

1 The importance of individual-to-society feedbacks in animal ecology and 2 evolution

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28

29 **Abstract**

30

31 1. The social decisions that individuals make – who to interact with and how frequently –
32 gives rise to social structure. The resulting social structure then determines how
33 individuals interact with their surroundings – resources and risks, pathogens and
34 predators, competitors and cooperators.

35 2. However, despite intensive research on (i) how individuals make social decisions and
36 (ii) how social structure shapes social processes (e.g. cooperation, competition and
37 conflict), there are still few studies linking these two perspectives. These perspectives
38 represent two halves of a feedback loop: individual behaviour scales up to define the
39 social environment, and this environment, in turn, feeds back by shaping the selective
40 agents that drive individual behaviour.

41 3. We first review well-established research areas that have captured both elements of this
42 feedback loop – host-pathogen dynamics and cultural transmission. We then highlight
43 areas where social structure is well studied but the two perspectives remain largely
44 disconnected. Finally, we synthesise existing research on 14 distinct research topics to
45 identify new prospects where the interplay between social structure and social processes
46 are likely to be important but remain largely unexplored.

47 4. Our review shows that the inherent links between individuals' traits, their social
48 decisions, social structure, and social evolution, warrant more consideration. By
49 mapping the existing and missing connections among many research areas, our review

50 highlights where explicitly considering social structure and the individual-to-society
51 feedbacks can reveal new dimensions to old questions in ecology and evolution.

52

53 **Keywords.** Fitness, individual differences, group-living, social evolution, social networks, social
54 structure, social transmission, coevolution, social dynamics

55

56 **1. Introduction**

57

58 Social interactions are a crucial component of animals' environments. As animals move and
59 interact with others, they generate an ever-changing social web. Within this web, each
60 individual experiences a unique social environment, and contributes to the social environment
61 of others. The characteristics of the individuals' social environment can have profound
62 implications for their reproduction and survival (e.g. Alberts 2019, and references therein). For
63 example, an individual's mating opportunities or risk of contracting a disease, depend on its
64 connections to other individuals. Explicitly accounting for the patterns of connections that form
65 individuals' social environment—how connections are formed, maintained, and their short- and
66 long-term consequences—represents a foundational shift in biological thinking in ecology and
67 evolution (Wilson 1975; Kurvers *et al.* 2014). Such thinking represents a move away from
68 models and assumptions that all individuals are connected (or connected equally) with one-
69 another. However, this accounting has traditionally been done by asking questions from one of
70 two perspectives: (i) how do individual traits influence their position in their social
71 environment?, and (ii) how does population structure shape social processes, such as
72 cooperation, competition, conflicts, and risks? Yet, these two perspectives are not independent.
73 Individual behaviour scales up to define the social structure of the population; the resulting

74 social structure, in turn, feeds back onto individuals' lives by modulating processes that can
75 shape their fitness. Thus, these two perspectives represent two halves of a feedback loop (Fig.
76 1a).

77

78 Studies over the past decades have substantially advanced our understanding of the
79 mechanisms by which social structure – the content, quality, and patterning of social
80 connections among individuals in a population (Hinde 1976) – arises, and how social structure
81 shapes social processes (Sueur *et al.* 2019). For example, (dis)assortativity around individual
82 traits and states – e.g. genetic relatedness, sex, age, dominance, promiscuity, behavioural
83 repertoire – can influence social interactions (Pike *et al.* 2008; Croft *et al.* 2009; Farine, Montiglio
84 & Spiegel 2015; McDonald *et al.* 2019); early-life conditions affect adult social decisions (Farine,
85 Spencer & Boogert 2015); and the social environment can affect collective decision-making
86 (Strandburg-Peshkin *et al.* 2017; Palacios-Romo, Castellanos & Ramos-Fernandez 2019) or
87 dispersal and recruitment (McDonald 2007; Ilany *et al.* 2013; Armansin *et al.* 2020). Sometimes,
88 who individuals are connected to, or the overall structure of populations, can also simply arise
89 from limitations in where individuals can move and, therefore, who they can encounter (e.g.
90 He, Maldonado-Chaparro & Farine 2019). There is also an increasing understanding of how
91 social structure shapes social processes. Different characteristics of social structure, such as the
92 density of connections among individuals or their tendency to form interconnected clusters, can
93 alter the breadth and diversity of behavioural repertoires (Cantor & Whitehead 2013; Aplin
94 2016), influence the resilience of a population against disturbances (Formica *et al.* 2017; Lantz &
95 Karubian 2017; Maldonado-Chaparro *et al.* 2018a), and shape social processes such as
96 competition (Sheppard *et al.* 2018) and the transmission of diseases and information (Aplin *et al.*
97 2012b; Stroeymeyt *et al.* 2018). Hence, structure and process are inherently linked.

98

99 Social structure represents a major substrate for evolutionary dynamics. It influences how
100 selection, arising from either physical or biotic interactions, operates on phenotypes, including
101 both social and non-social traits (Formica *et al.* 2011; Farine & Sheldon 2015; Sueur *et al.* 2019).
102 Social structure, in and of itself, can also determine how individuals respond to selection
103 (Montiglio, McGlothlin & Farine 2018), revealing the potential for co-evolution between the
104 structure of the social environment and social processes. Ultimately, co-evolutionary pathways
105 exist because both individuals and their social structures are coupled and dynamic systems (Box
106 1): individual social decisions underpin the social structures that, in turn, influences their
107 behaviour. Despite the broad understanding of the many factors affecting the emergence and
108 consequences of social structure, there are still few areas of research that explicitly capture the
109 feedback between individual animals and their social structures. We generally refer to the
110 factors that represent the two sides of the feedback as bottom-up and top-down effects, as they
111 correspond to individuals' actions shaping social structure (bottom-up) and to processes that
112 affect the environment that individuals experience (top-down).

113

114 Here, we highlight current efforts and recent opportunities for studying the individual-to-
115 society feedback. We first review two well-established topics that have captured the feedback
116 between individual behaviour and population-level processes: host-pathogen dynamics and
117 cultural transmission (Fig. 1b). We then highlight how multiple mechanisms and population
118 processes that have typically been explored separately could couple to form largely unexplored
119 feedbacks. Finally, we synthesise the literature on social structure from the past decade to
120 identify new prospects – research topics where evidence suggests that feedbacks between
121 individuals and social structures are important, but where social structure has not been strongly

122 considered. This synthesis provides a roadmap for strengthening existing, and arising, links
123 between currently disparate research topics (Fig. 2, Box 1), which we believe will help to
124 uncover new perspectives in the study of social evolutionary ecology.

125

126 **2. From individuals to societies and back: two established feedback loops**

127

128 Two well-studied dynamics in animal societies are the spread of infectious diseases and
129 resulting host-pathogen evolution, and the spread of information and resulting cultural
130 evolution. In both these examples, individual state (e.g. infected or not, informed or not) and
131 processes (disease and information transmission) that operate through social structure are
132 dynamic and tightly coupled (Fig. 1b), changing each other over time.

