

1 Recognising the key role of individual recognition in social networks

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6 Highlights

- 7 • The ability of individuals to recognise and keep track of others influences many social
8 processes (e.g. formation of social structure, social learning, and cooperation) yet the
9 role of individual recognition is rarely considered.
- 10 • Social network analysis entails quantifying the social associations among individuals to
11 provide insights in to patterns of individual behaviour, interactions, and social
12 structure.
- 13 • Integrating our understanding of individual recognition into the social network
14 approach allows for a better understanding of the basis for social relationships within
15 networks in different populations.
- 16 • Combining the currently largely distinct, but intimately related, areas of social
17 networks and individual recognition will lead to new perspectives in both and
18 improved understanding of the evolutionary and ecological causes and consequences
19 of sociality.

24 **Abstract:** Many aspects of sociality rely on individuals recognising one another.
25 Understanding how, when, and if individuals recognise others can yield insights into the
26 foundations of social relationships and behaviours. Through synthesising individual
27 recognition research in different sensory and social domains, and doing so across various
28 related social contexts, we propose that a social network perspective can help to uncover
29 how individual recognition may vary across different settings, species, and populations.
30 Specifically, combining individual recognition with social networks has unrecognised potential
31 for determining the level and relative importance of individual recognition complexity. This
32 will provide insights not only on the ecology and evolution of individual recognition itself, but
33 also on social structure, social transmission, and social interactions such as cooperation.

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35 **Keywords:** individual recognition, sociality, social networks, cooperation, social structure,
36 social transmission

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41 Understanding individual recognition

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43 Identifying stimuli within the environment and responding to the characteristics and
44 information associated with these stimuli over time is a key component of survival in almost
45 all animals. Particularly relevant to the social domain is **individual recognition** (see Glossary):
46 the ability to remember and recognise individuals [1]. Individual recognition abilities have
47 been studied widely, in amphibians, birds, cephalopods, crustaceans, fish, insects, mammals,
48 and reptiles [2–9]. Further, individual recognition can occur in many sensory domains within
49 species; zebra finches (*Taeniopygia guttata*) can recognise conspecifics not only through
50 vision [10] but also through their song [11] and chimpanzees (*Pan troglodytes*) can identify
51 individuals from other troops using the scent of their urine [12]. Some studies even show
52 evidence for cross-modal individual recognition [7,13,14]. For example, African lions
53 (*Panthera leo*) seem to match the roars (audio) of particular individuals to their physical
54 appearance (visual) and respond strongly to incongruent presentations of these cues [7;
55 reviewed Table 1].

56

Glossary

Binary IR: sometimes referred to as “individual discrimination,” cases where individuals from a population can be categorized in to two heterogenous groups, usually on the basis of previous experience; most often studied in terms of familiarity, kinship, or group membership more generally. This does not entail the use of individual-specific cues.

Class-level IR: an individual’s class (or phenotype) is matched to a representation of that class which contains information associated with individuals from it i.e. the phenotypes of individuals are associated with class-specific information that has been previously learned; can be on the basis of physical characteristics that are indicative of dominance, aggression, reproductive success, etc. This is similar to binary IR in that it does not entail the use of individual-specific cues, but different because it includes more than two classes/categories/groups. This may rely more heavily on left hemisphere because of the more general role in category-based distinctions [16]

Cooperation: behaviours initiated by an actor that have a benefit to a recipient (other than, or in addition to, themselves)

Individual recognition (IR): recognition where an individual, x (the receiver), learns cues related to another individual, y (the signaler), which are associated with relevant information about y and are used by x to identify y and adjust their behaviour towards them in future interaction (blanket term to refer to cases of true, class-level, and binary recognition)

Marker method: a possible mechanism for individual recognition – where there is no single representation or “template” for each individual but instead there are a large number of different categories (or markers) and different individuals fit in to unique combinations of them; in this case “true” individual recognition is not necessary because the cues that are learned are not themselves unique to the individual but the combination of cues is

Multiplicity of IR: the total number of sets (groups) that can be differentiated with individual recognition

Social network: the web of social connections between individuals within a group/population. Nodes (i.e. individuals) are connected by edges (i.e. associations, bonds, relationships) in a way that represents the overall social structure, and the position of each individual within this structure.

