.5565 | -0.2925 |
| a.12 | | 0.0516 | 0.5117 | -0.9987 |
| a.13 | | -0.0469 | 0.5029 | -1.1035 |
| a.15 | | -0.1839 | 0.5582 | -1.4293 |
| a.17 | | -0.1035 | 0.4858 | -1.1569 |
| a.18 | | -0.0389 | 0.4960 | -1.0845 |
| a.19 | | 0.0576 | 0.4766 | -0.9119 |
| a.21 | | 0.0992 | 0.4712 | -0.8493 |
| a.23 | | -0.1506 | 0.4918 | -1.2148 |
| a.27 | | -0.1355 | 0.4946 | -1.1982 |
| a.29 | | -0.1880 | 0.5596 | -1.4361 |
| a.3 | | 0.4109 | 0.5284 | -0.4951 |
| a.4 | | -0.0640 | 0.4926 | -1.1146 |
| a.5 | | 0.4015 | 0.4799 | -0.4205 |
| a.6 | | -0.1680 | 0.5660 | -1.4383 |
| a.7 | | -0.0963 | 0.5015 | -1.1632 |
| a.8 | | -0.0156 | 0.4713 | -1.0046 |
| a.9 | | -0.0723 | 0.4954 | -1.1364 |
| b.1 | | 0.4437 | 0.5006 | -0.4067 |
| b.10 | | -0.0470 | 0.4673 | -1.0091 |
| b.11 | | 0.2211 | 0.5068 | -0.7488 |
| b.12 | | -0.2033 | 0.5592 | -1.4531 |
| b.13 | | -0.2888 | 0.5511 | -1.5313 |
| b.14 | | 0.0886 | 0.5309 | -0.9551 |
| b.15 | | 0.7851 | 0.5636 | -0.1040 |
| b.16 | | -0.3576 | 0.5634 | -1.6439 |
| b.17 | | -0.0146 | 0.5054 | -1.0727 |
| b.19 | | -0.1684 | 0.5658 | -1.4266 |
| b.2 | | -0.1737 | 0.5641 | -1.4194 |
| b.20 | | 0.0378 | 0.5139 | -1.0019 |
| b.21 | | -0.1980 | 0.5630 | -1.4623 |
| b.23 | | -0.0992 | 0.5701 | -1.3251 |
| b.24 | | -0.1981 | 0.5153 | -1.3460 |
| b.26 | | -0.1628 | 0.5601 | -1.4150 |
| b.27 | | 0.0123 | 0.4570 | -0.9316 |
| b.28 | | 0.3412 | 0.4718 | -0.4987 |
| b.29 | | -0.3164 | 0.5455 | -1.5417 |
| b.3 | | -0.2997 | 0.5517 | -1.5403 |
| b.30 | | 0.1018 | 0.5296 | -0.9671 |
| b.5 | | 0.0238 | 0.4676 | -0.9187 |
| b.7 | | 0.6157 | 0.5314 | -0.2345 |
| b.8 | | -0.1691 | 0.5557 | -1.3899 |
| b.9 | | 0.0174 | 0.4740 | -0.9510 |
| c.1 | | 0.1064 | 0.5358 | -0.9340 |
| c.14 | | -0.1944 | 0.5582 | -1.4213 |
| c.15 | | 0.1404 | 0.4827 | -0.7939 |
| c.16 | | -0.0291 | 0.5102 | -1.1078 |
| c.18 | | -0.0456 | 0.4942 | -1.0941 |

| | | | | |
|------|---------|--------|---------|--------|
| c.19 | -0.3346 | 0.5456 | -1.5688 | 0.6093 |
| c.21 | -0.3778 | 0.5730 | -1.6820 | 0.6157 |
| c.22 | -0.2189 | 0.4934 | -1.3123 | 0.6788 |
| c.23 | 0.3492 | 0.4527 | -0.4388 | 1.3247 |
| c.24 | 0.0656 | 0.4422 | -0.8214 | 0.9836 |
| c.25 | -0.2373 | 0.5490 | -1.4752 | 0.7379 |
| c.27 | 0.3078 | 0.5000 | -0.5820 | 1.3934 |
| c.28 | -0.1041 | 0.5147 | -1.1949 | 0.9042 |
| c.29 | 0.6331 | 0.4716 | -0.1514 | 1.6094 |
| c.30 | -0.0050 | 0.4548 | -0.9450 | 0.9212 |
| c.4 | 0.1105 | 0.5272 | -0.9368 | 1.2271 |
| c.5 | 0.0716 | 0.5360 | -1.0150 | 1.1953 |
| c.7 | -0.2351 | 0.5454 | -1.4619 | 0.7528 |

Experimental assemble

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|-------------|----------|-----------|---------|--------|
| Assemble 1 | 0.0254 | 0.1830 | -0.3408 | 0.4505 |
| Assemble 3 | 0.0958 | 0.2026 | -0.2155 | 0.6155 |
| Assemble 4 | -0.0565 | 0.2012 | -0.5644 | 0.3007 |
| Assemble 5 | 0.0044 | 0.1885 | -0.3952 | 0.4322 |
| Assemble 6 | -0.0541 | 0.2120 | -0.5934 | 0.3205 |
| Assemble 7 | 0.0078 | 0.1871 | -0.3900 | 0.4286 |
| Assemble 8 | -0.0064 | 0.1868 | -0.4297 | 0.3908 |
| Assemble 9 | 0.0184 | 0.2151 | -0.4122 | 0.5118 |
| Assemble 10 | 0.0057 | 0.1986 | -0.4177 | 0.4440 |
| Assemble 11 | -0.0508 | 0.2187 | -0.5984 | 0.3477 |
| Assemble 14 | -0.0298 | 0.1875 | -0.4615 | 0.3544 |
| Assemble 15 | 0.0359 | 0.2041 | -0.3590 | 0.5273 |
| Assemble 16 | -0.0276 | 0.2029 | -0.5088 | 0.3721 |
| Assemble 17 | -0.0085 | 0.2000 | -0.4527 | 0.4128 |
| Assemble 18 | 0.0165 | 0.1980 | -0.3911 | 0.4740 |
| Assemble 19 | 0.0192 | 0.2139 | -0.4138 | 0.5168 |
| Assemble 20 | 0.0075 | 0.2050 | -0.4274 | 0.4625 |

Sex and reproductive state

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|--------------------|----------|-----------|---------|--------|
| Pregnant female | 0.0357 | 0.5771 | -1.0606 | 1.1694 |
| No pregnant female | -0.1673 | 0.5715 | -1.3428 | 0.8145 |
| Male | 0.1309 | 0.5710 | -0.8891 | 1.2870 |

Table A7. Conditional modes of random effects in the Aggressiveness betweenness centrality model. Random effects at the level of individuals, sex-pregnant interaction and experimental assemblages of individuals were controlled for in the model.

| Individual identity | Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|----------------------------|------------------|-----------------|------------------|-------------|--------------|
| a.1 | | -0.1406 | 0.2141 | -0.5570 | 0.2826 |
| a.11 | | -0.2391 | 0.2525 | -0.7229 | 0.2662 |
| a.12 | | 0.3292 | 0.2437 | -0.1358 | 0.8185 |
| a.13 | | -0.1765 | 0.2511 | -0.6592 | 0.3314 |
| a.15 | | -0.2276 | 0.2544 | -0.7121 | 0.2821 |
| a.17 | | 0.3241 | 0.2060 | -0.0686 | 0.7375 |
| a.18 | | -0.0676 | 0.2528 | -0.5503 | 0.4381 |
| a.19 | | 0.6533 | 0.2099 | 0.2473 | 1.0758 |
| a.21 | | 0.3293 | 0.1972 | -0.0532 | 0.7256 |
| a.23 | | -0.3779 | 0.1937 | -0.7558 | 0.0040 |
| a.27 | | -0.1504 | 0.2021 | -0.5376 | 0.2544 |
| a.29 | | -0.2553 | 0.2430 | -0.7192 | 0.2318 |
| a.3 | | 1.0178 | 0.2392 | 0.5600 | 1.4983 |
| a.4 | | -0.1419 | 0.2057 | -0.5398 | 0.2703 |
| a.5 | | 0.2112 | 0.2032 | -0.1795 | 0.6217 |
| a.6 | | -0.1505 | 0.2649 | -0.6664 | 0.3707 |
| a.7 | | -0.2791 | 0.2191 | -0.7084 | 0.1538 |
| a.8 | | -0.1329 | 0.2180 | -0.5550 | 0.3016 |
| a.9 | | -0.2113 | 0.2099 | -0.6187 | 0.2050 |
| b.1 | | 0.3614 | 0.2085 | -0.0382 | 0.7748 |
| b.10 | | 0.4257 | 0.2277 | -0.0094 | 0.8807 |
| b.11 | | -0.3465 | 0.2545 | -0.8422 | 0.1663 |
| b.12 | | -0.0701 | 0.2530 | -0.5540 | 0.4402 |
| b.13 | | -0.3405 | 0.2144 | -0.7544 | 0.0841 |
| b.14 | | -0.0860 | 0.2607 | -0.5883 | 0.4329 |
| b.15 | | 1.0988 | 0.2219 | 0.6702 | 1.5395 |
| b.16 | | -0.1101 | 0.2051 | -0.5061 | 0.3024 |
| b.17 | | -0.1060 | 0.2505 | -0.5852 | 0.3927 |
| b.19 | | -0.4234 | 0.2704 | -0.9493 | 0.1066 |
| b.2 | | -0.1810 | 0.2627 | -0.6920 | 0.3394 |
| b.20 | | -0.1283 | 0.2543 | -0.6198 | 0.3814 |
| b.21 | | -0.1351 | 0.2602 | -0.6345 | 0.3822 |
| b.23 | | -0.3444 | 0.2868 | -0.9070 | 0.2222 |
| b.24 | | -0.2030 | 0.2478 | -0.6886 | 0.2871 |
| b.26 | | -0.1474 | 0.2542 | -0.6386 | 0.3597 |
| b.27 | | -0.2644 | 0.2004 | -0.6485 | 0.1345 |
| b.28 | | 0.1105 | 0.2034 | -0.2862 | 0.5108 |
| b.29 | | -0.2963 | 0.1987 | -0.6801 | 0.1023 |
| b.3 | | -0.2146 | 0.2105 | -0.6242 | 0.2034 |
| b.30 | | -0.2284 | 0.2516 | -0.7126 | 0.2782 |
| b.5 | | -0.2574 | 0.2189 | -0.6886 | 0.1680 |
| b.7 | | 1.1787 | 0.2103 | 0.7714 | 1.5982 |
| b.8 | | -0.2004 | 0.2623 | -0.7069 | 0.3223 |
| b.9 | | -0.2644 | 0.2058 | -0.6616 | 0.1473 |
| c.1 | | 0.0795 | 0.2638 | -0.4253 | 0.6031 |
| c.14 | | -0.1200 | 0.2588 | -0.6234 | 0.3967 |
| c.15 | | 0.6719 | 0.2184 | 0.2486 | 1.1097 |
| c.16 | | -0.1783 | 0.2080 | -0.5803 | 0.2357 |
| c.18 | | 0.3495 | 0.1978 | -0.0384 | 0.7367 |
| c.19 | | -0.1207 | 0.2026 | -0.5139 | 0.2847 |

| | | | | |
|------|---------|--------|---------|--------|
| c.21 | -0.1530 | 0.2261 | -0.5925 | 0.2938 |
| c.22 | -0.2180 | 0.1889 | -0.5881 | 0.1571 |
| c.23 | 0.1328 | 0.1856 | -0.2262 | 0.4999 |
| c.24 | -0.1477 | 0.2077 | -0.5464 | 0.2682 |
| c.25 | -0.1601 | 0.2041 | -0.5588 | 0.2414 |
| c.27 | 0.4757 | 0.2271 | 0.0298 | 0.9282 |
| c.28 | -0.2346 | 0.2210 | -0.6640 | 0.2022 |
| c.29 | 0.5638 | 0.1644 | 0.2450 | 0.8891 |
| c.30 | -0.1300 | 0.1757 | -0.4687 | 0.2203 |
| c.4 | -0.0479 | 0.2492 | -0.5278 | 0.4469 |
| c.5 | 0.0920 | 0.2784 | -0.4477 | 0.6491 |
| c.7 | -0.0494 | 0.2200 | -0.4824 | 0.3814 |

Experimental assemble

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|-------------|----------|-----------|---------|--------|
| Assemble 1 | -0.0242 | 0.1024 | -0.2378 | 0.1750 |
| Assemble 3 | 0.1314 | 0.1155 | -0.0556 | 0.3850 |
| Assemble 4 | -0.1041 | 0.1270 | -0.3898 | 0.1113 |
| Assemble 5 | -0.2118 | 0.1506 | -0.5397 | 0.0175 |
| Assemble 6 | -0.0365 | 0.1253 | -0.3101 | 0.2012 |
| Assemble 7 | 0.0360 | 0.1098 | -0.1666 | 0.2787 |
| Assemble 8 | 0.0032 | 0.1116 | -0.2253 | 0.2365 |
| Assemble 9 | -0.0054 | 0.1413 | -0.2994 | 0.2883 |
| Assemble 10 | 0.0827 | 0.1280 | -0.1425 | 0.3777 |
| Assemble 11 | 0.0417 | 0.1306 | -0.2049 | 0.3329 |
| Assemble 14 | 0.0231 | 0.1132 | -0.1973 | 0.2664 |
| Assemble 15 | 0.0392 | 0.1240 | -0.2078 | 0.3072 |
| Assemble 16 | 0.0133 | 0.1206 | -0.2279 | 0.2708 |
| Assemble 17 | -0.0184 | 0.1149 | -0.2596 | 0.2120 |
| Assemble 18 | 0.1185 | 0.1271 | -0.0870 | 0.4046 |
| Assemble 19 | -0.0767 | 0.1385 | -0.3935 | 0.1655 |
| Assemble 20 | -0.0202 | 0.1211 | -0.2752 | 0.2204 |

Sex and reproductive state

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|--------------------|----------|-----------|---------|--------|
| Pregnant female | 0.0098 | 0.2604 | -0.4902 | 0.4965 |
| No pregnant female | 0.0162 | 0.2572 | -0.4745 | 0.4930 |
| Male | -0.0350 | 0.2596 | -0.5622 | 0.4094 |

Table A8. Conditional modes of random effects in the average aggression strength betweenness centrality model. Random effects at the level of individuals, sex-pregnant interaction and experimental assemblages of individuals were controlled for in the model.

| Individual identity | | | | |
|----------------------------|------------------|-----------------|------------------|-------------|
| | Intercept | Estimate | Est.Error | 2.5% |
| a.1 | | -0.0602 | 0.1041 | -0.2638 |
| a.11 | | -0.0146 | 0.1172 | -0.2417 |
| a.12 | | 0.0024 | 0.1210 | -0.2350 |
| a.13 | | -0.1208 | 0.1218 | -0.3620 |
| a.15 | | 0.1028 | 0.1181 | -0.1269 |
| a.17 | | 0.0837 | 0.1042 | -0.1196 |
| a.18 | | 0.0060 | 0.1243 | -0.2336 |
| a.19 | | -0.1337 | 0.1047 | -0.3427 |
| a.21 | | 0.1141 | 0.1041 | -0.0846 |
| a.23 | | -0.1207 | 0.0927 | -0.3049 |
| a.27 | | -0.0202 | 0.1006 | -0.2161 |
| a.29 | | -0.0911 | 0.1174 | -0.3232 |
| a.3 | | 0.0887 | 0.1179 | -0.1398 |
| a.4 | | -0.0657 | 0.1116 | -0.2854 |
| a.5 | | 0.0125 | 0.1018 | -0.1860 |
| a.6 | | 0.0870 | 0.1288 | -0.1582 |
| a.7 | | -0.0148 | 0.1053 | -0.2200 |
| a.8 | | 0.0057 | 0.1106 | -0.2102 |
| a.9 | | 0.1158 | 0.0985 | -0.0745 |
| b.1 | | 0.1839 | 0.1016 | -0.0116 |
| b.10 | | -0.1508 | 0.1104 | -0.3719 |
| b.11 | | -0.0025 | 0.1180 | -0.2314 |
| b.12 | | -0.0144 | 0.1212 | -0.2507 |
| b.13 | | 0.0064 | 0.1037 | -0.1992 |
| b.14 | | 0.0051 | 0.1221 | -0.2350 |
| b.15 | | -0.0358 | 0.1068 | -0.2445 |
| b.16 | | 0.1416 | 0.1051 | -0.0603 |
| b.17 | | -0.0709 | 0.1208 | -0.3078 |
| b.19 | | 0.1970 | 0.1243 | -0.0378 |
| b.2 | | 0.0803 | 0.1226 | -0.1583 |
| b.20 | | -0.0615 | 0.1205 | -0.3002 |
| b.21 | | -0.0814 | 0.1226 | -0.3224 |
| b.23 | | -0.0620 | 0.1258 | -0.3122 |
| b.24 | | 0.0365 | 0.1163 | -0.1897 |
| b.26 | | 0.0026 | 0.1220 | -0.2334 |
| b.27 | | -0.0510 | 0.1002 | -0.2462 |
| b.28 | | -0.0598 | 0.1048 | -0.2668 |
| b.29 | | -0.0548 | 0.0961 | -0.2442 |
| b.3 | | 0.0230 | 0.1043 | -0.1790 |
| b.30 | | -0.1458 | 0.1231 | -0.3889 |
| b.5 | | 0.0004 | 0.1081 | -0.2104 |
| b.7 | | -0.1238 | 0.1071 | -0.3347 |
| b.8 | | 0.0290 | 0.1218 | -0.2062 |
| b.9 | | -0.1139 | 0.1031 | -0.3209 |
| c.1 | | 0.0259 | 0.1246 | -0.2170 |
| c.14 | | -0.1350 | 0.1277 | -0.3882 |
| c.15 | | 0.0378 | 0.1090 | -0.1735 |
| c.16 | | -0.0605 | 0.1057 | -0.2665 |
| c.18 | | 0.2616 | 0.1035 | 0.0635 |
| | | | | 0.4700 |

| | | | | |
|------|---------|--------|---------|--------|
| c.19 | 0.0588 | 0.1022 | -0.1347 | 0.2633 |
| c.21 | 0.0741 | 0.1093 | -0.1351 | 0.2934 |
| c.22 | 0.1862 | 0.0992 | -0.0015 | 0.3847 |
| c.23 | -0.0840 | 0.0928 | -0.2649 | 0.1000 |
| c.24 | 0.2387 | 0.1082 | 0.0305 | 0.4556 |
| c.25 | -0.2062 | 0.1072 | -0.4173 | 0.0026 |
| c.27 | -0.0538 | 0.1081 | -0.2650 | 0.1595 |
| c.28 | -0.1186 | 0.1057 | -0.3247 | 0.0885 |
| c.29 | 0.4779 | 0.0926 | 0.2995 | 0.6640 |
| c.30 | -0.1519 | 0.0939 | -0.3368 | 0.0330 |
| c.4 | 0.0120 | 0.1218 | -0.2246 | 0.2550 |
| c.5 | -0.1495 | 0.1342 | -0.4211 | 0.1097 |
| c.7 | -0.0130 | 0.1055 | -0.2206 | 0.1930 |