133

134 **2.1. *Infectious disease and parasite transmission***

135

136 Social structure can fundamentally determine the pathways and consequences of pathogen
137 transmission (Silk *et al.* 2019). Evidence for this comes from studies showing that the basic
138 reproductive number (R_0), which is defined as the mean number of secondary infections in a
139 susceptible population resulting from contact with a single infected individual during its
140 infectious period (Macdonald 1952), typically misestimates the resulting rate of pathogen
141 spread in structured populations (Keeling 1999). Thus, the patterns of contacts among
142 individuals can generate differences in the propagation rate among populations, even with the
143 same pathogen. For example, propagation is locally higher but globally lower when
144 individuals' contacts are more clustered (Keeling 2005). The effects of social structure on disease
145 propagation are evident when looking at how disease dynamics differ across taxa with varying

146 social systems. Species where individuals have strongly-differentiated relationships are more
147 susceptible to long-lasting outbreaks of low-transmissibility infections (Sah, Mann & Bansal
148 2018). Social connections can also provide a stronger medium for the transmission of some
149 pathogens than alternative routes. For example, among giraffes (*Giraffa camelopardalis*),
150 pathogen transmission is more likely to occur among socially-connected than spatially-
151 connected individuals sharing a water-hole (VanderWaal *et al.* 2014). For endo- and ecto-
152 parasites, the transmission process may not be restricted to direct contacts, but can also occur
153 through indirect connections, such as shared space use (Silk *et al.* 2019). For example, the
154 transmission of gastrointestinal helminths among Eastern chipmunks (*Tamias striatus*) can be
155 temporally decoupled, by one or two weeks, from social contacts due to the life-cycle of the
156 parasite (Gear, Luong & Hudson 2013). Together, these studies demonstrate that the pattern of
157 the social structure and the nature of the pathogen or parasite interact to determine the
158 transmission pathways and dynamics of disease spread. More recently, a similar feedback has
159 been proposed regarding the dispersal of mutualistic and commensal microorganisms through
160 social contact – while the microbial transmission can be modulated by the hosts’ social
161 environment, the hosts’ physiology can in turn modulate the microbiota of that social
162 environment (see Sarkar *et al.* 2020).

163
164 Social structure can shape the pathways of pathogen transmission and thus, can act as an agent
165 of selection on the traits such as virulence and infectiousness, in both hosts and pathogens. Host
166 resistance and pathogen virulence are textbook examples of co-evolutionary forces –
167 increasingly virulent pathogens select for more resistant hosts. However, sociality presents an
168 alternative medium through which host organisms can respond to pathogen virulence. Changes
169 in host behaviour, such as to avoid pathogens (e.g. Prado *et al.* 2009), can drive selection on

170 pathogen traits. For example, by reducing the ability for pathogens to spread, clustering of
171 social interactions can select for lower pathogen infectivity (Boots & Meador 2007), lower
172 pathogen virulence (Best *et al.* 2011), and longer infection periods (Best *et al.* 2011). In turn, the
173 impact of increased clustering of social interactions on pathogen traits can then drive the
174 evolution of higher host resistance (Best *et al.* 2011); (Kiesecker *et al.* 1999; Behringer, Butler &
175 Shields 2006; Boillat *et al.* 2015). These examples highlight how the patterns of connections that
176 form social structure (e.g. clustered vs. unclustered), and not just the intensity of social
177 behaviours (e.g. the number of connections), can directly shape key parameters of infectious
178 diseases transmission dynamics.

179
180 Evolutionary changes in host or pathogen states could feed back onto social structure. Theory
181 suggests that the relationship between pathogen prevalence, virulence, and host sociality is
182 complex and, sometimes, counter-intuitive (Prado *et al.* 2009). In general, increasing pathogen
183 prevalence can drive decreases, either evolutionary or behavioural (e.g. Prado *et al.* 2009;
184 Stroeymeyt *et al.* 2018) in host-host contact rates, as individuals could be selected to avoid sick
185 conspecifics (Kiesecker *et al.* 1999; Behringer, Butler & Shields 2006; Boillat *et al.* 2015) and sick
186 individuals may even altruistically avoid kin (Heinze & Walter 2010; Bos *et al.* 2012; Stroeymeyt
187 *et al.* 2018). However, a pathogen that is sufficiently contagious as to be unavoidable can drive
188 an increase in host-host contact rates (Bonds *et al.* 2005), because the benefits of avoiding social
189 contacts are lost while the benefits of maintaining contacts are maintained. Such co-
190 evolutionary dynamics between host and pathogen parameters are potentially cyclical (Prado *et*
191 *al.* 2009). High host sociality facilitates rapid transmission of pathogens and evolution of higher
192 virulence, which, in turn, may drive a reduction in host sociality. As hosts evolve to have fewer
193 contacts, selection on pathogens can favour reduced virulence (if hosts die before the pathogens

194 can transmit). As virulence drops, host sociality increases, and the cycle continues. These
195 examples highlight some of the ways in which the social structure of the population is
196 important for cycling dynamics, and is also itself potentially dynamic.

197

198 From the perspective of studying animal social behaviour, one hypothesis for the evolution of
199 social structure suggests that host-pathogen dynamics have driven the choice of social contacts
200 (Freeland 1976). Specifically, can pathogens change the dynamics of social interactions within a
201 group by selecting for social connections based on specific health traits of potential associates,
202 thus leading to a clustered structure driven by the host-pathogen dynamics? If pathogens
203 manipulate host behaviour to their benefit (Poulin 2018), or hosts respond to pathogens, such as
204 by reducing social contacts when infected (Lopes, Block & Konig 2016), then host-parasite
205 interactions could impact social structure dynamically. Black ants (*Lasius niger*), for example, if
206 challenged with a pathogenic fungus, individual-level changes in the patterns of social contacts
207 increase transmission-inhibiting structural properties at the colony-level (Adelman *et al.* 2015).
208 However, individuals are not homogeneous; they can also vary in their infectiousness, in their
209 contact rates, and in their infectious period (VanderWaal, Ezenwa & Hawley 2016). Thus, we
210 could ask whether and how heterogeneity among individuals, or in their social relationships,
211 affect co-evolutionary dynamics between hosts and pathogens. For example, common vampire
212 bats (*Desmodus rotundus*) expressing sickness behaviour reduce their social interactions (such as
213 allogrooming with non-kin), but these reductions are smaller for social interactions that
214 generate greater benefits (such as food sharing with close kin) (Stockmaier *et al.* 2020). Some
215 individuals contribute disproportionately to propagations of pathogens, such as when 20% of
216 individuals contribute 80% of the transmission events (Lloyd-Smith *et al.* 2005; Adelman *et al.*
217 2015). If infectiousness and contact rates can be modulated through social behaviour, which can

218 be either host-driven (e.g. to avoid infection) or pathogen-driven (e.g. manipulating host
219 behaviour), and infectiousness and contact rates co-vary, then both the social structure and
220 disease parameters (e.g. virulence) should be dynamic in a given population.

221

222 2.2. *Information and cultural transmission*

223

224 Although fundamentally different, information and pathogens can sometimes spread through
225 populations in similar ways. Animals often use information from their social contacts when
226 making decisions about foraging, habitat choice, and predator avoidance (e.g. Doligez, Danchin
227 & Clobert 2002; Gil *et al.* 2018). However, since individuals rarely have access to all other
228 individuals in their population, social structure constrains where and when information can
229 spread (e.g. Aplin *et al.* 2012a), similar to social constraints on pathogen spread. Information
230 transmission can also fundamentally differ from pathogen spread. For instance, transmission
231 does not always follow a one-contact to one-spread rule ('simple contagion'), but can require
232 more than one contact and social reinforcement via multiple interaction partners ('complex
233 contagion') (Centola *et al.* 2007; Firth 2020). Complex contagion processes fundamentally alter
234 the properties of transmission through populations, especially in those where social interactions
235 are concentrated around a few individuals, or when individuals are somewhat segregated into
236 distinct social clusters (Centola *et al.* 2007). In simple contagion processes, clusters of highly
237 interconnected individuals impair transmission, but during complex contagion, clustering of
238 individuals can instead facilitate transmission, as found in startle responses in schools of golden
239 shiners (*Notemigonus crysoleucas*) (Rosenthal *et al.* 2015).