Social network approach: an approach aimed at understanding a range of different social phenomena and their evolutionary causes and consequences by quantifying diverse kinds of interactions among individuals within a population to create a social network.

Social transmission: the social spread of social information and behaviours between socially-connected individuals

Specificity of IR: the total number of individuals included in a set; together, specificity and multiplicity give us an indication of the total number of individuals that can be recognised

Template-matching: one proposed mechanism for individual recognition where the observer perceives the phenotype of the individual, saves some template or representation of that phenotype, and compares encountered phenotypes to saved recognition templates to figure out which one matches; phenotype matching, often discussed as a mechanism for kin recognition, is one specific application of template-matching

Temporality of IR: how long information about individual identity can be retained and used for individual recognition over time

True IR: cues that are specific to the individual are learned and associated with information (usually fitness related) specific to that particular individual. Neurologically, this may rely more heavily on right brain hemisphere because of the more general role in assessing novelty and encoding unique features of individual stimuli [reviewed in 16]

57

58 Because it has been studied in various different contexts and species, definitions of individual

59 recognition vary widely [15]. All forms of recognition are currently unobservable cognitive

processes, making it difficult to understand the mechanisms and the nature or complexity of the cues and representations that allow for individual recognition [16,17]. Furthermore, processes enabling recognition may be distinct from those that govern responses after initial recognition.

However, rather than considering separate kinds or discrete types of recognition, it seems more plausible that these different routes to recognition lie on a continuum [18]. **Binary individual recognition** requires only a discrimination between one group and another and is usually on the basis of familiarity (e.g. ‘familiar’ or ‘unknown’), kin (e.g. ‘parent’ or ‘non-parent’), or simply classifying individuals as “in-group” or “out-group” [19,20]. Taking things one step further, **class-level individual recognition** requires associations between different physical characteristics of the signaller, the traits that they represent, and how these traits may influence the signaller’s behaviour [21]. This kind of recognition can vary in complexity depending on the details of classification (e.g. within-species classification more difficult than between-species). **“True” individual recognition** may be even more complex, as individual-specific characteristics are matched to individual-specific information (which itself can vary in amount and type)[22]. Placing the recognition that we observe on this continuum can be difficult because it is unclear if animals are using individual cues or more general class-level cues. Indeed, whether or not “true” individual recognition is necessary for individual recognition, even in humans, can be debated.

Table 1 – types of cues that can be used for individual recognition with examples of their operation

Cue type	Examples
Auditory: on the basis of vocal cues; used most often (playback experiments); may be dependent on perceptual requirements and anatomical constraints	Olive frogs (<i>Babina adenopleura</i>) use the distinctive vocal signals of conspecifics to identify their neighbours and exhibit lower levels of aggression towards them in a vocally-mediated example of the dear-

may make it less likely that individual identity can be transmitted through calls in some species	enemy effect [19]. Shapiro [23] discusses the existence of “signature vocalizations” that allow for individual recognition. Vocal individual recognition is reviewed by [15].
Visual: on the basis of visual cues of distinctive physical appearance or distinctive behaviours/movements; the face may be the best identified where vision is the primary sense	Kendrick et al. [24] used both electrophysiological recordings of brain activity and behavioural measures to show that sheep (<i>Ovis aries</i>) can remember 50 other sheep faces for time periods of over two years, and suggest that sheep have specialized neural mechanisms for processing faces. Visual cues can also be based on movement. For example, Japanese macaques (<i>Macaca fuscata</i>) exhibit consistent individual differences in their movement patterns that can serve as cues for individual recognition [25].
Olfactory: on the basis of scent cues	Bumblebees (<i>Bombus terrestris</i>) can discriminate between the scents of conspecifics to identify locations where their nestmates have been before [26] and house mice identify conspecifics through the scent of their urine [27]. It is possible that, similar to vocal cues, individuals have “signature mixtures” that allow for individual recognition. Individual recognition on the basis of olfactory and chemical cues are reviewed by [28,29].
Tactile: on the basis of touch; only briefly studied in humans	The only studies of individual recognition through tactile cues are with human parents, who are able to recognise their new-born offspring by touch alone [30,31].
Multi-sensory: on the basis of multiple cues in conjunction; cue chosen may be on the basis of the primary sense of the species	Lions (<i>Panthera leo</i>) match audio-visual cues (roars and physical appearance) to identify individuals, as demonstrated by their strong reactions to incongruent presentations of these cues [7]. Individual recognition on the basis of multiple cues may also be used to identify individuals of other species; [32] found that domestic horses (<i>Equus caballus</i>) could match familiar humans to their voices.