Experimental assemble

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|-------------|----------|-----------|---------|--------|
| Assemble 1 | 0.0286 | 0.1052 | -0.1811 | 0.2387 |
| Assemble 3 | -0.0097 | 0.1074 | -0.2268 | 0.2019 |
| Assemble 4 | 0.0130 | 0.1147 | -0.2078 | 0.2462 |
| Assemble 5 | -0.0777 | 0.0951 | -0.2717 | 0.1040 |
| Assemble 6 | -0.0852 | 0.1104 | -0.3031 | 0.1310 |
| Assemble 7 | -0.0597 | 0.1067 | -0.2811 | 0.1428 |
| Assemble 8 | -0.1351 | 0.0995 | -0.3376 | 0.0560 |
| Assemble 9 | -0.0478 | 0.1511 | -0.3540 | 0.2446 |
| Assemble 10 | 0.0104 | 0.1299 | -0.2660 | 0.2516 |
| Assemble 11 | -0.1908 | 0.1395 | -0.4902 | 0.0623 |
| Assemble 14 | 0.1206 | 0.1134 | -0.0905 | 0.3571 |
| Assemble 15 | -0.1318 | 0.1437 | -0.4013 | 0.1748 |
| Assemble 16 | 0.3582 | 0.1399 | 0.1145 | 0.6639 |
| Assemble 17 | -0.0869 | 0.1191 | -0.3125 | 0.1602 |
| Assemble 18 | 0.3554 | 0.1090 | 0.1544 | 0.5828 |
| Assemble 19 | -0.1701 | 0.1384 | -0.4530 | 0.0956 |
| Assemble 20 | 0.1632 | 0.1333 | -0.0906 | 0.4376 |

Sex and reproductive state

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|--------------------|----------|-----------|---------|--------|
| Pregnant female | 0.1745 | 0.6825 | -0.4221 | 2.1075 |
| No pregnant female | 0.2370 | 0.6935 | -0.3398 | 2.2188 |
| Male | 0.1630 | 0.6838 | -0.4361 | 2.1089 |

Table A9. Conditional modes of random effects in the dominance status model. Random effects at the level of individuals, sex-pregnant interaction and experimental assemblages of individuals were controlled for in the model.

| Individual identity | | | | |
|----------------------------|------------------|-----------------|------------------|-------------|
| | Intercept | Estimate | Est.Error | 2.5% |
| a.1 | | -0.5924 | 0.6703 | -2.0578 |
| a.10 | | 0.0078 | 0.7149 | -1.4749 |
| a.11 | | 0.5655 | 0.8187 | -0.7791 |
| a.12 | | 0.0048 | 0.7276 | -1.4958 |
| a.13 | | 0.5096 | 0.7429 | -0.7699 |
| a.14 | | 0.0057 | 0.7263 | -1.5057 |
| a.15 | | -0.3633 | 0.6700 | -1.7959 |
| a.16 | | -0.0043 | 0.7231 | -1.4846 |
| a.17 | | -0.4210 | 0.5852 | -1.6785 |
| a.18 | | 0.0476 | 0.5721 | -1.1142 |
| a.19 | | -0.2725 | 0.6286 | -1.5917 |
| a.2 | | -0.0082 | 0.7284 | -1.5077 |
| a.20 | | 0.0004 | 0.7259 | -1.5069 |
| a.21 | | -0.1562 | 0.5418 | -1.2696 |
| a.23 | | -0.1064 | 0.5345 | -1.2397 |
| a.24 | | 0.0055 | 0.7237 | -1.4902 |
| a.25 | | -0.0030 | 0.7288 | -1.5251 |
| a.26 | | -0.0005 | 0.7288 | -1.5184 |
| a.27 | | -0.2551 | 0.5787 | -1.4994 |
| a.28 | | -0.0062 | 0.7247 | -1.4917 |
| a.29 | | -0.1133 | 0.5875 | -1.3319 |
| a.3 | | 0.4416 | 0.6980 | -0.8403 |
| a.30 | | -0.0092 | 0.7305 | -1.5338 |
| a.4 | | -0.1282 | 0.5757 | -1.3439 |
| a.5 | | 0.5575 | 0.6235 | -0.5181 |
| a.6 | | -0.1734 | 0.6037 | -1.4351 |
| a.7 | | -0.0494 | 0.6304 | -1.3690 |
| a.8 | | 0.0288 | 0.5942 | -1.1663 |
| a.9 | | 0.1075 | 0.5399 | -0.9616 |
| b.1 | | 0.2860 | 0.5530 | -0.7857 |
| b.10 | | 0.0020 | 0.7350 | -1.5223 |
| b.11 | | 0.2623 | 0.6054 | -0.9147 |
| b.12 | | -0.1728 | 0.5913 | -1.3827 |
| b.13 | | -0.7283 | 0.7537 | -2.4012 |
| b.14 | | 0.2838 | 0.6257 | -0.9125 |
| b.15 | | 0.6023 | 0.6522 | -0.5097 |
| b.16 | | -0.5376 | 0.6314 | -1.8405 |
| b.17 | | 0.3399 | 0.6453 | -0.9031 |
| b.18 | | 0.0023 | 0.7332 | -1.5254 |
| b.19 | | -0.2473 | 0.6383 | -1.6238 |
| b.2 | | -0.1585 | 0.6197 | -1.4779 |
| b.20 | | 0.3370 | 0.6398 | -0.8705 |
| b.21 | | -0.2493 | 0.6226 | -1.5508 |
| b.22 | | 0.0116 | 0.7344 | -1.5057 |
| b.23 | | 0.0357 | 0.6632 | -1.3264 |
| b.24 | | -0.0618 | 0.5653 | -1.2314 |
| b.25 | | -0.0032 | 0.7340 | -1.5304 |
| b.26 | | -0.2738 | 0.6216 | -1.5691 |
| b.27 | | 0.1644 | 0.5189 | -0.8650 |

| | | | | |
|------|---------|--------|---------|--------|
| b.28 | 0.3965 | 0.6918 | -0.8591 | 1.8794 |
| b.29 | -0.5427 | 0.6206 | -1.8547 | 0.5570 |
| b.3 | -0.3626 | 0.5557 | -1.5255 | 0.6844 |
| b.30 | 0.3361 | 0.6326 | -0.8836 | 1.6450 |
| b.5 | 0.1642 | 0.6633 | -1.0848 | 1.6530 |
| b.6 | -0.0025 | 0.7278 | -1.5204 | 1.4971 |
| b.7 | 0.5223 | 0.6488 | -0.5743 | 2.0141 |
| b.8 | -0.2797 | 0.6333 | -1.6342 | 0.9416 |
| b.9 | 0.1527 | 0.6066 | -1.0222 | 1.4459 |
| c.1 | -0.0128 | 0.6001 | -1.2666 | 1.2011 |
| c.10 | 0.0020 | 0.7253 | -1.4739 | 1.5102 |
| c.11 | 0.0014 | 0.7250 | -1.5023 | 1.5045 |
| c.12 | -0.0043 | 0.7345 | -1.5531 | 1.5086 |
| c.14 | -0.2920 | 0.6251 | -1.5872 | 0.9366 |
| c.15 | -0.2189 | 0.6131 | -1.5003 | 0.9836 |
| c.16 | 0.0394 | 0.6084 | -1.1879 | 1.3057 |
| c.18 | -0.3993 | 0.5868 | -1.6828 | 0.6660 |
| c.19 | -0.2042 | 0.5115 | -1.2572 | 0.8019 |
| c.2 | 0.0037 | 0.7223 | -1.4849 | 1.5278 |
| c.21 | -0.8219 | 0.7777 | -2.4857 | 0.4339 |
| c.22 | -0.1099 | 0.4900 | -1.0971 | 0.8739 |
| c.23 | 0.8367 | 0.6641 | -0.2533 | 2.2112 |
| c.24 | 0.3155 | 0.5387 | -0.7070 | 1.4504 |
| c.25 | -0.2983 | 0.5363 | -1.4119 | 0.7289 |
| c.26 | 0.0041 | 0.7265 | -1.5128 | 1.4964 |
| c.27 | 0.2586 | 0.5499 | -0.7889 | 1.4165 |
| c.28 | -0.0209 | 0.5881 | -1.1958 | 1.1956 |
| c.29 | 0.5716 | 0.5812 | -0.4750 | 1.7645 |
| c.3 | 0.0033 | 0.7395 | -1.5537 | 1.5296 |
| c.30 | 0.2998 | 0.5756 | -0.7504 | 1.5553 |
| c.4 | 0.2486 | 0.5945 | -0.9300 | 1.4870 |
| c.5 | 0.0871 | 0.6199 | -1.1502 | 1.3730 |
| c.6 | -0.0066 | 0.7280 | -1.5447 | 1.5101 |
| c.7 | -0.1706 | 0.5138 | -1.2230 | 0.8516 |
| c.8 | 0.0013 | 0.7170 | -1.4661 | 1.5018 |

Experimental assemble

| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
|-------------|----------|-----------|---------|--------|
| Assemble 1 | -0.0110 | 0.1842 | -0.4271 | 0.3831 |
| Assemble 2 | 0.0004 | 0.2127 | -0.4585 | 0.4621 |
| Assemble 3 | 0.0295 | 0.1851 | -0.3299 | 0.4804 |
| Assemble 4 | -0.0097 | 0.1887 | -0.4312 | 0.3804 |
| Assemble 5 | 0.0165 | 0.1773 | -0.3551 | 0.4244 |
| Assemble 6 | -0.0156 | 0.1872 | -0.4538 | 0.3628 |
| Assemble 7 | -0.0198 | 0.1862 | -0.4520 | 0.3574 |
| Assemble 8 | -0.0050 | 0.1948 | -0.4382 | 0.4137 |
| Assemble 9 | 0.0245 | 0.2074 | -0.3850 | 0.5066 |
| Assemble 10 | 0.0081 | 0.1901 | -0.3972 | 0.4346 |
| Assemble 11 | -0.0258 | 0.2032 | -0.5037 | 0.3661 |
| Assemble 12 | 0.0010 | 0.2124 | -0.4592 | 0.4593 |
| Assemble 13 | 0.0005 | 0.2135 | -0.4694 | 0.4564 |
| Assemble 14 | 0.0166 | 0.1918 | -0.3786 | 0.4624 |
| Assemble 15 | -0.0055 | 0.1963 | -0.4379 | 0.4220 |
| Assemble 16 | -0.0196 | 0.1956 | -0.4727 | 0.3768 |
| Assemble 17 | 0.0119 | 0.1887 | -0.3830 | 0.4443 |
| Assemble 18 | 0.0164 | 0.1872 | -0.3674 | 0.4557 |
| Assemble 19 | 0.0027 | 0.2009 | -0.4269 | 0.4545 |

| Assemble 20 | -0.0081 | 0.1880 | -0.4290 | 0.3951 |
|-----------------------------------|----------|-----------|---------|--------|
| Sex and reproductive state | | | | |
| Intercept | Estimate | Est.Error | 2.5% | 97.5% |
| Pregnant female | -0.0401 | 0.7704 | -1.7022 | 1.6001 |
| No pregnant female | -0.1996 | 0.7637 | -1.8916 | 1.3977 |
| Male | 0.2797 | 0.7820 | -1.2555 | 2.0759 |

CAPÍTULO IV

SOCIAL DYNAMICS REGULATED BY INTERNAL SOCIAL ORGANIZATION TRAITS OR BY INDIVIDUAL PERSONALITIES

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ABSTRACT

In social environments, individuals exhibit behavioral responses and competing preferences, leading to the emergence of dynamic self-organizing processes. Our study aimed to investigate the impact of interindividual relationships between personalities and individual intrinsic attributes on group dynamics at different levels: dyadic, modularity-based, and membership-based. To achieve this, we observed the aggregation behavior of *Porcellio scaber*, a common species of woodlouse, in laboratory conditions. Our findings revealed that the time spent in a social environment, individual personality traits, and group size all had significant effects on how individuals aggregated. Moreover, we found that the reproductive status and sex of individuals were predictors of membership in a particular social aggregate. Our examination of *Porcellio scaber* aggregation revealed that this process is subject to limitations of maximum group size and quorum rules, causing fluctuations over time. Furthermore, we identified that aggregation is governed by local individual preference, as individuals followed cues such as habitat suitability and the presence of conspecifics in the vicinity. Overall, our study highlights the importance of interindividual relationships and intrinsic attributes in shaping social aggregation dynamics and sheds light on the mechanisms underlying the emergence of self-organizing processes in social environments.

key words

Social system, social structure, social dynamic, *Porcellio scaber*, self-organization.

INTRODUCTION

The aggregation has been one of the most studied topics in ecology (Krause & Ruxton, 2002; Parrish & Edelstein-Keshet, 1999). There are multiple factors that can lead to the aggregation and formation of groups of individuals, and some of these factors are based on restrictions, while others are based on benefits. First, based on restrictions, the aggregation and group formation may result from environmental heterogeneity, where the resource distributions are concentrated in patches, and individuals are forced to interact to access resources (Camazine *et al.*, 2001). Second, based on benefits, aggregation may result from increased per capita survival. In this case, aggregation facilitates predator detection, decreases the per capita predation risk (dilution effect), increases resource detection, etc. (Foster & Treherne, 1981; Krause & Ruxton, 2002). Finally, aggregation can occur when not necessarily related conspecifics are directly attracted, causing behavioral responses that benefit the group and promote the simplest expression of sociality (Camazine *et al.*, 2001; Jeanson & Deneubourg, 2007; Theraulaz *et al.*, 2003). Independent of the mechanism forcing the aggregation, group composition may vary associated with proximate cues used by newcomers to guide their choices, and therefore, a nonrandom organization in the group formation (Jeanson & Deneubourg, 2007). The synergistic responses, the competition, and the quality of interactions between lead to complex and non-intuitive behaviors that promote the establishment of self-organized patterns and their spatial-temporal dynamics (Camazine *et al.*, 2001; Conradt & Roper, 2005; Danchin *et al.*, 2004; Deneubourg & Goss, 1989; Devigne *et al.*, 2004; Sumpter, 2006). In contrast, the agglomeration, resource constraints, or agonistic behaviors at high density can act as negative feedback loops restricting group size (Amé *et al.*, 2006; Courchamp *et al.*, 2008).

In invertebrates, aggregation behaviors are an effective response to environmental pressures by reducing the risk of predation (Hamilton, 1971; Johannesen *et al.*, 2014; Stankowich, 2003; Svádová *et al.*, 2014), buffering water loss (Broly *et al.*, 2013, 2014; Dambach & Goehlen, 1999), and body temperature regulation (Heinrich, 1993; Jones & Oldroyd, 2006). Aggregation also promotes social and spatial structuring, which social position have benefits by improving access to mates and reproductive resources (Beauché & Richard, 2013; Lubin *et al.*, 2001; Morrell & Romey, 2008; Wilson, 1974). Aggregation in terrestrial isopods (Crustacea: Isopoda: Oniscidea) is a particularly recurrent, rapid, and stable process that results from a trade-off between individual preferences and inter-attraction between individuals (Allee, 1926; Devigne *et al.*, 2011). Aggregation in Oniscidea is particularly interesting because it is a prerequisite for the development of other forms of cooperation and could be a social step in evolution (Thiel, 2011). This taxon includes species of primary soil macro decomposers that present a social system that allows them to adapt to terrestrial life (Broly *et al.*, 2013; Thiel, 2011; Warburg, 1965; Zimmer & Zimmer, 2002). Some of the main benefits of gregariousness in terrestrial isopods include reducing water loss (Broly *et al.*, 2013; Drahokoupilová & Tuf, 2012), decreasing oxygen consumption (Allee, 1926; Takeda, 1984), increasing body size (Takeda, 1984), increasing reproductive opportunity (Beauché & Richard, 2013; Lefebvre & Caubet, 2010), and maintenance of intestinal bacterial flora and coprophagy (Hassall *et al.*, 2005; Kautz *et al.*, 2002).