240

241 One property of information transmission, making it distinct from disease transmission, is that
242 individuals can make decisions about producing or using information. Such decisions can alter
243 transmission pathways and outcomes. For example, songbirds consider their social
244 environment when producing vocal information to recruit new members to a foraging site
245 (Suzuki & Kutsukake 2017; Hilleman *et al.* 2019) and chimpanzees (*Pan troglodytes*) adjust food-
246 associated vocalisations depending on the strength of the social bond they have with the
247 intended receiver (Slocombe *et al.* 2010). When individuals are faced with multiple sources of
248 information, how they decide what to learn or who to learn from can also impact the
249 information landscape (Kendal *et al.* 2018). Individuals may have different social learning
250 strategies and preferentially copy individuals that are more dominant, successful, or older
251 (Laland 2004; Kendal *et al.* 2015), thus shaping what information persists in a population. If
252 individuals bias their learning towards a more common behaviour, then one variant can
253 become entrenched in a population (Aplin 2016). For example, conformist transmission among
254 great tits (*Parus major*) can lead to stable socially-learned foraging behaviours that are
255 maintained across multiple generations (Aplin *et al.* 2015). However, the propensity for local
256 traditions to become established and be maintained can also largely be determined by the global
257 structure of the population, even when learning is conformist (Somveille *et al.* 2018). More
258 clustered and modular social structures can promote local traditions. For example, orcas
259 (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) live in multilevel societies with stable
260 social groups and show group-specific repertoires of acoustic, foraging and social behaviours
261 that are maintained over generations (Whitehead & Rendell 2014). Thus, the structure of
262 populations as well as learning rules will determine what information is available to transmit
263 and where it spreads, shaping the information landscape that individuals have available to
264 them in their social environment.

265
266 When behaviours are socially-learned, shared within subgroups of the population, and persist
267 over time, they are recognized as culture (Laland & Hoppitt 2003). Considering how learned
268 behaviours can affect individual social decisions reveals the potential for culture to underpin
269 the co-evolution between social structure and behaviour. For example, information state can
270 determine the propensity for two individuals to associate, through a process called behavioural
271 homophily (Centola *et al.* 2007; Cantor & Whitehead 2013). Information state can also determine
272 the maintenance of social bonds – having similar social traits can facilitate cohesion among
273 individuals by allowing them to synchronise and coordinate their activities (Coussi-Korbel &
274 Fragaszy 1995). For example, populations of bottlenose dolphins are often divided into social
275 communities assorted by learnt foraging tactics (Mann *et al.* 2012; Machado *et al.* 2019; Wild *et al.*
276 2019), illustrating the idea that the more individuals interact, the more opportunities they have
277 for copying each other, thus highlighting how social decisions can reinforce behavioural
278 homogeneity. Models have shown that the feedback between information transmission and social
279 decision-making can stimulate the formation of stable groups within otherwise unstructured,
280 well-mixed, populations with (Cantor *et al.* 2015) and without any complex decision-making
281 (Cantor & Farine 2018). Information state can also impact individual position within their social
282 environment. More knowledgeable individual lemurs (*Lemur catta*) become more connected in
283 their social environment (Kulahci, Ghazanfar & Rubenstein 2018); becoming more connected
284 can then promote information transmission (Kulahci & Quinn 2019). Thus, there is extensive
285 empirical and theoretical evidence for the feedback between information use and social
286 structure.
287

288 Beyond determining which individuals acquire information, social structure can also play a role
289 in shaping the quality and quantity of information, akin to pathogen virulence. Learning of new
290 behaviours can be error-prone, thus social structures that result in longer transmission
291 pathways (e.g. where information must take more steps to reach every individual in a
292 population) should not only slow information transmission but also mean that individuals may
293 acquire different, or lower quality information (reviewed in Cantor & Whitehead 2013). The
294 propensity for learning errors to accumulate in longer transmission chains can subsequently
295 promote diversity of information in populations (Whitehead & Lusseau 2012), with obvious
296 consequences on variation in behavioural repertoires within populations arising from the
297 correlation between connectedness in the social network and individual information state.

298

299 **3. Multiple bottom-up and top-down influences in individual-to-society** 300 **feedbacks**

301

302 There are a multitude of social drivers and population processes that, unlike the topics above,
303 are rarely considered in unison. We first synthesise how the state of individuals – including the
304 conditions experienced in early-life, average genetic relatedness to conspecifics, and social
305 dominance – can influence their social decisions and through these the emergent structure of
306 their societies. Next, we synthesise how the emergent social structure influences processes such
307 as population dynamics, social stability, and social selection, can translate to fitness outcomes
308 and drive evolutionary dynamics.

309

310 **3.1. *Bottom-up: individual states influencing social structure***

311

312 Social traits can be determined at young age. Early-life conditions can modulate later-life social
313 behaviour, shaping the population-level social patterns along the way. For instance, zebra finch
314 nestlings exposed to stress develop more gregarious social phenotypes, maintaining a greater
315 number of social partners but choosing partners more randomly (Boogert, Farine & Spencer
316 2014; Brandl *et al.* 2019a). The proximate mechanisms that underpin inter-individual differences
317 in the development of social behaviour are also becoming clearer. Early-life stress can influence
318 the expression and receptor-binding of the neuropeptides oxytocin and vasopressin (Veenema
319 2012), which are important for the expression of social behaviours. Zebra finches with
320 experimentally reduced vasotocin production are less gregarious (Kelly *et al.* 2011) and more
321 aggressive (Kelly & Goodson 2014). These changes in phenotype can alter the individual's social
322 environment with consequences on their later fitness.

323

324 A pillar of the social environment is the formation of preferred associations. Such social
325 preferences are evident from partner investments that require time and energy (e.g.
326 allogrooming) and consistent associations that cannot be explained by spatial ranging alone
327 (e.g. mutual attraction to resources). For example, chimpanzees associate preferentially with
328 individuals that reciprocate grooming (Mitani 2006), vampire bats that groomed and shared
329 food in captivity stay together when released back to the wild (Ripperger *et al.* 2019), and zebra
330 finches that bred synchronously in the same colony also foraged together outside of the
331 breeding period (Brandl *et al.* 2019b). It remains unclear to what extent such preferred
332 associations depend on prior experiences *versus* phenotypic traits. Individuals can have
333 preferences for conspecifics with traits that either match or differ from their own. Such
334 phenotypic assortment (Farine 2014) is a key driver of population-level social patterns (e.g.
335 Croft *et al.* 2009; Apicella *et al.* 2012; Carter *et al.* 2015) and central to social evolution (Centola *et*

336 *al.* 2007; McDonald *et al.* 2017). In some cases, associations themselves can drive phenotypic
337 similarity as in vocal convergence in the contact calls of unrelated female greater spear-nosed
338 bats (*Phyllostomus hastatus*) that form a group (Boughman 1998). However, the mechanisms by
339 which new preferred associations form, are maintained, and develop into higher-value social
340 relationships, is an important area for future research (Carter *et al.* 2020).

341

342 Kinship is perhaps the most well-known driver of social preferences. Kin-biased associations
343 can result from either prior association or phenotype matching, which allows identification of
344 unfamiliar kin (e.g. Holmes & Sherman 1982; Halpin 1991; Sharp *et al.* 2005). Although kin-
345 biased associations provide opportunities for increasing inclusive fitness through nepotism, the
346 benefits can be partially or completely negated by increases in the potential for inbreeding and
347 kin competition (Keller 2002; West, Pen & Griffin 2002). The costs of inbreeding and kin
348 competition vary with differences in dispersal and the spatial scale of competition. Therefore,
349 some species, such as Australian sleepy lizards (*Tiliqua rugosa*), show kin avoidance (Godfrey *et*
350 *al.* 2014), while others, such as sperm whales (*Physeter macrocephalus*), preferentially associate
351 with kin (Konrad *et al.* 2018). Kin-biased assortment or dispersal (e.g. budding dispersal)
352 (Gardner & West 2006) influences genetic structure and the potential for kin selection, with
353 major consequences for the evolution and maintenance of cooperative behaviours (Hatchwell
354 2009; Green & Hatchwell 2018).