82

83 One way to overcome issues with definitions is by focusing on the **multiplicity, specificity, and**
84 **temporality** of individual recognition without getting caught up in debate over true vs. untrue
85 individual recognition and the nature of the representations that are used to achieve it [18].

86 This can give us a better sense of the amount and complexity of the information that can be
87 transmitted through these processes. What are the causes of varying levels of individual
88 recognition? How are varying levels of complexity related to the social or physical
89 characteristics of a given population or species, and how do differences in these factors
90 influence the predictions we make about the consequences of individual recognition? For
91 example, higher specificity and multiplicity of individual recognition may be more likely to
92 lead to conditions favouring the emergence and maintenance of cooperative behaviours [18].

93

94 Individual recognition is most likely to evolve in situations when: individuals have varying
95 phenotypes, remembering conspecifics and responding according to their previous

behaviours will be advantageous, and there are low costs, i.e. necessary cognitive mechanisms are already present [33,34]. Having distinctive phenotypes (identity signals) is often expected to be selected for in social species because it allows for various forms of communication and familiarity (reduced aggression), and can increase genetic diversity that is beneficial at the individual level, and also potentially the kin-group level [35]. Pollard [36] modelled the benefits of individual recognition and four other “response strategies” to alarm calling signallers when deciding between “foraging,” “being wary,” or “hiding,” under various conditions. The individual recognition strategy was the most advantageous under most conditions, lending support to the idea that identity signalling may be selected for due to potential fitness benefits of individual recognition and the adjustments in behaviour that result from it. For example, facial distinctiveness may have evolved in order to allow for more precise individual recognition in some social species [37,38]. Further, features may evolve as signals of quality rather than identity, and it is possible that there is a trade-off between these signals on the basis of each species’ ecology and reproductive system [39,40].

Recent advances and general approaches in individual recognition

The ability to perceive and recall information about individuals based on previous interactions is an important component of many social behaviours [33]. As outlined below, Tibbetts & Dale [1] have previously identified the three areas that individual recognition was most widely studied as: 1) territoriality, 2) aggressive competition, and 3) parental care, and called for further work in the area of 4) mate choice/recognition (reviewed Table 2).

Territoriality

120 Individual recognition may play a large role in territoriality, where recognition of others
121 allows individuals to reduce or correctly divert aggression towards conspecifics, which can
122 reduce the costs of establishing dominance hierarchies and resolving conflict within or
123 between groups. This is often studied in terms of the “dear-enemy effect,” where individuals
124 that reside in a territory will be less aggressive towards familiar neighbours, and may even
125 “cooperate” with them; this decreases the costs of territory defence for both parties [19,41].
126

127 *Aggressive competition*

128 Similarly, by remembering the identity, temperament, and competitive ability of others,
129 individuals can make more accurate assessments of their chances of winning contests and
130 adjust their interactions accordingly. In one example, the “facial” markings of Australian
131 crayfish (*Cherax destructor*) engaging in contests were experimentally manipulated to assess
132 their ability to visually recognise other individuals [42] . After exposing focal individuals to
133 multiple manipulated individuals in a test arena, the authors report that crayfish recognise
134 others using facial cues that they encode in memory during aggressive contests, and can
135 remember this information for at least 24 hours and use it to adjust their behaviour in future
136 interactions for up to two weeks.