On the other hand, personality and interaction networks play a crucial role in modulating collective decision making and subsequent group behavior (Amé *et al.*, 2006; Croft *et al.*, 2005; Fewell, 2003). Personality is the consistency of behavioral traits at the individual level over different contexts or times (Dall *et al.*, 2004). It is expected that individuals in the same

group tend to perform similar behaviors by convergence (Krause & Ruxton, 2002), and all of this occurs within limits established by the personality (Aplin *et al.*, 2014; Planas & Deneubourg, 2018). One of the most studied convergence mechanisms that can affect how an individual expresses his personality in a group is social facilitation (Amé *et al.*, 2004; Michelena & Deneubourg, 2011; Webster & Ward, 2011) This process occurs when the presence of group mates causes an individual to change their behavioral patterns by changing the frequency of the expression of behaviors or performing behaviors that would not usually perform alone (Zajonc, 1965). Studies in woodlice have demonstrated the existence of personality, and that inter-individual behavioral variation will be crucial in the emergence of group-level behaviors (Drinkwater, 2020; Tuf *et al.*, 2015). Individuals' predisposition to express states of calm and excitation may directly influence on collective behaviors under the aggregation stage (Broly *et al.*, 2014; Broly & Deneubourg, 2015).

Because the individual response to environmental and social stimuli is unique, estimating the norm of behavior is essential to predict social skills (Deneubourg & Goss, 1989; Detrain & Deneubourg, 2006; Sumpster, 2006). Although there is a growing literature on animal personality and the social effects of grouping, little research has related the effect of interindividual variability in behavior and social organization, including aspects of life history, on the dynamics of complex interindividual interactions and their emergent patterns (Firth *et al.*, 2018; Ilany & Akçay, 2016; Jolles *et al.*, 2017; Van Oers *et al.*, 2005). Therefore, it is necessary to investigate jointly the mechanisms involved in each level of interaction that define the aggregation process and the subsequent emergence of complex collective patterns.

In this context, we investigated the effect of animal personality and the dynamics of group attributes, including relationship identity and group size, on grouping patterns in the common

rough woodlouse *Porcellio scaber* Latreille, 1804. Without any change in the environment or replacement of individuals, we aimed to identify the behavioral and cultural mechanisms that are behind processes driving grouping dynamics, such as group stability, modularity including dense-dependent aspect, and preferences that define the membership of individuals in groups. Previous studies have shown that the individual preferences of group members strongly govern aggregate location, but that aggregation dynamics and collective decision-making are controlled by interindividual social interaction and their ability to express triggering behaviors (Broly *et al.*, 2012; Devigne *et al.*, 2011). Additionally, group cohesion in terrestrial isopods is governed by behaviors amplified by social facilitation that depend on the density of individuals and the time spent in the group (Broly & Deneubourg, 2015). In this regard, we consider the spatiotemporal evolution of the groupings and the effects of cultural aspects and reproductive states of the individuals under evaluation. Social aggregation can be described in terms of three components that help better understanding the process. The first is a social organization that describes group size, sexual composition and spatiotemporal cohesion; the second is a mating system that includes cultural and reproductive aspects; and the third is a social structure that describes emerging social interaction patterns (Kappeler & Van Schaik, 2002).

To conduct the research, we defined the personality, and we first assessed the repeatability of their performance in an asocial context and then the repeatability of sociability attributes and aggression-based dominance in a social context. We then placed individuals in a common arena, and recorded grouping dynamics. Through social network theory approximation and generalized modeling, we assessed the effect of personality, attributes of social organization

on dyadic association intensity, group modularity, and the relationships that define membership in an aggregate.

MATERIALS AND METHODS

Collect and housing conditions

We collected ninety common rough woodlice (*P. scaber* Latreille, 1804) in teen localities in Valdivia city, Chile. The individuals were maintained by localities in plastic containers provided with organic matter in different states of decomposition (barks, roots, and leaves) and wet soil. We maintained the substrate constantly kept humid to avoid the desiccation of the individuals. The individuals were acclimatized for ten days under controlled conditions (temperature: $16 \pm 3^\circ\text{C}$ and humidity: $80 \pm 10\% \text{ RH}$). Everyone was sexed and marked with a unique identification code using a white non-toxic acrylic marker and isolated in a 95 mm diameter Petri dish with wet plaster as substrate and provided with decomposing organic matter. All individuals remained isolated for 24 h before the personality test.

Individual performance

We performed the estimation of individual behavioral traits under isolation. The performance test consisted of five-minutes video recording in a 94 mm Petri dish with a novel homogeneous substrate (sterilized paper filter) inside a dark chamber. From each recording, we quantified three types of behaviors. First, the exploratory behaviors including linear distance traveled, the average speed of travel, the average direction of travel based on the sexagesimal system, and the standard deviation of the direction. Second neophobia behaviors: involves the number of stops and the immobility time. Third, the audacity behaviors defined as the number of escape attempts from the arena and the mean time between escape attempts (modified from Anselme, 2015, 2018). To extract the information

on the behaviors from the video recordings, we used the free software BORIS (Friard & Gamba, 2016) and the R packages "pathtrackR" (Harmer & Thomas, 2019).

Social performance

To evaluate and describe social attributes, we established three groups of 30 individuals each, controlled by the identity of individuals, locality of origin, sex, and female pregnancy status. Each group was divided into two subgroups of 15 individuals and placed in a 40 cm diameter circular arena containing black painted plaster as substrate and flexible PVC walls for three days. Each day we record 5-minute video recordings every two hours, from 00:00 to 04:00 hours in the absence of light, amounting three video samples per assemblage (modified from Drahokoupilová & Tuf, 2012). We analyzed the data considering the day as time unit. These All records were realized using EZVIZ network video recorder (model EZWIRELESS X5C), and EZVIZ cameras (model C3W). From each recording, we constructed dyadic association matrices based on the time individuals spent together in each observation using a simple ratio index and dyadic aggression matrices based on the number of recorded aggressions (Whitehead, 2008). We consider an association when individuals are no more than one body length apart (approximately 10 mm) or when they are part of an aggregate and aggression when an individual performs a violent action causing an impact on another.

From the association matrices, we approximate the sociability attributes of individuals based on five network centrality metrics: degree centrality, closeness centrality, betweenness centrality, eigenvalue centrality, and average association strength (modified from Croft *et al.*, 2008). In addition, we calculated the dominance status of the individuals using David's score from the aggression matrices using the R package "EloRating" (Neumann *et al.*, 2011). To

build the network and obtain the metrics, we will use the R packages called "sna" (Butts, 2015) and "igraph" (Csardi & Nepusz, 2005).

Definition of Personality

To define personality, we first performed a Kendall correlation analysis between the asocial and social behaviors described above. We found significant correlations between behaviors defining individuals' exploration and neophobia (positive correlation between distance, speed, and negative correlation with immobility time), behaviors describing audacity (negative correlation between escape attempts and periods between escape attempts), and sociability attributes based on centrality measures (positive correlation between degree, betweenness, and eigenvalue centrality). We also observed a marginal positive correlation between exploratory ability and audacity behaviors, and a marginal negative correlation between neophobia and audacity (for more detail, see Table S1). We found no correlation between dominance status with any other behavioral attribute. Complementary, we performed a repeatability analysis, controlling sex and pregnancy in females, to evaluate the consistency of all behavioral attributes (Table S2). Repeatability can be defined as the proportion of the total variance explained by differences among groups through a number of measurements (Sokal & Rohlf, 1995). We quantified the repeatability of behavioral attributes using the R software (R Development Core Team, 2012) and the package "rptR" (Nakagawa & Schielzeth, 2010). Finally, given that all behavioral attributes showed repeatability, we averaged the values per individual. We considered the level of correlation to reduce the number of behaviors by eliminating those strongly correlated with some other behavior in the same category. The behavioral attributes we used to define personality were distance, number of stops, immobility, escape attempts, average direction, and direction standard

deviation. David's score dominance status, degree, closeness, betweenness, eigenvalue centrality, and average association strength were used to describe the sociability attributes that define personality.

Personality on group dynamics

We assessed the effect of personality and social organization on group dynamics. We reassembled the three groups of 30 individuals from the pre-established subgroups in the social performance test described above and placed each in a single arena with the same conditions as in the previous step (40 cm diameter with wet plaster as substrate). We recorded all inter-individual associations with a 5-min interval every two h, from 00:00 h to 04:00 h, for six consecutive days for groups 1 and 2, and five days for group 3 (modified from Drahokoupilová & Tuf, 2012). Each assessment day consists of three observations and considers information about the social organization such as total group size, the identity of aggregates of individuals, the spatial location of aggregates in the assessment arena (four quadrants of 90° sexagesimal degrees each), and the number of individuals in each aggregate. It should be noted that the identity of individuals was controlled throughout the evaluation process. All recordings were made with the EZVIZ network video recorder (model EZWIRELESS X5C) and EZVIZ cameras (model C3W). We calculated the dyad association index using a simple proportion index to construct the association matrices (Whitehead, 2008).

The analysis of group dynamics was carried out in three stages: the first at the dyad level, the second at the aggregation level, and the third at the aggregate identity level (considering the identity of the sub-aggregates and their members). The group dynamics considered the temporal sequence in which the observations were made at each level of analysis in

conjunction with the size of the aggregates. First, we evaluated the effect of dyad personality dissimilarity and social organization attributes on the association weights of dyads by groups. Because we evaluate the dynamics of interindividual associations by group we perform Generalized Additive Mixed Models (GAMM) that consider temporal sequence and social organization attributes as smooth terms. GAMMs have the advantage over GAMs in that the more complex stochastic structure allows the treatment of autocorrelation and repeated measures situations by combining linear mixed-effects and generalized additive models (Hastie, 1992; Wood, 2006). A square root transformation was performed on the response variable and the quasi-binomial family (logit link function) was fitted. Prior to selecting the best-fit model, we evaluated a series of grouping variables as random factors and incorporated only those that influenced the response variable to avoid saturating the model. Assessment group identity (*Likelihood*-ratio = 0.002, $p = 0.97$), dyadic dissimilarity in sex, locality of origin, and subgroup on the social performance test (*L*-ratio = 0.001, $p = 1$), and dyadic relationship identity at sex and pregnancy level (*L*-ratio = 3.163, $p = 0.21$) had no significant effect; while dyad identity (*L*-ratio = 70.487, $p = <.0001$) was significant, and therefore included to the model.

Second, regarding the level of aggregates of individuals, we use modularity index-based network theory to approximate a measure of aggregate quantification. Modularity is the level of division of a network into clusters, where values close to 0 represent a single cohesive aggregate, and as the value increases positively, it indicates a greater number of aggregates with few individuals (Newman, 2006; Newman & Girvan, 2004). In this sense, we performed GAMMs where the response variable was given by the modularity values, and the temporal sequence and group size as smooth terms. Quasi-binomial family (logit link function) was

fitted to models. Complementarily, we controlled for the effect of the identity of the evaluation groups as a random factor, but since did not effect on the response variable, we decided to exclude it from the model (L -ratio = 0.000001, p = 0.9998).

Third, we evaluated the effect of personality and social organization attributes at the aggregate identity level. We use a community structure detector based on network theory that allows us to identify individuals who have membership in each cluster (Newman & Girvan, 2004). The detection algorithm is incorporated in the R package "igraph" (Csardi & Nepusz, 2005). From these values we calculate the dissimilarity in cluster identity for the dyads in each group, where 0 indicates that the dyad has membership in the same cluster and 1 indicates dissimilarity in cluster membership. We then performed a GAMM with binomial family distribution with dissimilarity in cluster membership as a response variable, and dissimilarity in personality as a fixed variable. Temporal sequence, aggregate size, and spatial location of the aggregate in the arena were incorporated as smooth terms. The model was controlled for dyadic identity, evaluation group identity and dyadic relationship identity at sex, and pregnancy as random variables. AIC (Akaike information criterion), BIC (Bayesian information criterion), and the coefficient of determination (adjusted r^2) were calculated to select the best-fitting models for each of the evaluation scales. (Table S2).

We calculated the dyadic dissimilarity through Mean Euclidean distances with R software, using the base function "stats" (R Development Core Team, 2012). To build the network and obtain the metrics, we will use the R packages called "sna" (Butts, 2015) and "igraph" (Csardi & Nepusz, 2005). The models were performed with the R package "mgcv" (Bürkner, 2017) and compared with the R package "nlme" (Pinheiro *et al.*, 2022). We used a product interaction tensor (te) to evaluate the interaction between time series and group or aggregate

size because it produces a full product smooth tensor (Wood, 2006). AIC and BIC information criteria using the base R package "stats", and coefficient of determination using the R package "MuMIn" (Barton, 2022). Details of the selected models can be found in Supplementary Material 1.

RESULTS

In the analysis of the effect of personality and social organization on group dynamics at the level of the dyadic association, we found that dissimilarity in the number of escape attempts has a positive effect on group dynamics of the dyadic association (Estimate = 0.02 ± 0.01 , $t = 3.00$, $p = 0.003$; Figure 1-A). When we compare the residuals of the dyadic association model as a function of dyadic dissimilarity in the number of escapes, we can observe that the associations between individuals with greater dissimilarity in their behaviors are more predictable and present less variability than those between individuals who are more behaviorally similar (Figure 1-B). In addition, we found that both the spatial location of the individuals' aggregates ($edf = 1.39$, $F = 2.83$, $p = 0.011$), and the number of individuals in the aggregates as a function of time per evaluation group (Group 1: $edf = 16.71$, $F = 17.85$, $p < 0.001$; Group 2: $edf = 21.27$, $F = 28.46$, $p < 0.001$; Group 3: $edf = 19.32$, $F = 24.38$, $p < 0.001$) have significant effects on the dyadic association index (Figure 2). The quadrant with the most stable aggregates of individuals with the most stable associations was quadrant 2, corresponding to the southeast area of the evaluation arena ($X = 0.709$, CI 95% [0.691 – 0.728]), followed by quadrant 1 located in the northeast of the arena ($X = 0.667$, CI 95% [0.641 – 0.693]) and finally the quadrants 3 ($X = 0.652$, CI 95% [0.639 – 0.665]) and 4 ($X = 0.651$, CI 95% [0.630 – 0.672]) at the western zone (Figure S2). For more details of models, see Table 1 – A.

When we evaluate the effect of social organization characteristics on modularity in groups, we find that time, group size in each of the observations, and the interaction of these have a significant positive effect (Table 1 – B). As days passed, individuals decreased due to confrontations and stressful events with fatal outcomes. Modularity decreased as the days of evaluation elapsed (Figure 3 – A). In addition, modularity values when groups had less than twenty-five individuals had an upper limit of 0.25, while modularity in groups with more individuals had an upper limit of approximately 0.50 with a 95% confidence interval. (Figure 3 – B). Group size had a negative relationship with time. The highest values of modularity were observed during the first days of the experiment, corresponding to observations when the groups presented the highest number of individuals (Figure 3 – C).

Concerning to the evaluation of dyadic dissimilarity in cluster membership, we found no effect of personality dissimilarity on membership. On the other hand, we found that nesting by the interaction between sex and pregnancy status has a significant effect on membership dissimilarity (Likelihood-ratio: $LR_{22,21} = 302.56$, $p < 0.001$). We recorded 5227 associations between individuals showing membership similarity and 966 between individuals belonging to different clusters (84.40% and 15.60% of the total reported associations, respectively). Within clusters, we found that about half of the associations were between males and non-pregnant females (48.61%), followed by associations between non-pregnant females (25.35%) and males (22.08%). We find associations of pregnant females with males (1.11%), with non-pregnant females (2.74%) and with other pregnant females (0.11%) within clusters (Figure 4 – A). Moreover, we observed that the size of Aggregates over time affects membership dissimilarity ($edf = 23.29$, $F = 19.65$, $p < 0.001$). Aggregates with more individuals are more likely to contain dyads with the same membership, and aggregates with

fewer individuals are more likely to contain dyads with different memberships. Small aggregations observed outside aggregate were not stable. Regardless of the dyad type concerning membership, time causes aggregates to contain more individuals (Figure 4 – B). Finally, we also found an effect of the spatial location of the aggregates in the experimental arena by quadrant ($edf = 1.92$, $F = 28.26$, $p < 0.001$). We evidenced that most of the associations registered between individuals belonging to the same cluster were established in the third quadrant of the arena (49.91%), followed by the second (22.90 %), fourth (17.60 %) and the first quadrant (9.59%). The location with the highest number of associations in total was in the third quadrant (48.68%) and the lowest number in the first quadrant (8.09%) (Figure 4 – C). For more details on the cluster membership dissimilarity model, see Table 1 - C.