355

356 The structure of social relationships can also be moulded by many other factors, including
357 agonistic interactions, phenotypic composition, and competition for resources. Rank within the
358 dominance hierarchy can be determined by individual traits (Drews 1993), such as size, age or
359 sex, or by social state, such as winner-loser effects (Chase *et al.* 2002) and social alliances (Strauss

360 & Holekamp 2019). Aggression can lead to dominance-related spatial structure, where group
361 members position themselves closer or farther from each other depending on difference in rank
362 (Hemelrijk 2000). Agonistic interactions with other groups can also shape within-group social
363 structure. For example, the structure of lekking wire-tailed manakin (*Pipra filicauda*) populations
364 was less stable when more high-testosterone individuals were present (Dakin *et al.* in press).
365 When individuals compete for resources, the distribution and abundance of resources can
366 impact individuals' decisions to form groups and whether to associated with preferred
367 associates versus less preferred associates. For example, African lions (*Panthera leo*) associate
368 more equally within a pride when prey are larger and aggregated, but associate more
369 exclusively when prey are smaller or dispersed (Mbizah *et al.* in press).

370

371 3.2. *Top-down: social structures influencing individual states*

372

373 Social structure can influence social and larger-scale demographic and ecological processes,
374 such as social stability (the pattern of recurrent relationships among group members), resilience
375 (how a group responds and adjusts to external disturbances), and population dynamics, and
376 these can shape the state of individuals and drive selection. Demographic processes (birth,
377 death, emigration, immigration) can impact social stability (e.g. Beisner *et al.* 2011; Maldonado-
378 Chaparro *et al.* 2018a; Shizuka & Johnson 2020), and determine the ability for individuals to
379 express certain traits. For example, temporary splits in captive zebra finch colony membership
380 disrupted the social relationships among colony members; in turn, these changes in social
381 structure negatively affected foraging behaviour (Maldonado-Chaparro *et al.* 2018a). The same
382 structural properties of disturbed social networks in the zebra finches were also found to be
383 present in communities of Masai giraffes (*Giraffa camelopardalis tippelskirchi*) that overlapped

384 with human settlements (Bond *et al.* in press). Even the loss of a single key individual can
385 destabilize social structure (Flack *et al.* 2006) and alter patterns of mating or parental care (Silk
386 2007; Alberts 2019). Thus, there is extensive scope for demographic processes and social
387 instability to shape individual-level states.

388

389 Social structure can affect broader population dynamics by influencing individual survival
390 (Singleton & Hay 1983; Cameron, Setsaas & Linklater 2009) and life history traits, such as
391 reproductive investment (Singleton & Hay 1983; Cameron, Setsaas & Linklater 2009). In alpine
392 marmots (*Marmota marmota*), the number of helpers in the hibernaculum is positively correlated
393 with over-winter survival (Grimm *et al.* 2003), and changes in the group size of meerkats
394 (*Suricata suricatta*) determines the dynamics of female dispersal and birth rates (Bateman *et al.*
395 2013). A measure of direct and indirect early-life social connectivity (eigenvector centrality) also
396 predicts adult survival in male bottlenose dolphins (*Tursiops* sp.) (Stanton & Mann 2012).
397 Considering sociality beyond group size, composition, and density of social connections raises
398 new questions such as: Do individuals contribute differently to population growth based on
399 how well connected they are? Can phenotypic assortment shift the operational sex-ratio and
400 thus the reproductive output of a population? Which mechanisms give rise to variation in social
401 traits and how consistent are these traits over the course of an individual's lifetime? Identifying
402 the social trait that best influence demographic processes is, in itself, an interesting question
403 (Pelletier *et al.* 2007).

404

405 Social structure can influence how sexual and social selection are operationalised (McDonald *et*
406 *al.* 2017; McDonald & Pizzari 2018b) and thus shape evolutionary processes by creating
407 variation among individuals in their relative fit to their environment. For instance, male house

408 finches (*Carpodacus mexicanus*) with less elaborate plumage can increase their relative
409 attractiveness by moving more often between groups (Oh & Badyaev 2010). Dispersing great
410 tits (*Parus major*) that arrive late to the breeding grounds are less likely to acquire a territory,
411 unless they associate with other late arriving individuals (Farine & Sheldon 2015). Early-life
412 connectivity can also dictate the acquisition of sexual traits that are expressed as adults. For
413 example, juvenile male zebra finches acquire the song of their most strongly-associated adult
414 male (i.e. the song that juvenile males learn) (Boogert *et al.* 2018). Being more socially connected
415 as a juvenile predicts social rise to reproductive positions in long-tailed manakin males
416 (*Chiroxiphia linearis*) (McDonald 2007) and increase longevity and reproductive success later in
417 life in spotted hyenas (*Crocuta crocuta*) (Turner *et al.* in press). Thus, social structure across
418 different time scales can impact the acquisition and value of individual traits, and social
419 behaviour provides the scope for individuals to develop strategies that increase their chances of
420 reproduction if they are physically outcompeted. Studies of social networks in hybrid
421 populations provide opportunities to better understand the direct feedbacks between individual
422 social traits, fitness outcomes, and population-level consequences. For example, Zonana *et al.*
423 (2019) found strong links between social associations and mating outcomes in a hybrid
424 population of California (*Callipepla californica*) and Gambel's (*Callipepla gambelii*) quail, even in
425 the absence of structure in terms of genetic ancestry, suggesting an important role of social
426 relationships in maintaining genetic structure in the population.

427

428 Explicitly quantifying individual-to-society feedbacks can reveal the relative importance of
429 different levels of selection (Fisher & McAdam 2017), and their ecological or mechanistic bases
430 (Pruitt *et al.* 2018). For example, if the consequences of social interactions are mediated by a
431 genetic component in the individuals, the social interactions can provide an additional source of

432 heritable genetic variance (Agrawal, Brodie & Wade 2001). In such cases, population structure
433 can generate emergent variation in the social environment that each individual experiences,
434 which is correlated among connected individuals (i.e. assortment), thus generating ‘between-
435 group’ differences on which selection can act (Montiglio, McGlothlin & Farine 2018). Social
436 phenotypes that are selected for via social or sexual selection can therefore feed back onto the
437 social structure via distinct pathways. Many potential pathways exist, providing promising
438 avenues for future research on individual-to-society feedbacks.

439

440 **4. Future prospects for studying individual-to-society feedbacks**

441

442 The importance of the links between individuals’ traits, their social decisions, social structure,
443 and social evolution are likely to be much more prevalent than currently considered. The
444 concepts of bottom-up and top-down social influences are newly emerging across several
445 research fields, revealing rich opportunities for new research questions (Sueur *et al.* 2019;
446 Shizuka & Johnson 2020). Here we synthesise key research topics where individual-to-society
447 feedbacks are important yet remain underexplored.

448

449 **4.1. *Social inheritance***

450

451 Theory suggests that social structure can emerge and be maintained across generations by a
452 simple mechanism of offspring having a higher probability of establishing relationships with
453 their parents’ associates (Ilany & Akcay 2016b; Ilany & Akcay 2016a). This mechanism can help
454 explain social clustering and heterogeneity of social interactions across a range of taxa. The

455 process by which offspring inherit social traits from their parents via the social environment is
456 called social inheritance (Ilany & Akcay 2016b).

457

458 Social inheritance can underpin the transgenerational transmission of social roles and other
459 behaviours (Ilany & Akcay 2016b; Cantor & Farine 2018). For example, African elephants
460 (*Loxodonta africana*) live in multi-level (i.e. structured in hierarchically nested social levels of
461 organization), matrifocal (i.e. structured around a female), societies where the relationships
462 between the maturing young and the matriarch provide calves with opportunities to replicate
463 the matriarch's social environment (Goldenberg, Douglas-Hamilton & Wittemyer 2016).