137

138 *Offspring identification*

139 Identifying offspring correctly is crucial to accurately providing preferential care, safety, and
140 resources to offspring, especially in cases where the offspring of multiple individuals are
141 housed in the same area, when social group sizes are big, when intra- or interspecific brood
142 parasitism is at play, when extra-pair paternity rates are high, and/or in species where
143 reproduction occurs relatively simultaneously within the year/season. Offspring also benefit

144 from recognizing their parents because it allows them to respond appropriately to them vs.
145 unfamiliar adults. This is especially crucial in situations where offspring must follow parents,
146 find them in larger groups, and when other adults are particularly dangerous [43]. Parent-
147 offspring identification can also contribute to inbreeding avoidance strategies.

148

149 *Mate recognition*

150 Finally, the ability to identify one's mate has important consequences for initial mate choice,
151 monogamy, biparental care, and carry-over effects from reproductive periods [44]. It is also
152 advantageous because it allows individuals to assess the value of possible mates through
153 individually distinctive traits before deciding; "eavesdropping" on the behaviours and
154 interactions of potential mates can inform mating decisions and the pursuit of extra-pair
155 copulations.

156

157 There are many routes to studying the presence, multiplicity, specificity, and longevity of
158 individual recognition. Most often, interactions among individuals are observed in a
159 controlled setting to see if individuals behave differently in the presence of different
160 conspecifics immediately and over time [45]. Another method entails the presentation of
161 cues that are presumed to be used for individual recognition, and looking at the responses of
162 receivers. This can include playbacks of calls or other vocalizations, visual presentations of
163 faces or parts of the body with distinct markings, or the scent or chemical makeup of other
164 individuals. Cues can also be presented after altering them slightly to get a better
165 understanding of, first, whether individuals are engaging in individual recognition and,
166 second, which components of those cues are being used to signal individual identity.
167 Although playback experiments are the most common [reviewed by 15], physical

appearance, genes/hormones, and scents or chemical compositions can also be manipulated to look at how changing certain characteristics of the cues that would presumably be used for individual recognition can impact behaviour [31, described above]. All of these approaches can be taken alongside methods and set-ups detailed in Table 2, with varying numbers of individuals (specificity) and groups of individuals (multiplicity), and over different time periods (longevity).

Table 2 – main methods used to study individual recognition with examples of their application