DISCUSSION

In this study we explore how personality and social organization can influence the spatiotemporal dynamics of aggregations and the level of cohesion of groups. In woodlice, aggregation dynamics and collective decision-making are determined by social interactions and the behavioral nature of individuals, while the location of groups is driven by individual preferences (Devigne *et al.*, 2011). To carry out this proposal, we use three approaches based on network theory: dyadic association index, modularity, and membership. The analyses were relational at the individual level regarding the first and third attributes, while we used a general analysis by evaluation group for the second approach.

When we evaluated the dyadic association index, we found that personality (determined by the number of escape attempts) had a significant effect. Individuals with more different personalities tended to be associated longer and had less variability in their association

values, whereas individuals with more similar personalities had a high range of variability. These interindividual patterns in the intensity of association were consistent in each pair of individuals during the evaluation process. In this sense, we suggest that aggregation processes in *P. scaber* arise from the affinity and tolerance that exists between personality types, as well as the socially facilitating environment that this association confers (Webster & Ward, 2011; Zajonc, 1965); and not solely from amplification processes based on positive feedback loops between expressions of generalized behaviors as proposed in models of aggregation in invertebrates (Camazine *et al.*, 2001; Jeanson *et al.*, 2012; Sumpter, 2006).

We also observed that the interaction between aggregate size and time influences the dyadic association index, with larger aggregates showing a greater intensity of association between members that fluctuates in an oscillating manner as days pass, with moments of maximum association approximately every two days. Own results are congruent with the previous works, suggesting that aggregation in woodlice depends on the number of individuals and the time individuals spend in the group (Broly & Deneubourg, 2015). It is known that the group size implies more time individuals spend interacting, more potential interactions, and the greater the probability that aggregates will be consistently established (Hutchinson & Waser, 2007; Nicolis *et al.*, 2005). The temporal oscillation in dyadic association index values is probably due to circadian rhythms of activity, where the joint influence of environmental factors (light incidence mediated by photoperiod) and individual conditions (such as physiology and feeding behaviors) could lead to alterations in association amplification processes (Broly & Deneubourg, 2015; Donlea & Shaw, 2009; Eban-Rothschild & Bloch, 2012; Refinetti, 2000).

Concerning the spatial location of the aggregates of individuals, we found an asymmetric spatial distribution to the intensity of dyadic associations even though the environment was homogeneous. One possible explanation may be due to coprophagric feeding behaviors since it is common to observe accumulations of feces in spaces where groups were housed (Hassall & Rushton, 1982). Another pathway of grouping may be mediated through the amplification of chemical signals and pheromones (Takeda, 1984; Thiel, 2010). As a product of aggregation, the conditioning of space modifies the environment creating heterogeneities in the distribution of resources and strongly influencing the spatial establishment of groups (Broly *et al.*, 2016).

Social interactions, maximum environmental carrying capacity, and maximum aggregate size can act as covariate factors and could be important for understanding local aggregation patterns in woodlice. We developed an experimental design with high and constant recourses and space during the evaluation process with no replacement of individuals. This design allowed us to observe the outcome of the cooperation and competition processes limited by the carrying capacity of the evaluation arena. In this regard, when evaluating modularity through aggregation dynamics, we observed highest modularity values were recorded at the beginning of group formation and when the groups were still above 80% of the initial size (approximately 25 individuals). Subsequently, when the groups had less than 80% of the initial size due to clashes between individuals, the modularity values were lower than those recorded above 80% and with a constant trend. A high modularity value indicates that individuals tend to have more stable associations within the main aggregates, while associations with individuals from other aggregates in the periphery are weak. In our case, we noted that modularity did not vary when aggregates contained less than 80% of the initial

size, which means that most individuals tended to be mainly part of a single aggregate. Previous experiments in *P. scaber* also found that about 80% of individuals tend to aggregate consistently around a resource at low densities, referring to maximum group size (Broly *et al.*, 2012, 2016). Since we find that time, group size and their combined effects influence modularity, suggesting that group structuring in *P. scaber* depends on positive feedback mediated by amplification and reinforcement, which in turn induce negative feedback involving the physical constraints of the environment and competitive social interactions that define the maximum size of aggregates (Broly *et al.*, 2014, 2016; Jeanson *et al.*, 2012; Jeanson & Deneubourg, 2009).

On the other hand, when we evaluated which mechanisms influence association processes at the group membership level, we found that intrinsic aspects linked to reproductive behaviors, spatiotemporal dynamics, and aggregate size limit the access of individuals to aggregates. Predominant dyadic relationships within aggregates are between males and non-pregnant females. In contrast, pregnant females were rarely associated with other individuals, so they were rarely consistently found as part of an aggregate. Males, followed by non-pregnant females, actively established the most associations regardless of whether they occurred inside or outside the aggregates. Both groups spend approximately one-sixth of their inter-individual associations interacting with individuals who are not part of the aggregate of which they are a member. It is known that aggregation in Oniscidea has several reproductive benefits, such as: reducing the time spent on finding breeding partners and increasing mating opportunities mediated by chemical compounds (Henf *et al.*, 2008), as well as allowing an acceleration of vitellogenesis and synchronization of molting cycles of females in the presence of males (Caubet *et al.*, 1998; Lefebvre & Caubet, 1999, 2010). One of the precursor

aggregation mechanisms in terrestrial isopods is the response to pheromones emitted by conspecifics (Kuenen & Nooteboom, 2011). In *Armadillidium vulgare*, this olfactory response is more intense between individuals of different sexes and can discriminate females' physiological and reproductive states over short distances (Beauché & Richard, 2013).

Although terrestrial isopods do not exhibit pre-copulatory guarding behaviors, as occurs in aquatic species, it is known that there is scramble competition between males for priority access to receptive females (Henf *et al.*, 2008; Jormalainen, 2007; Lefebvre *et al.*, 2000). The first males mates with females have a higher probability of reproductive success because of the females' ability to store sperm and since mating induces an intermediate refractory period during which females reject mating attempts (Moreau *et al.*, 2002; Suzuki & Ziegler, 2005).

In conclusion, we showed that aggregation in *P. scaber* is generally a process limited by maximum group size and quorum rules that fluctuates over time, governed by the local preference of the individuals in the group and reproductive traits. Furthermore, we observed that the intensity of associations between pairs of individuals is consistent and depends on their personalities. On the other hand, we show that the most stable aggregates tend to be large groups (50-70 % of individuals) that are systematically composed of males and non-pregnant females due to aspects linked to the life history traits of the taxon.

REFERENCES

- Allee, W. C. (1926). Studies in animal aggregations: Causes and effects of bunching in land isopods. *Journal of Experimental Zoology*, 45(1), 255–277.
<https://doi.org/10.1002/jez.1400450108>

Amé, J.-M., Halloy, J., Rivault, C., Detrain, C., & Deneubourg, J. L. (2006). Collegial decision making based on social amplification leads to optimal group formation. *Proceedings of the National Academy of Sciences*, 103(15), 5835–5840.
<https://doi.org/10.1073/pnas.0507877103>

Amé, J.-M., Rivault, C., & Deneubourg, J.-L. (2004). Cockroach aggregation based on strain odour recognition. *Animal Behaviour*, 68(4), 793–801.
<https://doi.org/10.1016/j.anbehav.2004.01.009>

Aplin, L. M., Farine, D. R., Mann, R. P., & Sheldon, B. C. (2014). Individual-level personality influences social foraging and collective behaviour in wild birds. *Proceedings of the Royal Society B: Biological Sciences*, 281(1789), 20141016–20141016. <https://doi.org/10.1098/rspb.2014.1016>

Barton, K. (2022). MuMIn: Multi-model inference. R package 1.46.0 (1.46.0). <https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf>

Beauché, F., & Richard, F.-J. (2013). The Best Timing of Mate Search in *Armadillidium vulgare* (Isopoda, Oniscidea). *PLOS ONE*, 8(3), e57737.
<https://doi.org/10.1371/journal.pone.0057737>

Broly, P., & Deneubourg, J. L. (2015). Behavioural Contagion Explains Group Cohesion in a Social Crustacean. *PLoS Computational Biology*, 11(6), 1–18.
<https://doi.org/10.1371/journal.pcbi.1004290>

Broly, P., Deneubourg, J. L., & Devigne, C. (2013). Benefits of aggregation in woodlice: A factor in the terrestrialization process? *Insectes Sociaux*, 60(4), 419–435.
<https://doi.org/10.1007/s00040-013-0313-7>

Broly, P., Devigne, L., Deneubourg, J.-L., & Devigne, C. (2014). Effects of group size on aggregation against desiccation in woodlice (Isopoda: Oniscidea). *Physiological Entomology*, 39(2), 165–171. <https://doi.org/10.1111/phen.12060>

Broly, P., Mullier, R., Deneubourg, J. L., & Devigne, C. (2012). Aggregation in woodlice: Social interaction and density effects. *ZooKeys*, 176(SPECIAL ISSUE), 133–144.
<https://doi.org/10.3897/zookeys.176.2258>

Broly, P., Mullier, R., Devigne, C., & Deneubourg, J.-L. (2016). Evidence of self-organization in a gregarious land-dwelling crustacean (Isopoda: Oniscidea). *Animal Cognition*, 19(1), 181–192. <https://doi.org/10.1007/s10071-015-0925-6>

Bürkner, P. C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, 80(1), 1–28. <https://doi.org/10.18637/jss.v080.i01>

Butts, C. T. (2015). Social Network Analysis with sna. *Journal of Statistical Software*, 24(6).
<https://doi.org/10.18637/jss.v024.i06>

Camazine, S., Deneubourg, J.-L., Franks, N. R., Sneyd, J., Theraula, G., & Bonabeau, E. (2001). Self-Organization in Biological Systems. Princeton University Press.
<https://doi.org/10.1515/9780691212920>

Caubet, Y., Juchault, P., & Mocquard, J.-P. (1998). Biotic triggers of female reproduction in the terrestrial isopod *Armadillidium vulgare* Latr. (Crustacea Oniscidea). *Ethology*

Ecology & Evolution, 10(3), 209–226.
<https://doi.org/10.1080/08927014.1998.9522853>

Conradt, L., & Roper, T. J. (2005). Consensus decision making in animals. *Trends in Ecology and Evolution*, 20(8), 449–456. <https://doi.org/10.1016/j.tree.2005.05.008>

Courchamp, F., Berec, L., & Gascoigne, J. (2008). *Allee Effects in Ecology and Conservation*. Oxford University Press.
<https://doi.org/10.1093/acprof:oso/9780198570301.001.0001>

Croft, D. P., James, R., & Krause, J. (2008). Exploring animal social networks. Princeton University Press. <https://www.jstor.org/stable/j.ctt7sfqv>

Croft, D. P., James, R., Ward, A. J. W., Botham, M. S., Mawdsley, D., & Krause, J. (2005). Assortative Interactions and Social Networks in Fish. *Oecologia*, 143(2), 211–219.

Csardi, G., & Nepusz, T. (2005). The Igraph Software Package for Complex Network Research. *InterJournal, Complex Systems*, 1695.

Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters*, 7(8), 734–739. <https://doi.org/10.1111/j.1461-0248.2004.00618.x>

Dambach, M., & Goehlen, B. (1999). Aggregation density and longevity correlate with humidity in first-instar nymphs of the cockroach (*Blattella germanica* L., Dictyoptera). *Journal of Insect Physiology*, 45(5), 423–429.
[https://doi.org/10.1016/s0022-1910\(98\)00141-3](https://doi.org/10.1016/s0022-1910(98)00141-3)

Danchin, E., Giraldeau, L.-A., Valone, T. J., & Wagner, R. H. (2004). Public information: From nosy neighbors to cultural evolution. *Science* (New York, N.Y.), 305(5683), 487–491. <https://doi.org/10.1126/science.1098254>

Deneubourg, J. L., & Goss, S. (1989). Collective patterns and decision-making. *Ethology Ecology & Evolution*, 1(4), 295–311. <https://doi.org/10.1080/08927014.1989.9525500>

Detrain, C., & Deneubourg, J.-L. (2006). Self-organized structures in a superorganism: Do ants “behave” like molecules? *Physics of Life Reviews*, 3(3), 162–187. <https://doi.org/10.1016/j.plrev.2006.07.001>

Devigne, C., Broly, P., & Deneubourg, J. L. (2011). Individual preferences and social interactions determine the aggregation of woodlice. *PLoS ONE*, 6(2), e17389. <https://doi.org/10.1371/journal.pone.0017389>

Devigne, C., Renon, A. J., & Detrain, C. (2004). Out of sight but not out of mind: Modulation of recruitment according to home range marking in ants. *Animal Behaviour*, 67(6), 1023–1029. <https://doi.org/10.1016/j.anbehav.2003.09.012>

Donlea, J. M., & Shaw, P. J. (2009). Sleeping together using social interactions to understand the role of sleep in plasticity. *Advances in Genetics*, 68, 57–81. [https://doi.org/10.1016/S0065-2660\(09\)68003-2](https://doi.org/10.1016/S0065-2660(09)68003-2)

Drahokoupilová, T., & Tuf, I. H. (2012). The effect of external marking on the behaviour of the common pill woodlouse *Armadillidium vulgare*. *ZooKeys*, 176(SPECIAL ISSUE), 145–154. <https://doi.org/10.3897/zookeys.176.2375>

Drinkwater, E. (2020). How does inter-individual variation affect group level behaviour? [PhD, University of York]. <https://etheses.whiterose.ac.uk/29012/>

Eban-Rothschild, A., & Bloch, G. (2012). Social influences on circadian rhythms and sleep in insects. *Advances in Genetics*, 77, 1–32. <https://doi.org/10.1016/B978-0-12-387687-4.00001-5>

Fewell, J. H. (2003). Social Insect Networks. *Science*, 301(5641), 1867–1870. <https://doi.org/10.1126/science.1088945>

Firth, J. A., Cole, E. F., Ioannou, C. C., Quinn, J. L., Aplin, L. M., Culina, A., McMahon, K., & Sheldon, B. C. (2018). Personality shapes pair bonding in a wild bird social system. *Nature Ecology and Evolution*, 2(11), 1696–1699. <https://doi.org/10.1038/s41559-018-0670-8>

Foster, W. A., & Treherne, J. E. (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature*, 293(5832), 466–467. <https://doi.org/10.1038/293466a0>

Friard, O., & Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, 7(11), 1325–1330. <https://doi.org/10.1111/2041-210X.12584>

Hadrián Tuf, I., Drábková, L., & Šipoš, J. (2015). Personality affects defensive behaviour of *Porcellio scaber* (Isopoda, Oniscidea). *ZooKeys*, 2015(515), 159–171. <https://doi.org/10.3897/zookeys.515.9429>

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, 31(2), 295–311. [https://doi.org/10.1016/0022-5193\(71\)90189-5](https://doi.org/10.1016/0022-5193(71)90189-5)

Harmer, A. M. T., & Thomas, D. B. (2019). pathtrackr: An r package for video tracking and analysing animal movement. *Methods in Ecology and Evolution*, 2041-210X.13200. <https://doi.org/10.1111/2041-210X.13200>

Hassall, M., & Rushton, S. P. (1982). The role of coprophagy in the feeding strategies of terrestrial isopods. *Oecologia*, 53(3), 374–381. <https://doi.org/10.1007/BF00389017>

Hassall, M., Tuck, J. M., & James, R. (2005). Effects of density and spatial heterogeneity on foraging behaviour and fitness correlates of *Armadillidium vulgare* (Isopoda Oniscidea). *Ethology Ecology & Evolution*, 17(3), 233–247. <https://doi.org/10.1080/08927014.2005.9522594>

Hastie, T. J. (1992). Generalized Additive Models. In *Statistical Models* in S. Routledge.

Heinrich, B. (1993). Social Thermoregulation. In B. Heinrich (Ed.), *The Hot-Blooded Insects: Strategies and Mechanisms of Thermoregulation* (pp. 447–509). Springer. https://doi.org/10.1007/978-3-662-10340-1_17

Henf, C., Leupolt, B., & Zimmer, M. (2008). Mate-recognition, mate-choice and monopolisation in isopods: An inter-habitat comparison. In M. Zimmer, F. Charfi-Cheikhrouha, & S. Taiti (Eds.), *Proceedings of the International Symposium of Terrestrial Isopod Biology* (pp. 149–159).

Hutchinson, J. M. C., & Waser, P. M. (2007). Use, misuse and extensions of “ideal gas” models of animal encounter. *Biological Reviews of the Cambridge Philosophical Society*, 82(3), 335–359. <https://doi.org/10.1111/j.1469-185X.2007.00014.x>

Ilany, A., & Akçay, E. (2016). Social inheritance can explain the structure of animal social networks. *Nature Communications*, 7. <https://doi.org/10.1038/ncomms12084>

Jeanson, R., & Deneubourg, J. (2007). Conspecific Attraction and Shelter Selection in Gregarious Insects. *The American Naturalist*, 170(1), 47–58. <https://doi.org/10.1086/518570>

Jeanson, R., & Deneubourg, J. L. (2009). Positive Feedback, Convergent Collective Patterns and Social Transitions in Arthropods. In J. Gadau & J. H. Fewell (Eds.), *Organization of insect societies: From genome to sociocomplexity* (pp. 460–482). Harvard University Press.