464 Similarly, in spotted hyenas, the amount of social support, rather than intrinsic attributes (e.g.
465 physical strength and aggressiveness), explains the outcome of one-on-one interactions in the
466 process of establishing dominance, and thus offspring social rank (Strauss & Holekamp 2019;
467 Vulllioud *et al.* 2019). In theory, social inheritance can also facilitate phenotypic assortativity by
468 causing individuals to be more connected with kin or otherwise similar groupmates. For
469 example, populations can become assorted by personality if both personality and social contacts
470 are heritable (Ilany & Akcay 2016a). Despite its explanatory power, social inheritance, and other
471 mechanisms such as genetic inheritance of behavioural traits, remains an underexplored
472 bottom-up driver of real animal societies and the evolution of other social interactions, such as
473 dominance interactions (but see Strauss, Shizuka & Holekamp 2019). Further, little is known
474 about the top-down consequences of inheriting social contacts in other aspects of an individual
475 animal's life, such as survival and lifetime reproductive success.

476

477 4.2. *Predator-prey dynamics*

478

479 Predation risk plays a major role in group living, and there is increasing evidence that it shapes
480 social structure. Individual predation events cause flocks of great tits (*Parus major*) to rapidly
481 reconfigure (Voelkl, Firth & Sheldon 2016), while long-term predation pressure promotes more
482 stable schools in Trinidadian guppies (*Poecilia reticulata*) (Heathcote *et al.* 2017) and drives more
483 complex social interactions in cooperatively-breeding cichlids (*Neolamprologus pulcher*)
484 (Groenewoud *et al.* 2016). There is also a growing body of work showing how social interactions
485 between predators can drive the evolution of prey traits. Studies of great tits as predators
486 illustrate how social interactions – specifically social learning – can reinforce the evolution of
487 prey defences, such as aposematic warning signals (Landova *et al.* 2017; Thorogood, Kokko &
488 Mappes 2018).

489

490 However, how the social structure of predators can feed back on the prey's, and vice-versa, has
491 yet to be explored in detail. If social relationships in either predator or prey populations exhibit
492 phenotypic structure (e.g. assortment by predator or anti-predator traits), then this could alter
493 the 'landscape of fear' by generating non-random social or spatial structure in susceptibility to
494 predation (Gotanda *et al.* 2019). In turn, social structure could shape the strength and direction
495 of selection for different individuals (Pruitt *et al.* 2017). For example, if predators overlap with
496 multiple prey groups, then the traits of one prey group can affect the predator's behaviour (e.g.
497 whether it becomes satiated or not), which can, correspondingly, create an indirect effect on the
498 predation pressure that another prey group experiences (e.g. whether it is attacked or not)
499 (Montiglio *et al.* 2018). The interplay of social structures within and across trophic levels, and
500 across meta-populations, remains a rich area for future research, with co-evolutionary dynamics
501 arising from social structure potentially taking place between predators and prey, and within
502 both predator and prey communities.

503

504 4.3. *Collective decision-making*

505

506 Theory suggests that animals moving together cant maintain cohesion and coordinate
507 behaviours by following simple rules such as attraction, repulsion and alignment to other group
508 members (Couzin *et al.* 2002). In species that maintain preferred relationships, individual social
509 preferences can determine closest neighbours (Farine *et al.* 2017), and thus the composition of a
510 unit of interacting individuals. Simulations suggest that preferred associations can generate
511 sub-group formation, and cause more socially-connected individuals to be closest to the group
512 centre (Bode, Wood & Franks 2011). In this way, emergent group-level behaviours can directly
513 affect fitness by driving local variation in how individuals experience their environment, such
514 as their relative predation risk.

515

516 Not only can individuals' social preferences in collective movement influence social structure,
517 but the structure itself can also impact collective movement and decision-making. Social
518 relationships can determine the relative influence of each individual on their group
519 (Strandburg-Peshkin *et al.* 2018). For example, individual chacma baboons (King *et al.* 2011) and
520 Geoffroy's spider monkeys (*Ateles geoffroyi*) (Palacios-Romo, Castellanos & Ramos-Fernandez
521 2019) are more likely to be followed by close associates when initiating movement. If
522 followership is explained by relatedness or affiliations to others, then individuals that are more
523 socially connected can be more influential by being more effective at recruiting a majority
524 (Strandburg-Peshkin *et al.* 2015). Collective actions, such as joint territory defence, can also feed
525 back onto affiliative behaviours and fitness. For example, green woodhoopoes (*Phoeniculus*
526 *purpureus*) increase allopreening rates (increasing the connectivity among group members) after

527 coordinating their behaviours during inter-group conflicts (Radford 2008), whereas groups of
528 banded mongoose (*Mungos mungo*) express lower within-group agonistic interactions after
529 simulated intergroup conflicts (thereby reducing social connectivity within the group) (Preston
530 *et al.* in press). A ripe direction for future research is to integrate the study of how social
531 structure shapes the properties of animal collectives with the feedback that collective decision-
532 making has on individual interaction rules and social structure.

533

534 **4.4. Dispersal behaviour**

535

536 Dispersal to, and subsequent reproduction in, newly-settled environments is the primary driver
537 of gene flow and connectivity across populations (Bowler & Benton 2005). The outcomes of
538 individual dispersal decisions can also generate social structure. In most species, the young of
539 one sex disperse sufficiently far to reduce the chances of encountering related individuals
540 (Clobert 2012). If there is limited dispersal (Hamilton 1964a), budding dispersal (Gardner &
541 West 2006), or any pattern where dispersing individuals are more likely to encounter kin
542 (Leedale *et al.* 2018), then kin-structured populations can emerge, which can be important for
543 the evolution of cooperative breeding (Hatchwell 2009; Green & Hatchwell 2018).

544

545 Dispersal decisions fundamentally drive social structure, which has reciprocal consequences for
546 individual dispersal decisions. Local density increases competition for resources, which can
547 determine when individuals disperse and where they go (Maag *et al.* 2018). Aggressive
548 (Christian 1970) and affiliative (Bekoff 1977) interactions can also underpin decisions to disperse
549 or not. In yellow-bellied marmots (*Marmota flaviventris*), females that are more socially-
550 embedded in their natal group are less likely to disperse (Blumstein, Wey & Tang 2009). Social

551 interactions can also influence patterns of settlement. In songbirds, associations during the
552 winter predict breeding and territorial proximity in the following spring (Firth & Sheldon 2016).
553 In group-living birds (Williams & Rabenold 2005) and primates (Cheney & Seyfarth 1983),
554 individuals often disperse between neighbouring groups, highlighting a link between global
555 social structure and dispersal decisions. Finally, social structure can determine how difficult
556 new social environments are for dispersers to penetrate (Armansin *et al.* 2020). In rock hyraxes
557 (*Procapra capensis*), some groups are more resistant to immigrants if the addition of a group
558 member disrupts otherwise stable social associations (Ilany *et al.* 2013).

559
560 Studies of the transience stage of dispersal may provide opportunities to explore the feedback
561 between animals' dispersal decisions and social structure. Transience represents a key point
562 where individual decisions directly translate to social structure. During transience, dispersing
563 coalitions of Kalahari meerkats (*Suricata suricatta*) avoid territories of unrelated groups (Cozzi *et*
564 *al.* 2018) and disperse shorter distances when cohorts are larger and contain more males (Maag
565 *et al.* 2018). Despite being a critical stage in the interplay between top-down and bottom-up
566 processes, transience behaviours remain understudied, especially in social species (Mabry *et al.*
567 2015). A promising avenue for future work is quantifying the role of population-level social
568 structure (i.e. the social landscape) in shaping the movement and prospecting behaviours of
569 dispersers (e.g. Armansin *et al.* 2020) which can, in turn, alter patch-level social structure
570 through settlement.