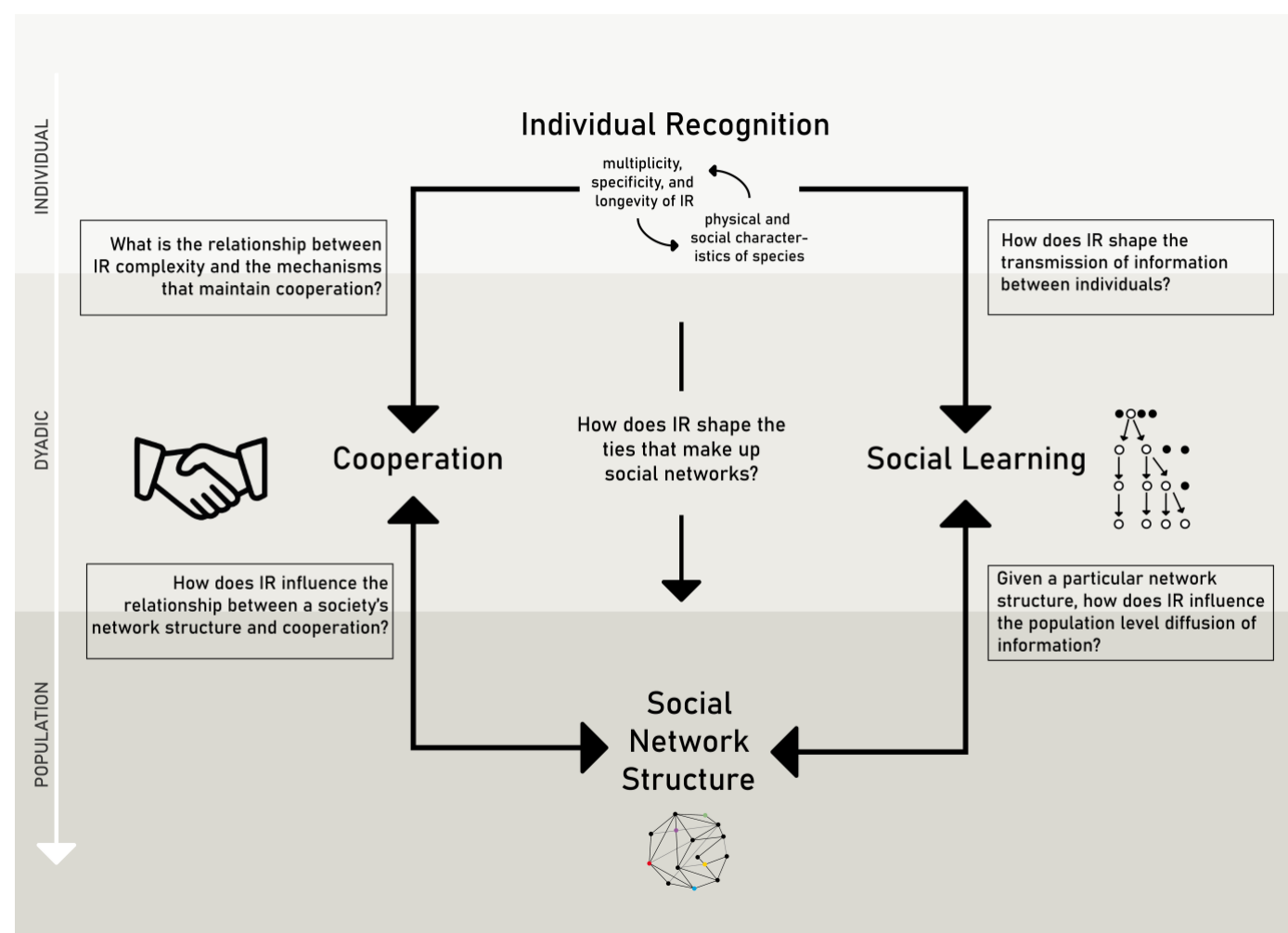
Method	Description	Examples
Partner choice tests	The focal individual is given the ability to show their preference for a partner by joining them or their identifying cues in physical space. If the individual chooses the more familiar or “target” individual, they are said to be recognizing that individual. This can be done with the y-maze and other set-ups that allow for a choice between individuals (or their calls, smells, etc.), or by quantifying the amount of time individuals spend in the presence of others/looking at others.	[Australian sea lion (<i>Neophoca cinerea</i>) - 43, Red jungle fowl (<i>Gallus gallus</i>) - 46]
Contests	Individuals are placed in an arena and subject to multiple contests. The focal individuals’ level of aggression or tolerance is noted in each instance. If they adjust their behaviour on the basis of familiarity or their previous experiences with the “rivals” it is assumed that recognition is occurring.	[Crayfish (<i>Procambarus clarkii</i>) - 6, Golden-crowned sparrows (<i>Zonotrichia atricapilla</i>) - 47]
Habituation/dishabituation	A stimulus is repeatedly presented to the focal individual until they stop or decrease their responding to it (habituation). Then, a new stimulus is presented to them. If they perceive the new stimulus as different to the previous one, they will start responding to it (dishabituation); whereas if they do not perceive the difference, they will continue to ignore it.	[Superb fairy-wrens (<i>Malurus cyaneus</i>) - 22, Greater false vampire bat (<i>Megaderma lyra</i>) - 48]
Violation of expectancies	The responses of a focal individual to the presentation of cues in a manner that is physically impossible are used to ascertain if individuals pick up on this irregularity. For example, the calls of the same individual can be played from two distinct locations. If the focal is more attentive (looking time, vigilance, etc.) in this scenario than in a “normal” one, it suggests that recognition is occurring.	[African lions (<i>Panthera leo</i>) - 7, Domestic cat (<i>Felis catus</i>) - 14]