Jeanson, R., Dussutour, A., & Fourcassié, V. (2012). Key factors for the emergence of collective decision in invertebrates. *Frontiers in Neuroscience*, 0(AUG), 121. <https://doi.org/10.3389/fnins.2012.00121>

Johannesen, A., Dunn, A. M., & Morrell, L. J. (2014). Prey aggregation is an effective olfactory predator avoidance strategy. *PeerJ*, 2, e408. <https://doi.org/10.7717/peerj.408>

Jolles, J. W., Boogert, N. J., Sridhar, V. H., Couzin, I. D., & Manica, A. (2017). Consistent Individual Differences Drive Collective Behavior and Group Functioning of

Schooling Fish. Current Biology, 27(18), 2862-2868.e7.

<https://doi.org/10.1016/J.CUB.2017.08.004>

Jones, J., & Oldroyd, B. (2006). Nest Thermoregulation in Social Insects. *Advances in Insect Physiology*, 33, 153–191. [https://doi.org/10.1016/S0065-2806\(06\)33003-2](https://doi.org/10.1016/S0065-2806(06)33003-2)

Jormalainen, V. (2007). Mating Strategies in Isopods: From Mate Monopolization to Conflicts. In J. E. Duffy & M. Thiel (Eds.), *Evolutionary Ecology of Social and Sexual Systems: Crustaceans as Model Organisms* (p. 0). Oxford University Press.

<https://doi.org/10.1093/acprof:oso/9780195179927.003.0008>

Kappeler, P. M., & Van Schaik, C. P. (2002). Evolution of primate social systems. International Journal of Primatology, 23(4), 707–740.

<https://doi.org/10.1023/A:1015520830318>

Kautz, G., Zimmer, M., & Topp, W. (2002). Does *Porcellio scaber* (Isopoda: Oniscidea) gain from coprophagy? *Soil Biology and Biochemistry*, 34(9), 1253–1259. [https://doi.org/10.1016/S0038-0717\(02\)00065-2](https://doi.org/10.1016/S0038-0717(02)00065-2)

Krause, J., & Ruxton, G. D. (2002). Living in groups. Oxford University Press. https://books.google.pt/books?id=HAoUFFfVFtMcC&dq=Krause,+J.+%26+Ruxton,+G.D.+2002.+Living+in+Groups.+Oxford:+Oxford+University+Press.&lr=&hl=es&source=gbs_navlinks_s

Kuenen, D., & Nooteboom, H. (2011). Olfactory orientation in some land-isopods (Oniscoidea, Crustacea). *Entomologia Experimentalis et Applicata*, 6, 133–142. <https://doi.org/10.1111/j.1570-7458.1963.tb00610.x>

Lefebvre, F., & Caubet, Y. (1999). On the male-effect in the terrestrial Crustacean *Armadillidium vulgare* (Latreille, 1804). Invertebrate Reproduction & Development, 35(1), 55–64. <https://doi.org/10.1080/07924259.1999.9652367>

Lefebvre, F., & Caubet, Y. (2010). Female-extended control over their reproductive investment: The role of early mating interactions on oocyte maturation in the terrestrial crustacean *Armadillidium vulgare* (Latreille, 1804). Invertebrate Reproduction & Development, 54(4), 177–186. <https://doi.org/10.1080/07924259.2010.9652331>

Lefebvre, F., Limousin, M., & Caubet, Y. (2000). Sexual dimorphism in the antennae of terrestrial isopods: A result of male contests or scramble competition? Canadian Journal of Zoology, 78(11), 1987–1993. <https://doi.org/10.1139/z00-128>

Lubin, Y., Henschel, J. R., & Baker, M. B. (2001). Costs of Aggregation: Shadow Competition in a Sit-and-Wait Predator. Oikos, 95(1), 59–68.

Michelena, P., & Deneubourg, J.-L. (2011). How Group Size Affects Vigilance Dynamics and Time Allocation Patterns: The Key Role of Imitation and Tempo. PLOS ONE, 6(4), e18631. <https://doi.org/10.1371/journal.pone.0018631>

Moreau, J., Seguin, S., Caubet, Y., & Rigaud, T. (2002). Female remating and sperm competition patterns in a terrestrial crustacean. Animal Behaviour, 64(4), 569–577. <https://doi.org/10.1006/anbe.2002.4000>

Morrell, L. J., & Romey, W. L. (2008). Optimal individual positions within animal groups. Behavioral Ecology, 19(4), 909–919. <https://doi.org/10.1093/beheco/arn050>

Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews*, 85(4), no-no.
<https://doi.org/10.1111/j.1469-185X.2010.00141.x>

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., Widdig, A., & Engelhardt, A. (2011). Assessing dominance hierarchies: Validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour*, 82(4), 911–921.
<https://doi.org/10.1016/j.anbehav.2011.07.016>

Newman, M. E. . J. (2006). Modularity and community structure in networks. *Proceedings of the National Academy of Sciences of the United States of America*, 103(23), 8577–8582. <https://doi.org/10.1073/pnas.0601602103>

Newman, M. E. J., & Girvan, M. (2004). Finding and evaluating community structure in networks. *Physical Review E - Statistical, Nonlinear, and Soft Matter Physics*, 69(2), 026113. <https://doi.org/10.1103/PhysRevE.69.026113>

Nicolis, S. C., Theraulaz, G., & Deneubourg, J. L. (2005). The effect of aggregates on interaction rate in ant colonies. *Animal Behaviour*, 69(3), 535–540.
<https://doi.org/10.1016/j.anbehav.2004.06.007>

Parrish, J. K., & Edelstein-Keshet, L. (1999). Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science*, 284(5411), 99–101.
<https://doi.org/10.1126/science.284.5411.99>

Pinheiro, J., Bate, D., & R Core Team. (2022). *Nlme: Linear and Nonlinear Mixed Effects Models.* R package version 3.1-159 (3.1-159). <https://CRAN.R-project.org/package=nlme>

Planas, I., & Deneubourg, J.-L. (2018). The role of personality variation, plasticity and social facilitation in cockroach aggregation. *Biology Open*, 7, bio036582. <https://doi.org/10.1242/bio.036582>

R Development Core Team. (2012). *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing. <https://www.r-project.org/>

Refinetti, R. (2000). Circadian Rhythm of Locomotor Activity in the Pill Bug, *Armadillidium vulgare* (Isopoda). *Crustaceana*, 73(5), 575–583.

Sokal, R. R., & Rohlf, F. J. (1995). *Biometry: The Principles and Practices of Statistics in Biological Research* (Cop. W. H. Freeman and Company, Ed.).

Stankowich, T. (2003). Marginal predation methodologies and the importance of predator preferences. *Animal Behaviour*, 66, 589–599. <https://doi.org/10.1006/anbe.2003.2232>

Sumpter, D. J. T. (2006). The principles of collective animal behaviour. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 361(1465), 5–22. <https://doi.org/10.1098/rstb.2005.1733>

Suzuki, S., & Ziegler, A. (2005). Structural investigation of the female genitalia and sperm-storage sites in the terrestrial isopod *Armadillidium vulgare* (Crustacea, Isopoda).

Arthropod Structure & Development, 34(4), 441–454.

<https://doi.org/10.1016/j.asd.2005.06.002>

Svádová, K. H., Exnerová, A., & Štys, P. (2014). Gregariousness as a defence strategy of moderately defended prey: Experiments with *Pyrrhocoris apterus* and avian predators. *Behaviour*, 151(11), 1617–1640. <https://doi.org/10.1163/1568539X-00003208>

Takeda, N. (1984). The aggregation phenomenon in terrestrial isopods.

Theraulaz, G., Gautrais, J., Camazine, S., & Deneubourg, J. L. (2003). The formation of spatial patterns in social insects: From simple behaviours to complex structures. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 361(1807), 1263–1282.

<https://doi.org/10.1098/RSTA.2003.1198>

Thiel, M. (2010). Chemical Communication in Peracarid Crustaceans. In T. Breithaupt & M. Thiel (Eds.), *Chemical Communication in Crustaceans* (pp. 199–218). Springer New York. https://doi.org/10.1007/978-0-387-77101-4_10

Thiel, M. (2011). The Evolution Of Sociality: Peracarid Crustaceans As Model Organisms (pp. 285–297). Brill. https://brill.com/view/book/edcoll/9789047427711/Bej.9789004174252.i-354_026.xml

Van Oers, K., Klunder, M., & Drent, P. J. (2005). Context dependence of personalities: Risk-taking behavior in a social and a nonsocial situation. *Behavioral Ecology*, 16(4), 716–723. <https://doi.org/10.1093/beheco/ari045>

Warburg, M. R. (1965). The Microclimate in the Habitats of Two Isopod Species in Southern Arizona. *American Midland Naturalist*, 73(2), 363. <https://doi.org/10.2307/2423460>

Webster, M. M., & Ward, A. J. W. (2011). Personality and social context. *Biological Reviews*, 86(4), 759–773. <https://doi.org/10.1111/j.1469-185X.2010.00169.x>

Whitehead, Hal. (2008). *Analyzing Animal Societies: Quantitative Methods For*. University of Chicago Press.

Wilson, D. S. (1974). Prey Capture and Competition in the Ant Lion. *Biotropica*, 6(3), 187–193. <https://doi.org/10.2307/2989651>

Wood, S. N. (2006). Low-Rank Scale-Invariant Tensor Product Smooths for Generalized Additive Mixed Models. *Biometrics*, 62(4), 1025–1036. <https://doi.org/10.1111/j.1541-0420.2006.00574.x>

Zajonc, R. B. (1965). Social Facilitation. *Science*, 149(3681), 269–274. <https://doi.org/10.1126/science.149.3681.269>

Zimmer, M., & Zimmer, M. (2002). Nutrition in terrestrial isopods (Isopoda: Oniscidea): An evolutionary-ecological approach. 455–493.

TABLES

Table 1. Estimated parameters obtained from GAMMs testing the effect of personality dissimilarity and social organization on group dynamics attributes at the scale of: A. Dyadic associations; B. Modularity; and C. Dissimilarity in aggregate membership.

| A. DYADIC ASSOCIATION | | | | |
|---|------------|-------------------------|----------------|------------------|
| Smooth terms | <i>edf</i> | Ref. <i>df</i> | <i>F</i> | <i>p-value</i> |
| s(Spatial location) | 1.395 | 2.00 | 2.83 | 0.011 |
| te(Time, Aggregate size) in Group 1 | 16.706 | 16.71 | 17.85 | <0.001 |
| te(Time, Aggregate size) in Group 2 | 21.268 | 21.27 | 28.46 | <0.001 |
| te(Time, Aggregate size) in Group 3 | 19.318 | 19.32 | 24.38 | <0.001 |
| Fixed factors | Estimate | SE | <i>t value</i> | <i>p-value</i> |
| Intercept | 1.56 | 0.19 | 8.18 | <0.001 |
| Diss. degree centrality | 0.00 | 0.01 | 0.04 | 0.969 |
| Diss. Closeness centrality | 0.20 | 0.19 | 1.08 | 0.282 |
| Diss. Betweenness centrality | 0.00 | 0.00 | 0.34 | 0.733 |
| Diss. Eigen value centrality | 0.02 | 0.91 | 0.03 | 0.980 |
| Diss. Association strength | -0.42 | 0.64 | -0.66 | 0.511 |
| Diss. Distance | 0.00 | 0.00 | 0.89 | 0.373 |
| Diss. Stops | 0.00 | 0.02 | 0.27 | 0.788 |
| Diss. Immobility | -0.06 | 0.13 | -0.48 | 0.635 |
| Diss. Escape attempts | 0.02 | 0.01 | 3.00 | 0.003 |
| Diss. Average direction | 0.00 | 0.00 | 0.55 | 0.583 |
| Diss. Sd. direction | 0.00 | 0.00 | 1.04 | 0.299 |
| Diss. Dominance status | 0.03 | 0.04 | 0.58 | 0.564 |
| Random factors | <i>df</i> | <i>Likelihood Ratio</i> | | <i>p-value</i> |
| Dyad identity | 31, 30 | 70.49 | | <0.001 |
| B. GROUP MODULARITY | | | | |
| Smooth terms | <i>edf</i> | Ref. <i>df</i> | <i>F</i> | <i>p-value</i> |
| te(Time, Group size) | 2.767 | 24.00 | 0.43 | 0.009 |
| Fixed factors | Estimate | SE | <i>t value</i> | <i>p-value</i> |
| Intercept | -1.94 | 0.19 | -10.31 | <0.001 |
| C. DISSIMILARITY IN CLUSTER MEMBERSHIP | | | | |
| Smooth terms | <i>edf</i> | Ref. <i>df</i> | <i>F</i> | <i>p-value</i> |
| s(Spatial location) | 1.92 | 2.00 | 28.26 | <0.001 |
| te(Time, Aggregate size) | 23.29 | 23.28 | 19.65 | <0.001 |
| Fixed factors | Estimate | SE | <i>t value</i> | <i>p-value</i> |
| Intercept | -2.29 | 0.19 | -11.80 | <0.001 |
| Diss. degree centrality | 0.04 | 0.03 | 1.30 | 0.194 |
| Diss. Closeness centrality | -0.14 | 0.39 | -0.37 | 0.714 |
| Diss. Betweenness centrality | 0.01 | 0.01 | 0.72 | 0.472 |
| Diss. Eigen value centrality | -2.88 | 1.90 | -1.52 | 0.129 |
| Diss. Association strength | -0.13 | 1.29 | -0.10 | 0.920 |
| Diss. Distance | 0.00 | 0.00 | 0.22 | 0.828 |
| Diss. Stops | -0.03 | 0.04 | -0.82 | 0.410 |
| Diss. Immobility | -0.19 | 0.26 | -0.73 | 0.469 |
| Diss. Escape attempts | 0.00 | 0.01 | -0.17 | 0.862 |
| Diss. Average direction | 0.00 | 0.00 | 1.10 | 0.271 |
| Diss. Sd. direction | -0.01 | 0.01 | -1.64 | 0.101 |
| Diss. Dominance status | -0.06 | 0.09 | -0.62 | 0.537 |
| Random factors | <i>df</i> | <i>Likelihood Ratio</i> | | <i>p-value</i> |
| Dyad identity | 22, 21 | 526.77 | | <0.001 |
| Group identity | 22, 21 | 122.04 | | <0.001 |
| Dyadic relation by Sex: Pregnant | 22, 21 | 302.56 | | <0.001 |

edf: effective degree of freedom; Ref.*df*: relative degree of freedom; s(): smooth term; te: tensor product interaction; Diss.: Dissimilarity. Significant probability was highlighted in bold.

Table S1. Kernel correlation between personality attributes.

| | Distance | Speed | Av. direction | Sd. direction | Stops | Immobility | Escape att. | Escape int. | David's score | Degree | Closeness | Betweenness | Eigen value |
|-------------------------------|----------|---------|---------------|---------------|--------|------------|-------------|-------------|---------------|---------|-----------|-------------|-------------|
| Speed | 0.87*** | | | | | | | | | | | | |
| Average direction | 0.29* | 0.27 | | | | | | | | | | | |
| Sd. direction | 0.15 | 0.20 | 0.04 | | | | | | | | | | |
| Stops | -0.13 | -0.14 | -0.12 | -0.05 | | | | | | | | | |
| Immobility | -0.39*** | -0.27** | -0.31* | -0.13 | 0.32* | | | | | | | | |
| Escape attempts | 0.29* | 0.22 | 0.22 | 0.01 | -0.26* | -0.41** | | | | | | | |
| Escape interval | -0.28* | -0.22 | -0.14 | -0.07 | 0.24* | 0.39** | -0.82*** | | | | | | |
| David's score | 0.10 | 0.07 | -0.13 | 0.04 | -0.02 | -0.11 | 0.02 | -0.06 | | | | | |
| Degree | 0.05 | 0.05 | 0.08 | 0.02 | -0.01 | -0.06 | 0.15 | -0.17 | -0.02 | | | | |
| Closeness | 0.08 | 0.05 | 0.03 | 0.06 | -0.05 | -0.01 | 0.07 | -0.09 | 0.00 | 0.38 | | | |
| Betweenness | 0.07 | 0.05 | 0.06 | -0.04 | 0.00 | -0.12 | 0.11 | -0.09 | -0.03 | 0.51** | 0.10 | | |
| Eigen value centrality | 0.01 | 0.01 | 0.08 | 0.00 | -0.02 | -0.09 | 0.20 | -0.20 | -0.04 | 0.74*** | 0.14 | 0.52*** | |
| Av. Assoc. strength | -0.08 | -0.02 | 0.10 | 0.04 | -0.03 | 0.05 | -0.08 | 0.00 | 0.01 | 0.24 | 0.08 | -0.02 | 0.15 |

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Table S2. Behavioral repeatability analysis at the individual level.