571

572 4.5. Cooperative behaviour

573

574 Cooperation involves providing benefits to social partners. How cooperation evolves and is
575 maintained in animal populations has sparked debate on the relative merits of competing
576 theoretical frameworks: inclusive fitness, multilevel selection, reciprocity, and biological
577 markets (West, Griffin & Gardner 2007; Carter 2014). Although these theories differ, they all
578 imply that the evolutionary stability of costly cooperation requires some form of spatial,
579 phenotypic, or behavioural assortment (Hamilton 1964b) where individuals with a greater
580 tendency to cooperate preferentially interact with each other to avoid the costs of defection by
581 non-cooperators (Fletcher & Doebeli 2009; Apicella *et al.* 2012; Marcoux & Lusseau 2013).

582

583 Considering social structure is therefore essential for an ecologically realistic understanding of
584 the evolution and maintenance of social cooperation. Cooperation can be favoured by repeated
585 interactions (Axelrod & Hamilton 1981), caused by strong pairwise social ties (Allen *et al.* 2017),
586 but disfavoured in populations with a high density of social connections as these are more
587 easily invaded by non-cooperators (Ohtsuki *et al.* 2006). In addition, higher levels of cooperation
588 can be maintained when individuals choose their associates – as cooperators prune their social
589 ties with defectors – thereby affecting social structure by creating clusters of highly cooperative
590 individuals (Fehl, van der Post & Semmann 2011). This process can occur through kin selection,
591 but costly nonkin cooperation can also be maintained via conditional partner choice and partner
592 control. By monitoring their experiences with others, individuals can choose more cooperative
593 partners, reward cooperative behaviour, and punish defection (Agren, Davies & Foster 2019).
594 For example, flycatcher pairs preferentially mobbed with neighbouring pairs that helped them
595 mob previously (Krams *et al.* 2007; Krama *et al.* 2012), vervet monkeys received more grooming
596 after their ability to provide food was experimentally elevated (Fruteau *et al.* 2009), and dwarf

597 mongoose received more grooming after their perceived contributions to cooperative sentinel
598 behaviour were experimentally elevated by playbacks (Kern & Radford 2018).
599
600 Some experimental evidence suggests that individuals that experience cooperation with one set
601 of partners are more likely to cooperate with a different set of partners (generalized reciprocity)
602 (e.g. Rutte & Taborsky 2007; Barta *et al.* 2011). In other words, when deciding to cooperate,
603 individuals might not only monitor the cooperativeness of specific individuals but also their
604 overall social environment. This possibility opens interesting new questions about individual-
605 to-society feedbacks. While experiments suggest that the regularity of social interactions can
606 promote cooperation in humans (Rand, Arbesman & Christakis 2011), would the social stability
607 or quality of social relationships influence the cooperation strategies of individuals within non-
608 human societies? For example, does a more stable social environment reward vampire bats with
609 fewer stronger relationships, while unstable social environments favour bats with more but
610 weaker social ties (Carter, Farine & Wilkinson 2017)? If an individual grows up in a more
611 cooperative society, does that experience make it more likely to cooperate with new individuals
612 in a different society?

613

614 4.6. *Mating systems*

615

616 Mating systems are influenced by two main factors, the spatiotemporal distribution of males
617 and females, and the extent to which each sex invests in parental care (Emlen & Oring 1977).
618 However, mating systems are also impacted by social structure since males and females do not
619 interact homogeneously, either within or between sexes. Heterogeneity in social interactions can
620 result from intrinsic (e.g. homophily) or extrinsic (e.g. predation risk, habitat structure) factors,

621 and can influence the spatial and temporal distribution of individuals, thus leading to
622 individual variation in competitive environments and mate availabilities (McDonald *et al.* 2013;
623 Maldonado-Chaparro *et al.* 2018b). Local differences in density and operational sex ratio
624 (Kasumovic *et al.* 2008) or in the phenotypic composition of the social environment (Farine,
625 Montiglio & Spiegel 2015) can generate fine-scale differences in the strength and direction of
626 sexual selection on individual morphological or behavioural traits.

627
628 Individuals can also express differences in mating strategies (e.g. in promiscuity) and can
629 respond to experienced selection pressures. For instance, males that mate with many females
630 might also mate with the most polyandrous females (McDonald & Pizzari 2018a), or males
631 might decide to leave a highly competitive area, which can feed back to social and mating
632 structure (Watters & Sih 2005). For instance, in water striders the presence of aggressive
633 individuals drives other individuals to leave the area shaping new local group compositions
634 (Eldakar *et al.* 2009). In such a case a male's reproductive success will not only depend on his
635 direct competitors, but also on females' connections to their potential mates. Thus, males who
636 have the greatest copulation success also suffer from the highest intensity of sperm competition,
637 thus generating post-copulatory sexual selection (Fisher, Rodriguez-Munoz & Tregenza 2016).
638 The mating structure of animal populations represents a clear example of how social structure
639 both acts to shape selection and how it can be shaped by individuals responding to competition
640 for reproductive success.

641

642 4.7. *Physiological interactions and stress transmission*

643

644 Behavioural endocrinologists have long recognized a two-way relationship between physiology
645 and behaviour. Even indirect social interactions can affect an individual's physiology. For
646 example, observing agonistic interactions increases androgen levels of uninvolved cichlid fish
647 (*Oreochromis mossambicus*) (Oliveira *et al.* 2001), and the heart beat rate of bystanders in greylag
648 geese (*Anser anser*) (Wascher, Scheiber & Kotrschal 2008). Social position, including rank in the
649 social hierarchy, can also impact stress levels and health (Sapolsky 2005). Just as social structure
650 and interactions shape individuals' physiological states (comprising reproductive state,
651 metabolic state, seasonal variation in hormone levels, and other aspects), these states can
652 influence who individuals associate with, potentially driving assortment by physiological traits.
653 Very simple processes can promote non-random clustering among individuals. For example,
654 individuals sharing physiological traits might move at the same speed or have similar
655 nutritional demands and therefore have a higher propensity for spatial and social clustering
656 (Gersick & Rubenstein 2017). The divergent behavioural outcomes linked to the physiological
657 phenotypes of individuals (re)shape their social environment. For example, if closely associated
658 individuals are more (dis)similar in their physiological states, such (dis)assortativity could
659 indicate another link between individual traits and processes mediated by social structure.
660

661 One physiological aspect with potential for an integrative study of feedbacks between
662 individuals and societies is the stress response within the social environment. Activation of the
663 neuroendocrine stress axis usually leads to an elevation of stress-associated glucocorticoids,
664 which are known to play a role in various forms of social behaviour of vertebrates (Spencer
665 2017) and can shape how individuals interact with others (DeVries *et al.* 1996). Physiological
666 expression of individual states, such as stress, might transmit to other individuals via social
667 interactions (Noguera, Kim & Velando 2017). On the other hand, social support in the group can

668 mitigate stress responses (Furtbauer & Heistermann 2016) and facilitate coping with stressful
669 events (social buffering) (Kikusui, Winslow & Mori 2006). For instance, lactating chacma
670 baboon females that are strongly connected to males have lower glucocorticoid levels when
671 faced with newly immigrated, and potentially infanticidal, males (Engh *et al.* 2006). The absence
672 of such social support (i.e. social isolation) can, in turn, have negative effects on fitness: in
673 greylag geese, solitary confinement or mate-loss affects immuno-reactive corticosterone
674 metabolites, percentage of red blood cells, and intestinal parasite loads (Ludwig *et al.* 2017).
675
676 Integrating the individual's state, the response of the group, and following it back to the
677 individual might generate new insights on how social groups respond to environmental
678 stressors. Observing individuals under environmental pressures that push their physiological
679 limits, such as food or water shortages, high temperatures, or increased predation, can provide
680 an opportunity to study feedbacks and behavioural drivers. Experimental approaches might
681 involve changing the composition of physiological phenotypes in groups to test whether it
682 changes the social structure. While traditional studies might have ended at this point, observing
683 follow up changes in individual states, resulting from a shift in selective agents of the social
684 environment, might generate new insights on feedback mechanisms. While the investigation of
685 the link between physiology and the social environment is slowly emerging (Seebacher &
686 Krause 2017), a thorough empirical framework for an integrative study of the feedback of
687 physiological states remains an exciting and promising new avenue for research.