| Attribute | Repeatability | SE | Confidence Interval | | <i>p</i> |
|--------------------------|---------------|------|---------------------|-------|----------|
| | | | 2.5% | 97.5% | |
| Distance | 0.70 | 0.11 | 0.46 | 0.86 | <0.001 |
| Speed | 0.68 | 0.11 | 0.43 | 0.85 | <0.001 |
| Average direction | 0.76 | 0.07 | 0.55 | 0.81 | <0.001 |
| Sd direction | 0.80 | 0.06 | 0.63 | 0.86 | <0.001 |
| Stops | 0.68 | 0.07 | 0.49 | 0.78 | <0.001 |
| Immobility | 0.81 | 0.05 | 0.66 | 0.86 | <0.001 |
| Escape attempts | 0.93 | 0.05 | 0.77 | 0.94 | <0.001 |
| Escape interval | 0.86 | 0.05 | 0.72 | 0.90 | <0.001 |
| David's score | 0.76 | 0.06 | 0.59 | 0.82 | <0.001 |
| Degree centrality | 0.67 | 0.06 | 0.51 | 0.75 | <0.001 |
| Closeness centrality | 0.66 | 0.09 | 0.44 | 0.79 | <0.001 |
| Betweenness centrality | 0.67 | 0.06 | 0.53 | 0.75 | <0.001 |
| Eigen value centrality | 0.67 | 0.06 | 0.51 | 0.74 | <0.001 |
| Av. Association strength | 0.39 | 0.08 | 0.23 | 0.53 | <0.001 |

Table S3. Model selection based on Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC) and coefficient of determination (r^2).

| Model | df | $\Delta AICc$ | BIC | -2LL | Adj. R^2 / Pseudo R^2_{marginal} |
|--|----|---------------|---------|-------|---|
| (A) DYADIC ASSOCIATION INDEX | | | | | |
| DISS. PERSONALITY + s(Spatial ubication) + te(Time, Aggregate size, by=Group) + (1 Dyad identity) | 31 | 26.1 | 22962.8 | 22692 | 0.81 |
| DISS. PERSONALITY + s(Spatial ubication) + te(Time, Subgroup size, by=Group) | 30 | 94.6 | 23024.6 | 22763 | 0.82 |
| (B) GROUP MODULARITY | | | | | |
| te(Time, Group size) | 5 | 0 | 189.0 | 173 | 0.23 |
| s(Time) + s(Group size) | 4 | 4.4 | 195.3 | 176 | 0.04 |
| s(Group size) | 4 | 11.0 | 33724.9 | 177 | 0.21 |
| (C) DISSIMILARITY IN AGGREGATE MEMBERSHIP | | | | | |
| DISS. PERSONALITY + s(Spatial ubication) + te(Time, Aggregate size) + (1 Dyad identity) + (1 Group identity) + (1 Dyadic relation by Sex: Pregnant) | 22 | 0 | 34020.9 | 33829 | 0.28 |
| DISS. PERSONALITY + s(Spatial ubication) + te(Time, Subgroup size) | 19 | 162.9 | 34311.5 | 34146 | 0.34 |

s: smooth term; te: tensor product interaction; DISS. PERSONALITY is the concept that includes dyadic dissimilarity in degree centrality, closeness centrality, interrelatedness centrality, eigenvalue centrality, mean association strength, distance traveled, number of stops, immobility time, escape attempts, average direction, standard deviation in direction, and David's score dominance status.

FIGURES

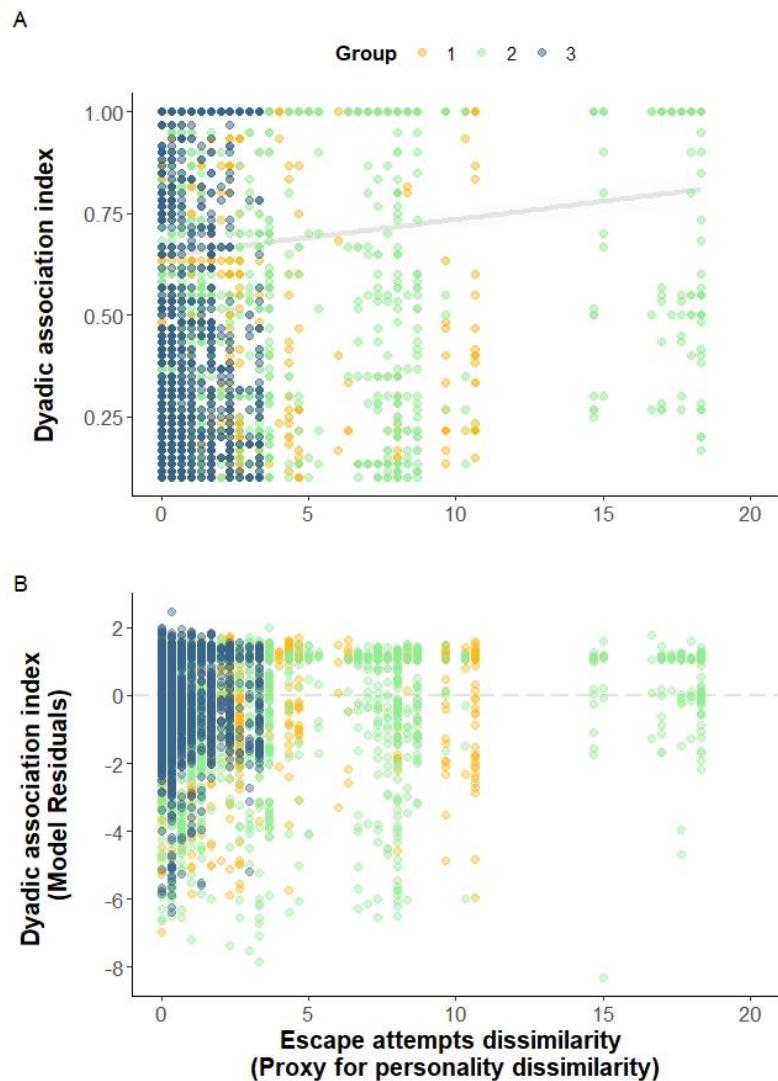


Figure 1. Effect of personality dissimilarity on dyadic association index in *Porcellio scaber*. A. Regression plot of dissimilarity in personality and dyadic association index; B. Partial regression plot of dissimilarity in personality and residuals from the dyadic association index model. We use the dyadic dissimilarity of escape attempts, performed in an asocial environment, as a proxy for personality. It is shown that the weight of dyadic associations has higher variability and a lower mean when the dyad of individuals has similar personality values. As the dyadic dissimilarity in personality increases, the dyadic association weight reduces variability and homogenizes to intermediate values. This trend is repeated in all three assessment groups, regardless of the range in which personality dissimilarity is distributed in each group.

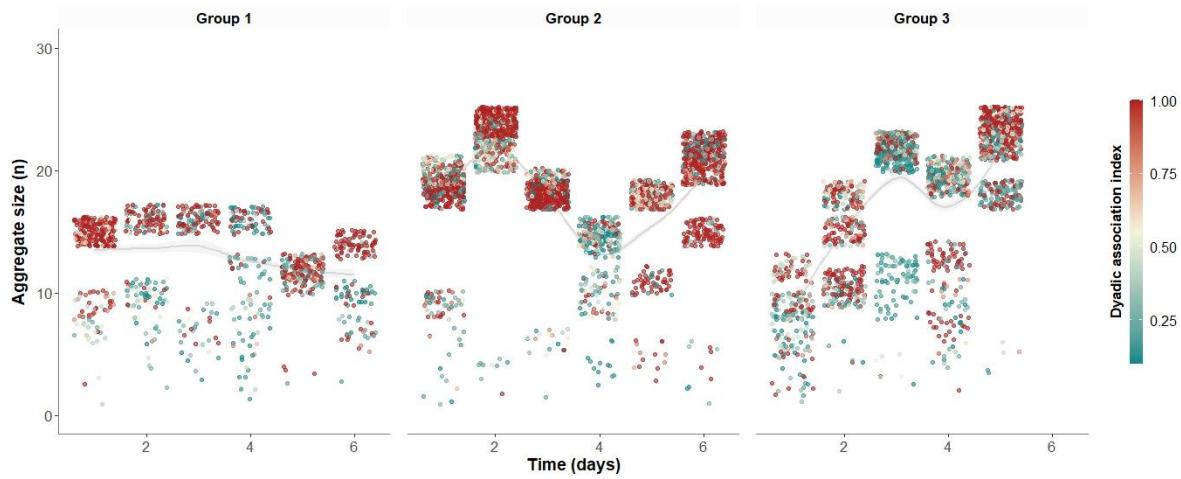


Figure 2. Relationship between aggregate formation dynamics and dyadic association index by evaluation group in *P. scaber*. The dynamics of aggregate formation is represented by aggregate size as a function of elapsed time. The color gradient represents the index of dyadic associations as a function of the proportion of time that two individuals were associated per observation.

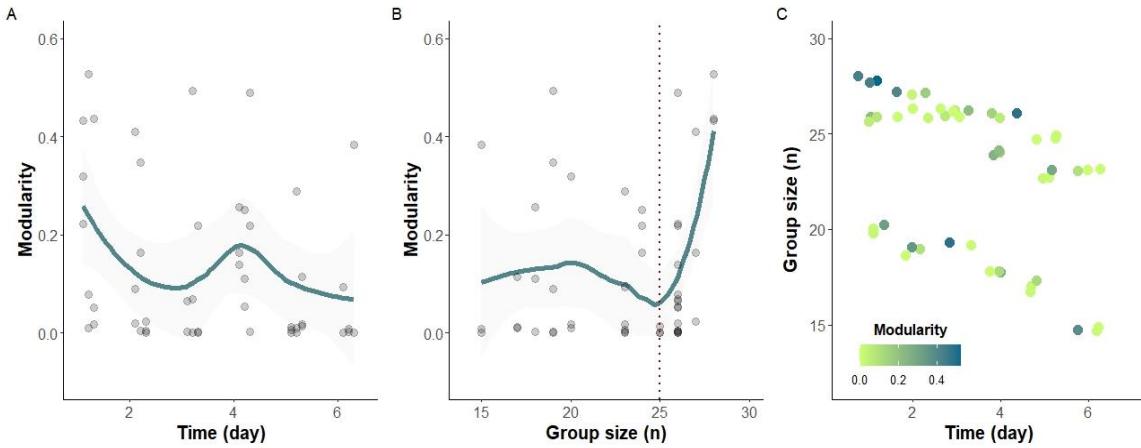


Figure 3. Denso-dependence and temporality of modularity in *Porcellio scaber*. A. Relationship between time and modularity; B. Relationship between group size and modularity; C. Relationship between time-size interaction and modularity. We found that modularity decreases over time. We also observed an increase in modularity values when the group size exceeds twenty-five individuals. Below this group size, modularity has an upper limit value of 0.25 at 95% confidence. While above twenty-five individuals, modularity can reach an upper bound of up to 0.50. Modularity quantifies the level of aggregation (clustering) in a graph based on network theory.

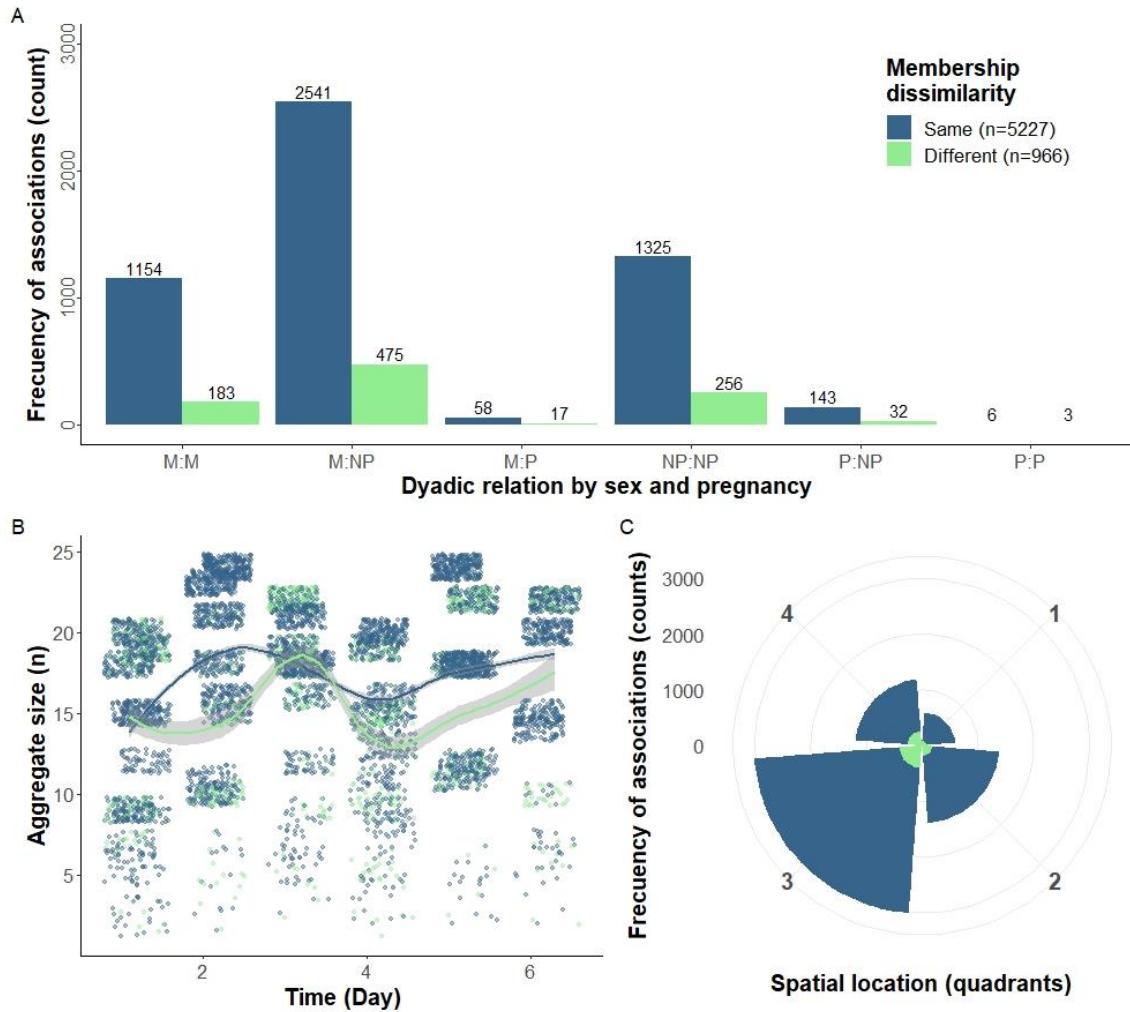


Figure 4. Attributes influencing membership preferences in *Porcellio scaber*. A. Frequency of dyadic associations by sex and pregnancy status. It is observed that the predominant associations are mainly between males and non-pregnant females, followed by associations between non-pregnant females and male pairs. The least frequent associations are those between pregnant females and other individuals. M: male, NP: non-pregnant female, P: pregnant female. B. Denso-dependence and temporality of associations. Most associations between individuals with the same membership occur in larger groups compared to associations between individuals who differ in membership. C. Frequency of dyadic associations per quadrant. A preference for location in the third quadrant of the arena was observed. Dissimilarity in the membership of dyadic associations by quadrant: first (same = 501, different = 100); second (same = 1197, different = 192); third (same = 2609, different = 406); fourth (same = 920, different = 268).



Figure S1. Distribution of behavioral variables by groups.

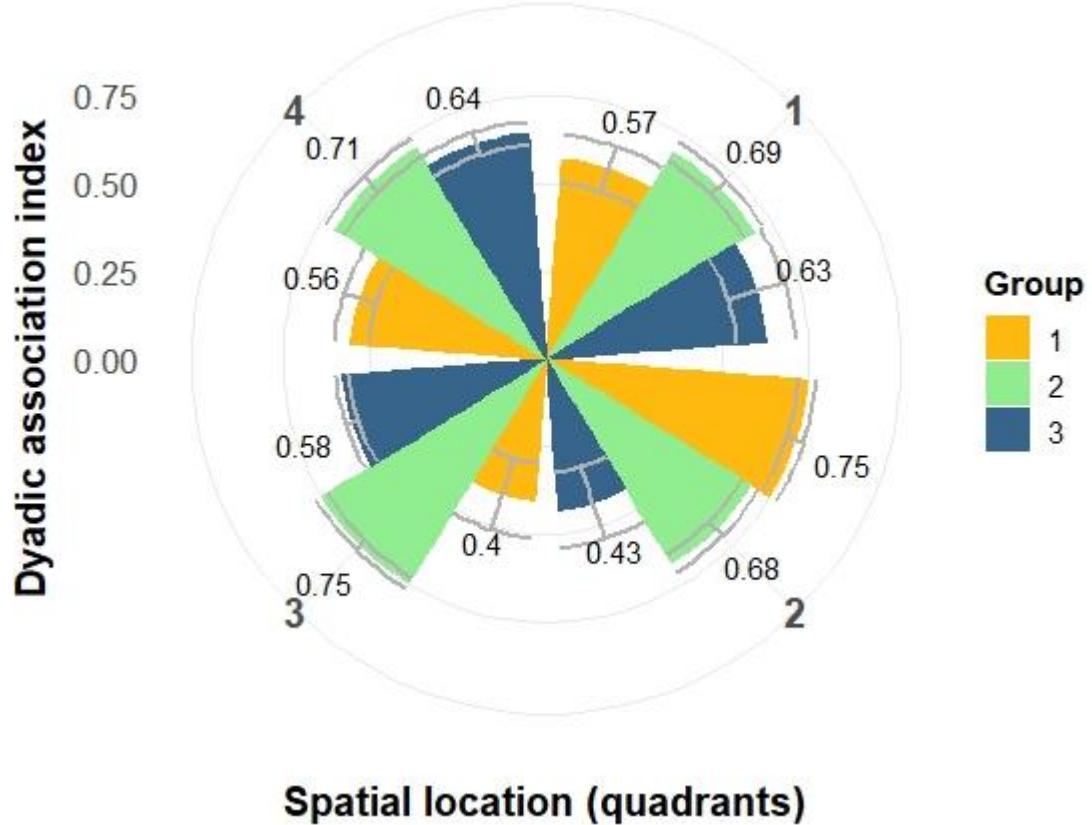


Figure S2. Value of the dyadic association index in each of the quadrants of the evaluation arena.

SUPPLEMENTARY MATERIAL 1

DETAILS OF THE MODELS USED IN THE ANALYSES

Library("mgcv")

- a) **Influence of personality dissimilarity and interindividual relationships by intrinsic attributes on dyadic association index in group formation dynamics:**

Dyadic association index model

```
= gamm(sqrt(weight) ~ dis.degree + dis.closeness  
+ dis.betweenness + dis.evcent + dis.oas + dis.distance  
+ dis.stops + (dis.inmobility/300) + dis.escape.attempts  
+ dis.average_direction + dis.deviation_direction + dis.ds  
+ s(spatial location, bs = "cc", k = 4) + te(time, aggregate size, bs  
= c("cr", "tp"), by = factor(Group)), random = list(Dyad identitiy  
= ~1), family = quasibinomial, method = "REML")
```

- b) **Influence of group attributes on group modularity in group formation dynamics:**

Modularity model = gam(modularity~te(Time, Group size, bs = c("cs", "tp")),
family = quasibinomial, method = "REML")

- a) Influence of personality dissimilarity and interindividual relationships by intrinsic attributes on dissimilarity in aggregate membership in group formation dynamics:

Membership dissimilarity model

```
= gamm(dissimilarity in membership ~ dis.degree + dis.closeness
+ dis.betweenness + dis.evcent + dis.oas + dis.distance
+ dis.stops + (dis.inmobility/300) + dis.escape.attempts
+ dis.average_direction + dis.deviation_direction + dis.ds
+ s(apatial location, bs = "cc", k = 4) + te(time, aggregate size, bs
= c("cr", "tp")), random = list(Group = ~1, dyad identity
= ~1, sex: pregnant = ~1), family = binomial, method = "REML")
```

CAPÍTULO V

DISCUSIÓN GENERAL Y CONCLUSIONES

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Un sistema social está representado por la suma propiedades emergentes que surgen de las interacciones y estrategias conductuales de los individuos (Hinde, 1976). La capacidad de los individuos para relacionarse con sus conespecíficos se encuentra ampliamente influenciada por la interacción entre los factores ecológicos, los condicionamientos basados en atributos intrínsecos y la personalidad. Sin embargo, el mismo entorno social, constituido por la organización social, la estructura social y las condiciones denso-dependientes, también restringe el comportamiento social de los individuos e influye sobre la manifestación de las conductas individuales generando un proceso complejo de retroalimentación (Bergmüller & Taborsky, 2010; Kappeler & Van Schaik, 2002; Terborgh & Janson, 1986; Wolf & Krause, 2014). En este sentido, esta tesis estuvo centrada en determinar cómo la personalidad influye sobre la estructuración social a través de diferentes contextos sociales usando como modelo de estudio la especie de isópodo terrestre *Porcellio scaber*.

En esta tesis se evidenció que tanto la personalidad como el entorno social modulan la expresión de sociabilidad en los individuos y sus respuestas conductuales, motivando una estructuración social no aleatoria (*Capítulo II*). Además, se encontró evidencia que sugiere un proceso de especialización de nicho social conducido indirectamente por la percepción del estatus de dominancia y directamente por interacciones agonísticas entre pares de individuos. Donde la personalidad de los individuos definió la intensidad de las agresiones de manera consistente y el desempeño de ciertas conductas plásticas reflejó el impacto de la participación en eventos de agresión (*Capítulo III*). Asimismo, también se demostró el efecto de la personalidad, las relaciones basadas en aspectos reproductivos y las preferencias sobre

los procesos dinámicos de agregación social, donde se observó un comportamiento que alterna entre fases de mayor y menor cohesión (*Capítulo IV*).

Aproximación mediante teoría de redes

El estudio de los sistemas sociales ha cobrado fuerza a partir del surgimiento del análisis de redes sociales. La teoría de redes facilita establecer un vínculo entre la funcionalidad de un grupo y los atributos de los individuos que lo constituyen (Fewell, 2003). Además, permite caracterizar las estructuras sociales emergentes para entender los procesos ecológicos y evolutivos que determinan la socialidad en animales (Pinter-Wollman *et al.*, 2014). En esta tesis se empleó el cuerpo teórico del análisis de redes para definir los atributos sociales a nivel de grupo y de individuos. Complementariamente, se utilizaron modelos de inferencia bayesiana ajustados a la naturaleza de los atributos sociales para evaluar la influencia de la personalidad y el ambiente social. Este enfoque ha sido recientemente propuesto debido a las limitaciones que presentan los métodos de permutación de redes tradicionales, los cuales son deficientes al considerar la no-independencia de las observaciones cuando se evalúan atributos de redes sociales (Hart *et al.*, 2022). Esta aproximación para el estudio de la personalidad y el entorno social en grupos de organismos permitió analizar las propiedades emergentes de los agrupamientos sociales a múltiples escalas. Esto fue de mucha utilidad en los análisis a nivel nodal, en los análisis relacionales que incluyen diadas de individuos y en la evaluación de atributos de grupo.

El uso de modelos de inferencia resulta ser una buena opción cuando el interés de estudio es la identificación de las fuentes de dependencia de los atributos de las redes y no la estructura

emergente como tal. Una de las grandes ventajas de trabajar con modelos de inferencia causal es que estos poseen una serie de herramientas que permiten especificar rigurosamente los supuestos y modelar explícitamente la interdependencia entre los datos en múltiples niveles. Una de la limitantes de trabajar con modelos de inferencia es que estas requieren grandes capacidades de cómputo cuando se analizan modelos multinivel complejos. En el caso de esta tesis, los modelos con mayor demanda de capacidad de cómputo fueron aquellos que incluían comparaciones en diadas, donde la multimembresía estuvo compuesta por solo dos factores.

Personalidad y ambiente social

La personalidad animal describe las diferencias interindividuales en la expresión de conductas que son consistentes en el tiempo y a través de diferentes entornos sociales (Dall *et al.*, 2004; Réale & Dingemanse, 2010). Estos patrones conductuales individuales han sido reportados en diferentes contextos en el que los individuos están inmersos, como por ejemplo en el uso diferencial del hábitat, en interacciones agonísticas y de agresión, en situaciones de depredación, y principalmente, en ambientes novedosos (Réale *et al.*, 2007). La personalidad animal es asumida a ser el resultado de diferencias adaptativas en la capacidad de respuesta de los individuos frente al ambiente ecológico y social asociado (Bergmüller & Taborsky, 2010; Smith & Blumstein, 2008; Wolf *et al.*, 2007). El ambiente social como concepto incluye el número de compañeros en el grupo, los efectos denso-dependientes, la composición del grupo y la naturaleza de las relaciones que ocurren (Webster & Ward, 2011). En este sentido, el efecto de las interacciones que un individuo tiene con sus conespecíficos y con el entorno es inherente a su desempeño conductual (Dingemanse *et al.*, 2010). En esta

tesis se evaluó la personalidad de los individuos de manera aislada y en entorno novedoso, para posteriormente relacionar estas conductas con conductas sociales desempeñadas en un ambiente social. Las conductas individuales que se cuantificaron con los individuos aislados se agruparon principalmente en dos grupos, donde el primero describió la capacidad de desplazamiento de los individuos y el segundo agrupó una serie de conductas estereotipadas. En términos generales, la mayoría de las conductas evaluadas presentó consistencia a nivel individual. Las conductas que no presentaron consistencia a nivel individual en algunos casos fueron la dirección de desplazamiento promedio, la desviación direccional y el número de cambios de dirección por más de 45°, todas relacionadas al desplazamiento y la noción del espacio por parte del individuo. Los mayores valores de repetibilidad conductual fueron encontrados antes de someter a los individuos a entorno social y luego de exponerlos al ambiente social de manera sostenida en un mismo grupo, pudiendo alcanzar valores de hasta el 90% en algunos casos (*Capítulo II* y *IV*), mientras que cuando los individuos fueron sometidos a entornos sociales cambiantes los valores de repetibilidad conductual se redujeron aproximadamente a la mitad, haciendo referencia a un efecto de la inestabilidad en el entorno social (*Capítulo III*). Pese a que existió variabilidad en la expresión de conductas, la personalidad de los individuos en nuestro modelo de estudio pudo ser constatada y definida sin problemas según los lineamientos sugeridos en el cuerpo teórico.

Una de las preguntas que comúnmente surgen con respecto a la relación entre la personalidad y el ambiente social es si la personalidad, aproximada a partir de la evaluación aislada del resto de individuos, puede predecir la expresión de conductas efectuadas en un entorno social. En el caso propuesto en esta tesis, se evidenció que en efecto la expresión de conductas por parte de un individuo es repetible y puede predecir su comportamiento cuando se encuentran

conformando un grupo social. Diferentes procesos sociales han sido propuestos para explicar como el ambiente social modula la expresión conductual. Entre estos resaltan la conformidad como la tendencia a efectuar una conducta generalizada conducida por la mayoría de los individuos y la facilitación social como un proceso que motiva la expresión de conductas en respuesta a situaciones desencadenantes (Webster & Ward, 2011). En esta tesis se observó que el ambiente social influye de forma diferenciada sobre los tipos de personalidad, donde individuos con personalidades más reactivas tienen a asociarse de manera más estable y a desempeñar conductas colectivas con otros miembros del grupo haciendo referencia a un proceso de conformidad, mientras que los individuos con personalidades proactivas tienen un alcance similar que los individuos reactivos pero suelen presentar asociaciones efímeras que en la mayoría de los casos motivan cambios de estados conductuales en los compañeros a los que se asocian. Además, este tipo conductual presentó una menor responsividad conductual al ambiente social por lo que se sugiere un proceso de facilitación social más que un proceso de conformidad (*Capítulo II*). Estos patrones de respuesta conductual por tipos de personalidades pueden variar entre especies, en el caso de nuestro modelo de estudio fue esperado encontrar que los individuos que conforman el núcleo del grupo desempeñen una conducta generalizada de quiescencia (Hendricks *et al.*, 2000).

Durante el desarrollo de esta tesis, el ambiente social siempre fue incluido como una fuente de variación en el desempeño conductual de los individuos. Cuando se analizaron los modelos de efectos se pudo observar que los grupo de evaluación (*Capítulo II y IV*) o ensambles aleatorios (*Capítulo III*) variaron en su efecto uno del otro. Es presumible que esto ocurrió principalmente a que el comportamiento de los individuos o la mera presencia de compañeros puede influenciar rasgos conductuales en los mismos individuos que terminan

modificando las propiedades emergentes del grupo, y en consecuencia el ciclo de retroalimentación.

Sistema social, sociabilidad y la especialización de roles

La descripción y comprensión de los sistemas sociales en animales es compleja debido a las interacciones multinivel que ocurren entre sus miembros, por lo que los investigadores han identificado componentes que permiten un mejor entendimiento de los atributos de manera disagregada y facilitan el uso de aproximaciones para su estudio. Estos son la estructura social, la organización social y el sistema de apareamiento (Kappeler & Van Schaik, 2002). En esta tesis se abordó principalmente la estructura social pero también se incorporó la organización social y el sistema de apareamiento de manera directa e indirecta mediante el uso de teoría de redes sociales. La aproximación a partir de redes sociales provee un método cuantitativo de la estructura social, el cual incorpora información de los miembros, relativa a su naturaleza física, conductual y sexual, así como también atributos del grupo como la cantidad de individuos. Aquí se complementó el análisis de redes sociales con el uso de modelos multinivel que incluyeron precisamente información acerca de la organización social y las relaciones sexuales-reproductivas.

Desde un punto de vista ecológico, la evaluación de la estructura social es importante ya que la estructuración propia del grupo y la posición que los individuos tienen en ella pueden tener efectos importantes en la dinámica social, la aptitud de los miembros y la funcionalidad del grupo, por lo tanto, la estructura social específica puede afectar a la evolución del comportamiento social (Sih *et al.*, 2009). Partiendo desde la premisa de que cada individuo experimenta y reacciona de manera diferenciada al resto, es presumible que la cantidad y calidad de sus interacciones en un ambiente social también sea diferente y se encuentre

determinadas por las restricciones de su desempeño conductual. Estas diferencias pueden persistir en el tiempo y a través de diferentes tipos de interacción social, evidenciando rasgos de personalidad animal en atributos de sociabilidad. En esta tesis se evidenció que la personalidad animal, descrita a partir de conductas efectuadas en un ambiente aislado y novedoso, determina la capacidad de asociación de los individuos y, en consecuencia, sus conductas sociales basadas en posición y centralidad en la estructura de redes sociales (*Capítulo II*). Además, cuando se evaluaron los mecanismos conductuales que conducen el establecimiento de los grupos en ambientes sociales cambiantes, se encontró que la fuerza de las interacciones agonísticas que definen la estructura de los grupos está determinada por la personalidad de los individuos (*Capítulo III*). La versatilidad del uso de medidas de centralidad de redes para definir la sociabilidad de los individuos radica en la posibilidad de utilizar aproximaciones dependiendo del atributo que se busca describir y del tipo de interacción que se use para describir la topología de la red. Por ejemplo, algunas métricas utilizan el número de conexiones que el individuo tiene, otras utilizan la frecuencia de interacciones, y otras miden la importancia social de las conexiones de un individuo particular (Lusseau & Newman, 2004). En esta tesis se utilizaron principalmente las centralidad de grado, la intermedialidad, la centralidad del valor propio, la cercanía y la fuerza de interacción media para explicar diferentes atributos de la sociabilidad individual.

Se tienen suficiente evidencia para sugerir que la personalidad animal impacta en como los individuos se desempeñan y establecen sus posiciones en los grupos sociales. El hecho que un individuo se encuentre haciendo parte de un entorno social amerita una serie de interacciones reiterativas con sus conespecíficos que conducen el desarrollo de conductas sociales consistentes o roles sociales. Esta tesis se enfocó en la retroalimentación que existe

entre el ambiente social y la personalidad animal para explicar la consistencia de los roles sociales haciendo uso de la hipótesis de nicho social (Bergmüller & Taborsky, 2010; Montiglio *et al.*, 2013). La consistencia en las conductas sociales puede ser ventajosa en los grupos, en especial cuando los miembros del grupo especializan sus preferencias y roles con la finalidad de mantener ciertos niveles de estabilidad. El reforzamiento social, en este caso, permite que los individuos puedan percibir y predecir las conductas de sus conespecíficos y modificar sus respuestas sociales propias (Dall *et al.*, 2005). En esta tesis se encontró que los individuos presentaron consistencia a nivel individual en conductas sociales ligadas a la intermedialidad en la asociación y en el grado e intermedialidad en interacciones agonísticas a través de múltiples ambientes sociales. También se pudo evidenciar consistencia individual en el estatus de dominancia de los individuos en diferentes ensambles sociales (*Capítulo III*). Por otro lado, nosotros encontramos que cuando los individuos tenían posibilidad de establecerse en ambientes sociales sostenidos expresaron consistencia individual en todas las métricas de centralidad que describían conductas sociales basadas en asociación, por lo que se encontró evidencia para considerar la sociabilidad como un atributo de la personalidad (*Capítulo IV*). Esta diferencia en la expresión de repetibilidad de las conductas sociales asociativas puede deberse principalmente a que el mecanismo que predomina en las fases iniciales de establecimiento de grupo es el conducido por la agresión o interacciones agonísticas.

La hipótesis de nicho social hace referencia a que el ambiente social modula la consistencia en la expresión de conductas mediado por el conflicto y disponibilidad de opciones sociales. En consecuencia, es esperable que el ambiente social tenga influencia en la expresión de personalidad en períodos cortos de tiempo cuando surge inestabilidad en los grupos y se

motiva el conflicto social. En el desarrollo de esta tesis, en efecto se pudo observar que la expresión de conductas sociales descritas por el grado de centralidad basado en interacciones agonísticas en ambientes sociales cambiantes guarda relación o impacta sobre la expresión de ciertas conductas plásticas, aun cuando un individuo se encuentra aislado (*Capítulo III*).

Los resultados presentados en esta sección describen la naturaleza social de nuestra especie de estudio y como estos interactúan motivando el surgimiento de patrones conductuales y propiedades emergentes del entorno. Existe una base teórica-experimental sólida acerca de la relación entre las conductas individuales, los atributos sociales producto de los sistemas sociales y su posición en las estructuras sociales emergentes (Aplin *et al.*, 2012, 2015; Krause *et al.*, 2010; Krause *et al.*, 2016; Kulahci *et al.*, 2018; Wilson *et al.*, 2013).

Organización y comportamiento del grupo

Basándose en el concepto de sistemas social propuesto por Kappeler & Van Schaik (2002), El componente que describe los atributos conformacionales de los grupos es la organización social. Este concepto engloba el tamaño, la composición y el grado de cohesión de un sistema social, y puede ser distinguido en tres tipos: vida solitaria en un vecindario, vida en parejas y vida en grupo. El modelo de estudio utilizado (*Porcellio scaber*) presenta vida en grupo con establecimiento de agregaciones sociales. En esta tesis se utilizaron métricas de redes sociales, y relaciones diádicas entre tipos de personalidades y sexos ligados a estados reproductivos para describir el comportamiento del grupo, el efecto del tamaño y las relaciones que delimitan los agregados.