688

689 **5. Closing remarks**

690

691 Our synthesis captures the growing evidence that individual decisions leading to social
692 structures can influence a wide range of social and ecological processes, and that these can, in
693 turn, influence how individuals behave and interact further. Theoretical and empirical research
694 on host-pathogen dynamics and cultural transmission clearly illustrates how social structure is
695 at the centre of a feedback between the social decisions that individual animals make and social
696 structure, and how social processes that are shaped by social structure can impact individual
697 traits. However, the implications of such feedback loops for the ecology and evolution of animal
698 societies are likely to go beyond these well-established areas of study, potentially affecting more
699 processes than those considered here.

700

701 We highlight existing opportunities to integrate disparate areas of research (Fig. 2) into the
702 study of individual-to-society feedback loops. Some topics (and their relationships to each
703 other) are quite well explored, such as relatedness, cooperation, and information and cultural
704 transmission. However, there are many gaps—for example how relatedness links to the stability
705 and resilience of societies—with some linkages between topics having only been tentatively
706 explored. Further, animal societies are likely to be simultaneously shaped by multiple factors.
707 For example, relatedness could determine the susceptibility of individuals to the pathogens that
708 their social contacts have, and therefore the parameters of pathogen transmission. Thus, most
709 top-down processes could act in unison with other top-down processes, or represent a feedback
710 to most bottom-up processes. Addressing such aims will be challenging, requiring a
711 combination of tools, such as high-resolution tracking, experimental manipulations, study
712 systems that are amenable to such manipulations, and analytical techniques that can clearly
713 identify the process or effect of interest amongst the competing drivers.

714

715 Individuals and societies are both dynamic, adaptive systems. Yet, most of the research being
716 conducted in animal societies focuses on either top-down or bottom-up approaches. Here, we
717 suggest that an integrative approach that explicitly considers the feedback between current
718 individual states and the social environments they experience will generate new insights on the
719 ecology and evolution of animal social systems. In generalizing the individual-to-society
720 feedbacks to include a more diverse array of bottom-up and top-down influences, we can gain a
721 broader understanding of the dynamics of social systems and the evolution of animal societies.

722

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739

740 **Authors' contributions**

741 DRF developed the concept and scope of the synthesis. MC, AMC, DRF defined the structure of
742 the manuscript and led the writing. All authors contributed to writing and revising sections,
743 overseen by DRF, MC, AMC. Authors are otherwise listed alphabetically.

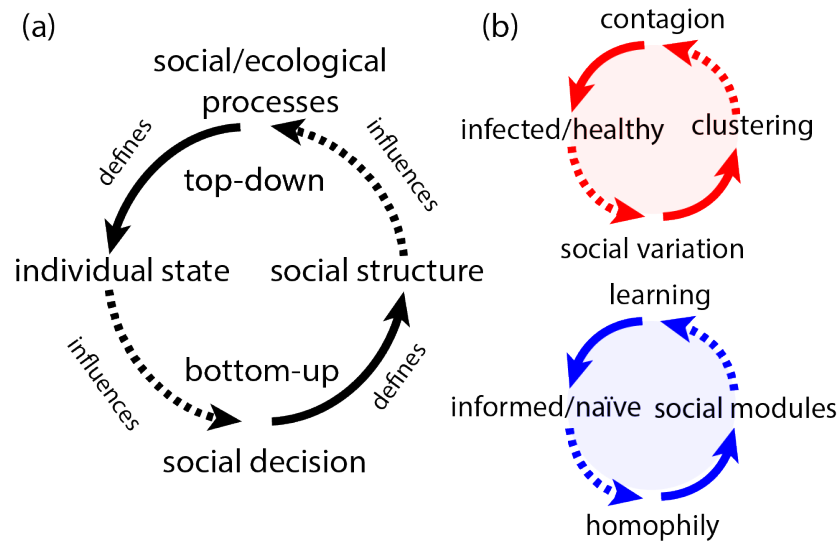
744

745 **Data accessibility**

746 The search terms and the closely-related terms used to perform the bibliographical review, the
747 list of publications gathered from Web of Knowledge, and the R code to replicate the network
748 analysis are available in Supporting Information S1.

749

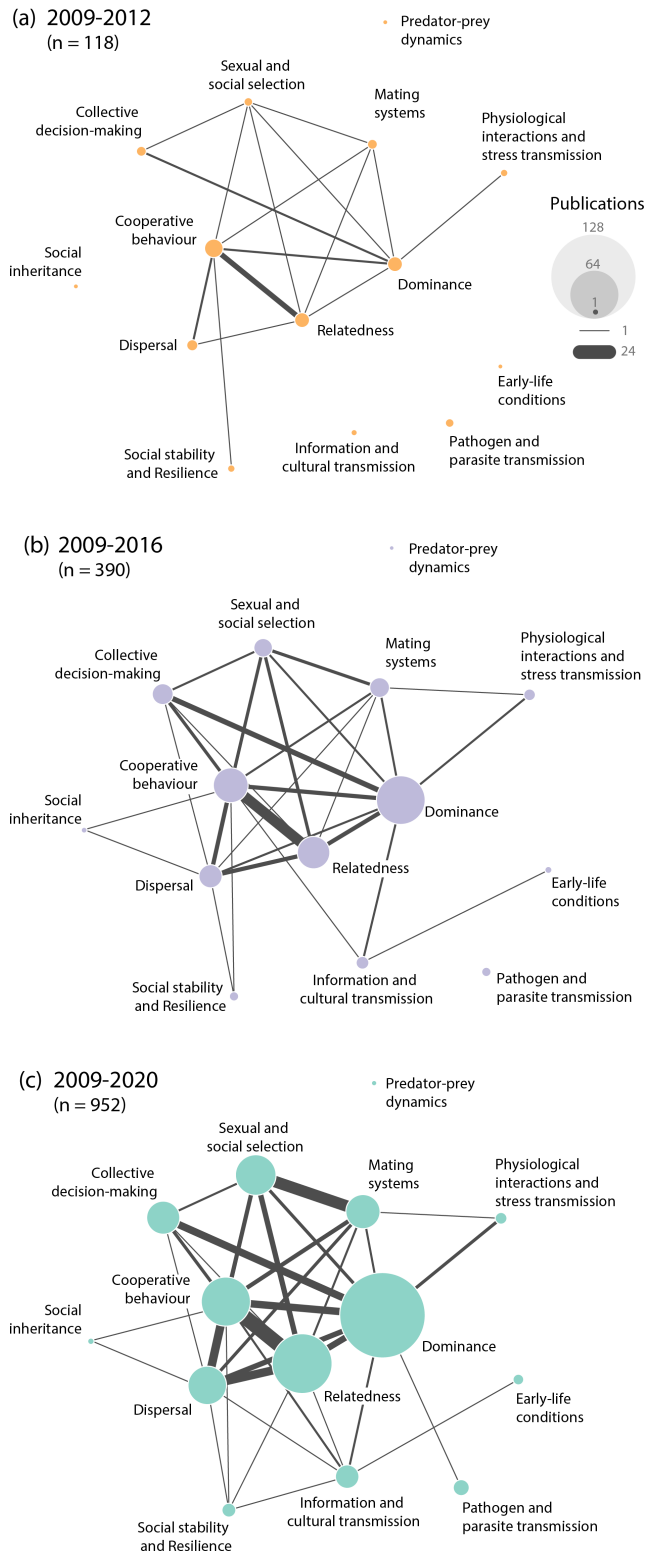
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751