Con respecto al comportamiento del grupo, se pudo observar que estos se establecen espacialmente según la preferencia de los individuos que lo conforman (a partir de pistas sociales probablemente desencadenadas por los individuos iniciadores). El diseño experimental contempló una distribución homogénea de recursos en ausencia de refugios, por lo que experimentalmente no se motivó direccionalidad en la elección de un espacio físico (*Capítulo IV*). Además, haciendo uso de las métricas de redes, se encontró que los grupos tuvieron un nivel de densidad variable en la fase de establecimiento de grupo, entre 50 – 97% de los individuos, pero cuando alcanzaban cierta estabilidad con el paso del tiempo la densidad se estableció entre 80-90%. Usualmente se registró un agregado conteniendo a la mayoría de los individuos con presencia de otros agregados más pequeños e individuos dispersos. En aspectos generales, los agregados presentaron un alto nivel de cohesión con pasos cortos entre individuos y bajos niveles de modularidad, pero presentaron variabilidad con respecto a su conformación (*Capítulo II*).

Para tener un entendimiento completo acerca del desempeño conductual de los individuos en un entorno social es necesario que se contemplen las fuentes de variación que influyen en condiciones naturales. Uno de los condicionantes que mayor importancia tienen en entornos naturales es el tamaño del grupo y su efecto denso dependiente sobre la expresión conductual y los mecanismos que lo regulan. La cuantificación de este efecto puede ser dificultosa debido a que las especies que comúnmente se usan en estudios conductuales habitan grupos más grandes que los que se usan en ensayos de laboratorio. En *Porcellio scaber* se tiene conocimiento de la existencia de reglas de quorum y límites máximos del tamaño de los agregados, donde a densidades bajas los individuos suelen establecer agregados conteniendo aproximadamente el 80% de la población, mientras que a densidades mayores suelen

establecerse mayor cantidad de agregados limitados por la disponibilidad a recursos (Broly *et al.*, 2012, 2016). En esta tesis se trabajaron con tamaños máximos de grupo de 30 individuos y en efecto se pudo observar que los agregados contenían aproximadamente el 80% de los individuos (*Capítulo II*). Complementariamente, se notó que bajo los 25 individuos la capacidad de modulación del grupo fue baja y constante, mientras que sobre los 25 individuos la modularidad fue superior (*Capítulo IV*). Estas observaciones fueron hechas con un tamaño de arena y disponibilidad de recursos constantes. Por otro lado, con respecto al efecto del tamaño del grupo sobre la personalidad, no se encontró evidencia para sugerir que este influya en la expresión de conductas sociales más allá de la relación esperable entre el grado de asociación (aproximado a partir de la centralidad de grado) y el tamaño de grupo. Se debe considerar que los resultados aquí obtenidos no estuvieron limitados por la disponibilidad de recursos por lo que cabe la posibilidad que aplicando un gradiente en dicha disponibilidad las conductas sociales pueden verse alteradas.

Cuando se evaluó la composición de los agregados de individuos, se observó que estos se encontraban principalmente conformados a partir de interacciones entre hembras no preñadas y machos, siendo las interacciones hembra no preñada- macho las predominantes, mientras que las hembras preñadas presentaron menores tasas de asociación y una menor participación en los agregados (*Capítulo IV*). La aproximación propuesta en esta tesis permitió de manera indirecta realizar una revelación práctica del sistema de apareamiento de la especie modelo, además de brindar la posibilidad de evaluar en conjunto atributos relacionales basados en comparaciones en expresión de conductas y atributos intrínsecos de los individuos.

Uno de los aspectos mas controversiales con nuestro modelo de estudio es debido a los elevados valores de cohesión grupal basado en la densidad de grupos. Durante nuestra

evaluaciones nosotros observamos que los agregados mas grandes albergan sobre el 50% de los individuos dando una sensación de saturación de redes. Por este motivo nosotros realizamos comparaciones a través de modelos nulos y pudimos evidenciar que la estructuración emergente de los grupos fue diferente a la esperada por aleatorización, por lo que podemos asumir que cada grupo se estructura en función del ensamble único de individuos. Una alternativa para conducir la saturación de redes sociales en *P. scaber* puede ser modificando los criterios utilizados para definir la asociación interindividual. En nuestro caso nosotros consideramos que dos individuos se encontraban asociados cuando su separación espacial no superaba un cuerpo (~12 mm) por al menos 15 segundos. Entonces, en futuras investigaciones se podría considerar trabajar con tipos de interacciones o contactos directos que ocasionen respuestas conductuales para aumentar la resolución de las redes y disminuir enlaces generalizados que ocasionen ruido.

Dinámica de los sistemas sociales

La evaluación de los cambios en la topología de la estructura social a través del tiempo y de diferentes configuraciones ecológicas puede esclarecer los moduladores y las funciones de la organización social (Whitehead, 2008). El conjunto de personalidades que conforman los grupos conduce los procesos que determinan su dinámica principalmente debido a que la personalidad influye en los patrones de interacción, en la percepción de estatus y en la transmisión y limitación a la información (Croft *et al.*, 2008, 2009; Fox *et al.*, 2009; Hoare & Krause, 2003).

En aspectos generales, en esta tesis se encontró que el tamaño de los agregados y el tiempo que los individuos permanecen en él influyen sobre las dinámicas de asociación, modulando

el nivel de cohesión de los agregados. En el *Capítulo IV* se evidenció que la intensidad de las asociaciones entre individuos varía de manera ondulatoria conforme estos gastan su tiempo en el grupo, independientemente del tamaño del grupo a bajas densidades. Además, se observó que la modularidad de los grupos es dependiente del tamaño del grupo (como lo vimos en la sección anterior), del tiempo que los individuos gastan perteneciendo a un agregado y de las interacciones agonísticas que perturban el ambiente social.

Con respecto al efecto de la personalidad sobre la dinámica de los grupos, en esta tesis se encontró evidencia que sugiere un efecto sostenido de la diferencia de personalidades sobre la intensidad de asociación diádica a través del tiempo. Es importante señalar que la conducta consistente que tuvo efecto fue el número de intentos de escape, una conducta evaluada en un ambiente aislado y novedoso. No se encontró que la diferencia en personalidades basada en conductas sociales ni el estatus de dominancia desempeñados en un entorno referencial tenga efecto alguno sobre la dinámica social. En consecuencia, es posible asumir que las dinámicas espaciotemporales del ambiente social basadas en interacciones diferenciales entre tipos de personalidades son predominantes sobre la organización social a largo plazo, a diferencia de los eventos de establecimiento de grupos en ambientes sociales cambiantes, donde los mecanismos son definidos por las relaciones de estatus y percepción son dominantes (*Capítulo III y IV*).

Recomendaciones y futuras direcciones

- Una de las principales recomendaciones sugeridas a partir de esta tesis tiene que ver con la definición de réplicas y el número de estas por ensayo. Como es conocido, el comportamiento de los individuos en un grupo y las propiedades emergentes del set

de individuos son raramente repetibles, debido a que los animales experimentan procesos de habituación y aprendizaje que constantemente modifican sus conductas.

Para esta tesis se tomó en consideración trabajar con tres grupos de 30 individuos por ensayo (90 individuos en total por ensayo). Esto permitió tener cierto nivel de resolución con respecto al registro de la variabilidad en la expresión de conductas por ensamble, pero la recomendación siempre estará dirigida a incluir la mayor cantidad de réplicas posibles para realizar análisis estadísticos más potentes, eficaces y fiables.

- En esta tesis, la identificación y rastreo de los individuos en un entorno social fue realizado de manera manual debido a que la capacidad de reconocimiento de los softwares de tracking libres fue limitada porque los individuos constantemente se solapaban cuando conformaban los agregados y porque la arena de evaluación fue de color negro (para evitar perturbaciones en el comportamiento de los individuos) por lo que no existía contraste entre arena e individuos. Esta situación ameritó una inversión de tiempo mayor en el registro de las interacciones entre individuos, pero fue igualmente útil. Se recomienda en futuros estudios validar los softwares y la resolución de los registros antes de realizar los ensayos.
- Se recomienda el uso de modelos de inferencia sobre los modelos de permutación clásicos de análisis de redes cuando se desea determinar la causalidad o influencia de los atributos nodales o de relación diádica sobre los atributos emergentes de las redes sociales.

- La aproximación de estudio aquí propuesta puede ser de utilidad para evaluar cualquier organismo social desde una perspectiva de redes sociales. La posibilidad de ampliar los análisis a niveles mayores de interacción está abierta, por lo que se pueden hacer estudios que van desde el nivel nodal hasta lo que la capacidad de cómputo lo permita. Aquí encontramos que los análisis a nivel de díadas brindan el suficiente soporte para evidenciar efectos relacionales a nivel de personalidad y de atributos intrínsecos.
- Se sugiere que futuras investigaciones contemplen la manipulación de la conformación de los grupos, incluyendo gradientes en la proporción de individuos y recambio por tipos de personalidad con la finalidad de complementar la información aquí generada acerca del rol de la personalidad animal. Como se ha visto a lo largo del desarrollo de la tesis, la modificación del ambiente social ayuda a evidenciar patrones en el comportamiento de los individuos mediante el establecimiento de normas de reacción. En este sentido, los experimentos de manipulación pueden ser útiles en la determinación de la importancia del rol que cumplen los tipos de personalidades en su entorno. Ser capaces de predecir los roles sociales según los tipos de personalidades puede ser de gran valor en el éxito de procesos de conservación de especies y reintroducción.

LITERATURA CITADA

- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, 518(7540), 538-541. <https://doi.org/10.1038/nature13998>
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., & Sheldon, B. C. (2012). Social networks predict patch discovery in a wild population of songbirds. *Proceedings. Biological sciences*, 279(1745), 4199-4205. <https://doi.org/10.1098/rspb.2012.1591>
- Bergmüller, R., & Taborsky, M. (2010a). Animal personality due to social niche specialisation. *Trends in Ecology and Evolution*, 25(9), 504-511. <https://doi.org/10.1016/j.tree.2010.06.012>
- Bergmüller, R., & Taborsky, M. (2010b). Animal personality due to social niche specialisation. *Trends in Ecology and Evolution*, 25(9), 504-511. <https://doi.org/10.1016/j.tree.2010.06.012>
- Broly, P., Mullier, R., Deneubourg, J. L., & Devigne, C. (2012). Aggregation in woodlice: Social interaction and density effects. *ZooKeys*, 176(SPECIAL ISSUE), 133-144. <https://doi.org/10.3897/zookeys.176.2258>
- Broly, P., Mullier, R., Devigne, C., & Deneubourg, J. L. (2016). Evidence of self-organization in a gregarious land-dwelling crustacean (Isopoda: Oniscidea). *Animal Cognition*, 19(1), 181-192. <https://doi.org/10.1007/s10071-015-0925-6>
- Croft, D. P., James, R., & Krause, J. (2008). *Exploring animal social networks*. Princeton University Press. <https://www.jstor.org/stable/j.ctt7sfqv>

Croft, D. P., Krause, J., Darden, S. K., Ramnarine, I. W., Faria, J. J., & James, R. (2009).

Behavioural trait assortment in a social network: Patterns and implications. *Behavioral Ecology and Sociobiology*, 63(10), 1495-1503. <https://doi.org/10.1007/s00265-009-0802-x>

Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005).

Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, 20(4), 187-193. <https://doi.org/10.1016/j.tree.2005.01.010>

Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters*, 7(8), 734-739. <https://doi.org/10.1111/j.1461-0248.2004.00618.x>

Dingemanse, N. J., Kazem, A. J. N., Réale, D., & Wright, J. (2010). Behavioural reaction norms: Animal personality meets individual plasticity. *Trends in Ecology and Evolution*, 25(2), 81-89. <https://doi.org/10.1016/j.tree.2009.07.013>

Fewell, J. H. (2003). Social Insect Networks. *Science*, 301(5641), 1867-1870. <https://doi.org/10.1126/science.1088945>

Fox, R. A., Ladage, L. D., Roth, T. C., & Pravosudov, V. V. (2009). Behavioural profile predicts dominance status in mountain chickadees, *Poecile gambeli*. *Animal Behaviour*, 77(6), 1441-1448. <https://doi.org/10.1016/j.anbehav.2009.02.022>

Hart, J. D. A., Weiss, M. N., Brent, L. J. N., & Franks, D. W. (2022). Common permutation methods in animal social network analysis do not control for non-independence.

Behavioral Ecology and Sociobiology, 76(11), 151. <https://doi.org/10.1007/s00265-022-03254-x>

Hendricks, J. C., Finn, S. M., Panckeri, K. A., Chavkin, J., Williams, J. A., Sehgal, A., & Pack, A. I. (2000). Rest in *Drosophila* is a sleep-like state. *Neuron*, 25(1), 129-138. [https://doi.org/10.1016/S0896-6273\(00\)80877-6](https://doi.org/10.1016/S0896-6273(00)80877-6)

Hinde, R. A. (1976). Interactions, Relationships and Social Structure. *Man*, 11(1), 1-17. <https://doi.org/10.2307/2800384>

Hoare, D. J., & Krause, J. (2003). Social organisation, shoal structure and information transfer. *Fish and Fisheries*, 4(3), 269-279. <https://doi.org/10.1046/j.1467-2979.2003.00130.x>

Kappeler, P. M., & Van Schaik, C. P. (2002). Evolution of primate social systems. *International Journal of Primatology*, 23(4), 707-740. <https://doi.org/10.1023/A:1015520830318>

Krause, J., James, R., & Croft, D. P. (2010). Personality in the context of social networks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 4099-4106. <https://doi.org/10.1098/rstb.2010.0216>

Krause, S., Wilson, A. D. M., Ramnarine, I. W., Herbert-Read, J. E., Clément, R. J. G., & Krause, J. (2016). Guppies occupy consistent positions in social networks: Mechanisms and consequences. *Behavioral Ecology*, 28(2), arw177. <https://doi.org/10.1093/beheco/arw177>

Kulahci, I. G., Ghazanfar, A. A., & Rubenstein, D. I. (2018). Consistent individual variation across interaction networks indicates social personalities in lemurs. *Animal Behaviour*, 136, 217-226. <https://doi.org/10.1016/j.anbehav.2017.11.012>

Lusseau, D., & Newman, M. E. J. (2004). Identifying the role that animals play in their social networks. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271(suppl_6), S477-81. <https://doi.org/10.1098/rsbl.2004.0225>

Montiglio, P. O., Ferrari, C., & Réale, D. (2013). Social niche specialization under constraints: Personality, social interactions and environmental heterogeneity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1618), 20120343. <https://doi.org/10.1098/rstb.2012.0343>

Pinter-Wollman, N., Hobson, E. A., Smith, J. E., Edelman, A. J., Shizuka, D., De Silva, S., Waters, J. S., Prager, S. D., Sasaki, T., Wittemyer, G., Fewell, J., & McDonald, D. B. (2014). The dynamics of animal social networks: Analytical, conceptual, and theoretical advances. *Behavioral Ecology*, 25(2), 242-255. <https://doi.org/10.1093/beheco/art047>

Réale, D., & Dingemanse, N. J. (2010). Personality and individual social specialisation. In T. Székely, A. J. Moore, & J. Komdeur (Eds.), *Social Behaviour* (pp. 417-441). Cambridge University Press. <https://doi.org/10.1017/CBO9780511781360.033>

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2), 291-318. <https://doi.org/10.1111/j.1469-185X.2007.00010.x>

Sih, A., Hanser, S. F., & McHugh, K. A. (2009). Social network theory: New insights and issues for behavioral ecologists. En *Behavioral Ecology and Sociobiology* (Vol. 63, Número 7, pp. 975-988). Springer-Verlag. <https://doi.org/10.1007/s00265-009-0725-6>

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: A meta-analysis. *Behavioral Ecology*, 19(2), 448-455. <https://doi.org/10.1093/BEHECO/ARM144>

Terborgh, J., & Janson, C. H. (1986). The Socioecology of Primate Groups. *Annual Review of Ecology and Systematics*, 17(1), 111-136. <https://doi.org/10.1146/annurev.es.17.110186.000551>

Webster, M. M., & Ward, A. J. W. (2011). Personality and social context. *Biological Reviews*, 86(4), 759-773. <https://doi.org/10.1111/j.1469-185X.2010.00169.x>

Whitehead, Hal. (2008). *Analyzing Animal Societies: Quantitative Methods For*. University of Chicago Press.

Wilson, A. D. M., Krause, S., Dingemanse, N. J., & Krause, J. (2013). Network position: A key component in the characterization of social personality types. *Behavioral Ecology and Sociobiology*, 67(1), 163-173. <https://doi.org/10.1007/s00265-012-1428-y>

Wolf, M., & Krause, J. (2014). Why personality differences matter for social functioning and social structure. *Trends in Ecology and Evolution*, 29(6), 306-308. <https://doi.org/10.1016/j.tree.2014.03.008>

Wolf, M., Van Doorn, G. S., Leimar, O., & Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, 447(7144), 581-584.
<https://doi.org/10.1038/nature05835>