752 **Figure 1. The individual-to-society feedback.** (a) A generalized feedback loop between
753 individual states and social structure considering that animals and their societies are linked.
754 Bottom-up influences represent social decisions that contributes to the resulting social structure.
755 Top-down influence are the effects of social structure (i.e. the distribution of social ties among
756 individuals) on social and ecological processes that ultimately determine the state of the
757 individuals. (b) Individual-to-society feedbacks illustrated for pathogen (top) and information
758 transmission (bottom). Whether or not individuals are infected by a pathogen or parasite can
759 influence the number of social connections they have, shaping social structure, which will
760 define properties of spread in populations (including pathogen traits), and ultimately determine
761 the future state of individuals (infected or healthy). Similarly, individuals that are informed or
762 naïve to a behavioural tactic can have a higher tendency to interact among themselves
763 (homophily), shaping the population into social modules; such modular structure will define
764 how the tactic will spread in the population via learning and ultimately define the future state
765 of individuals (informed or naïve).

766



767

768

Figure 2. Strong, weak, and missing links among research topics on the ecology and

769

evolution of animal social structure. Networks of co-occurrence of topics in original peer-

770 reviewed scientific articles between 2009 and 2020. Each node represents one of 14 research
771 topics. Node sizes representing the number of articles that address that topic, while edge widths
772 represent the number of articles where pairs of topics (i.e. the connected nodes) were addressed
773 in the same article. The networks represent the accumulation of articles over three 4-year
774 periods: (a) 118 articles published between 2009 to 2012, (b) 390 articles published from 2009 to
775 2016, and (c) 952 articles from 2009 to July 2020. See Box 1 and Supporting Information S1 for
776 more information on how these networks were constructed.
777

778 **Box 1. Identifying potential and realized connections in individual-to-society**
779 **feedback loops**

780

781 Over the past two decades, the two major perspectives in animal behaviour – the ethological
782 approach concerned with its evolutionary causation and the behavioural ecology approach
783 concerned with its functions and fitness consequences – have been bridged by network-thinking
784 (Whitehead 2008). The bulk of work on causes and consequences of animal social structures,
785 especially the recent cohort of studies inspired by network theory, have depicted social
786 structure as being static, overlooking the inherent dynamism of any social system (Pinter-
787 Wollman *et al.* 2014). Both individuals and societies are dynamic systems. Over time, societies
788 can change in size and composition and the distribution of social relationships can be
789 restructured (Shizuka & Johnson 2020). At the same time, each individual is in itself a dynamic
790 system, changing states over time. For instance, through the course of their lives individuals
791 learn from the environment and/or their peers (Kulahci & Quinn 2019), change in behavioural
792 motivations as they cross life stages (e.g. Berman 1982), and grow in social competences as they
793 mature within their social environments (Taborsky & Oliveira 2012). Thus, societies are rewired
794 as new individuals enter and old ones change or leave; as new social ties are formed and old
795 ones collapse. These social dynamics, when accounted for, are typically considered
796 independently from one another, although they are best considered as bidirectional (Gross &
797 Blasius 2008; Farine 2018).

798

799 Feedback loops between individuals and societies mean that the evolution of social structure
800 and the state of the individuals reciprocally influence each other (Fig. 1). In this review, we look
801 at linkages between multiple drivers of individual state and the processes influenced by social

802 structure, and where new connections can be made. To highlight the strong existing connections
803 and identify the general gaps in individual-to-society feedback loops, we reviewed the
804 literature addressing causes and consequences of animal social structures.

805
806 We first identified 14 of the common and emerging research topics in the study of animal social
807 structures, and then quantified how many publications addressed each topic together and
808 separately (Fig. 2). Although the use of network methods in the field of animal behaviour dates
809 back to the 1970's (Brent, Lehmann & Ramos-Fernández 2011), our focus is on the last decade
810 when the networks methodology gained popularity due to the publication of two influential
811 books (Croft, James & Krause 2008; Whitehead 2008; Whitehead 2009; Croft *et al.* 2011; Farine &
812 O'Hara 2013; Farine & Whitehead 2015). We based our search of original peer-reviewed papers
813 by identifying the studies citing the most influential methodological (Croft, James & Krause
814 2008; Whitehead 2008; Whitehead 2009; Croft *et al.* 2011; Farine 2013; Farine & Whitehead 2015)
815 and review papers (Wey *et al.* 2008; Krause, Lusseau & James 2009; Sih, Hanser & McHugh
816 2009; Pinter-Wollman *et al.* 2014) on animal social network analysis. We extracted the citations
817 of these influential publications from the Web of Science database on the 10th of July 2020. The
818 initial search yielded 1885 citations. After removing duplicates and 276 review articles and book
819 chapters, we analysed a total of 952 original peer-reviewed articles. We then analysed the title
820 and keywords of these articles to quantify which of them contained each of the 14 research
821 topics (and closely-related terms, e.g. 'relatedness', 'kinship', 'kin'; see Supplementary Material
822 1). We then generated a network depicting edges as the co-occurrence of topics in the same
823 articles (Fig. 2).

824

825 The cumulative publication networks revealed a core of well-connected research topics along
826 with a set of more peripheral topics (Fig. 2). The most studied topics in the last 12 years include
827 bottom-up drivers of individual states (e.g. 'relatedness', 'dominance'), while the top-down
828 influences are usually underrepresented (e.g. 'social stability and resilience', 'early-life
829 conditions'). Well-known cross-disciplinary research is represented by strong links (e.g.
830 'relatedness' – 'cooperative behaviour', and 'mating systems' – 'sexual and social selection').
831 The rapid increase in publications is clear from the accumulation of published articles by the
832 end of each of the three period (2009-2012: n=118; 2009-2016: n=390; 2009-2020: n=936; Fig. 2).
833 There was a visible increase in the network connectivity from 2009-2012 (connectivity = 18.7%)
834 to 2009-2016 (33.0%), but this largely stagnated over the following years 2009-2020 (39.6%) even
835 though the number of articles more than doubled (Fig. 2). These patterns suggest some
836 branching out from the first to the second period, and greater focus on classical topics (e.g.
837 'dominance', 'cooperative behaviour'), and somewhat less exploitation of new areas in the last
838 period. Some exceptions are 'cultural transmission' and 'social stability and resilience', whose
839 degrees increased from 0 to 7 and 1 to 4, respectively.

840

841 Importantly, our analysis reveals that there are still under-represented and weakly-connected
842 topics, revealing promising areas for further cross-disciplinary research. Among the missing
843 links, we highlight (i) the completely disconnected topic 'predator-prey dynamics'; (ii) the
844 potential links from 'social inheritance' to 'dominance', to 'relatedness' and to 'information and
845 cultural transmission'; and (iii) all potential links among the topics 'early-life conditions',
846 'dispersal', 'social stability' and 'physiological interactions and stress transmission'. Among the
847 weak links, we highlight (iv) those to and from 'social stability and resilience', (v) links from
848 'social inheritance' to 'dispersal', as well as (vi) links from 'pathogen and parasite transmission'

849 to 'dominance' and to 'physiological interactions'. We discuss these prominent areas for future
850 research in the "Future prospects for studying individual-to-society feedbacks" section.
851

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