1. Studying individual recognition with a social network approach

Over the past decade, **social network** analysis has become an increasingly influential method for understanding a range of different social phenomena and their evolutionary causes and consequences [49,50]. By quantifying diverse types of interactions among individuals within a

182 population, the **social network approach** allows for a generalised quantification of social
183 structure which can, in turn, provide insights into empirical patterns of individual behaviour
184 and interactions. In this way, it provides a platform for examining how social network
185 characteristics may lead to emergent properties that can make way for, and influence, other
186 social processes such as social transmission of information, behaviours, or contagious
187 disease. In addition to the areas discussed, individual recognition plays a key role in social-
188 bonds that are not motivated by kinship, territoriality, or future reproduction [51]. For
189 example, domestic donkeys (*Equus asinus*) show preferences for their ‘friends’ (individuals
190 that are most often their nearest-neighbour) over other individuals, suggesting that donkeys
191 recognise those that they have the strongest social bonds with, and use this information to
192 decide who to spend time with [52]. It seems plausible that individual recognition can have
193 an important influence on all types of interactions and relationships, necessarily influencing
194 social network structure. However, direct incorporation of the effects and influence of
195 individual recognition into the social network approach remains relatively limited, despite
196 much potential for doing so.

197 The intergration of social network analysis with investigations of individual recognition
 198 creates multiple opportunities to improve our understanding of how individual recognition
 199 interacts with other social processes (see Figure 1). For example, social network analysis can
 200 be used to advance insights into mate choice [53–55]. In many avian species, individuals
 201 recouple with the same partner over many breeding seasons; whether or not individual
 202 recognition is playing a role is important. What is the null expectation if individuals are
 203 choosing based on preference (for physical attributes, e.g. size, coloration, signalling
 204 characteristics, etc.) rather than identity? Are partners chosen repeatedly over time through
 205 the use of recognition or solely based on preference? Incorporating the study of individual
 206 recognition can bring another layer of understanding.



207 *Figure 1 – Pathways that link individual recognition and other social phenomena, and questions that can potentially be*
 208 *answered (ranging from the individual to population level) using a social network approach to studying individual*
 209 *recognition.*

210

211 Finally, studying individual recognition with a social network approach is advantageous
212 because of the potential broader role of individual recognition in shaping individual
213 differences. McNamara, et al [56] model the effects of “social awareness” on the trait of
214 trustworthiness, demonstrating that in populations where individuals trust conspecifics
215 based on their previous behaviour, variability in individual trustworthiness increases in the
216 population. It is possible that the ability to recognise and track conspecifics can lead to
217 variation in observable traits that influence social network structure, the rate and mode of
218 **social transmission**, and **cooperation**. Marrying studies of social network structure and
219 dynamics with findings about individual recognition can now lead to novel insights and new
220 support for conclusions in many lines of inquiry that have not been considered in conjunction
221 with individual recognition before (Figure 1).

222

223

224 Social structure and individual recognition

225 Previous studies have demonstrated that the presence or absence of individual recognition
226 can have consequences for social organization, the formation of dominance hierarchies, and
227 the way various phenomena may shape social structures [6,47]. Although many mechanisms
228 shape and maintain the structure of social networks in any species, recent simulation studies
229 have shown that the complexity of individual recognition can influence social dynamics in
230 group formation and the resulting numbers or size of various groups [57]. This may be due to
231 cognitive limitations on individual recognition that could potentially lead to further
232 limitations on how social networks form and are maintained [58]. Understanding the relative
233 impact of varying levels of complexity of individual recognition can give us insights into how

234 and why different populations are structured in the ways that they are which, in turn, can
235 inform our understanding of individual and group-level social processes (Figure 1). For
236 instance, network analysis allows for the quantification of various characteristics of social
237 structure, such as quantifying the level of non-random clustering (i.e. how much a social
238 network is structured by friend-of-a-friend relationships in comparison to what would be
239 expected from the general network structure in terms of number of individuals and number
240 of observed associations between these individuals), or quantifying the extent of between-
241 individual variation in social positions (how different individuals are from one another in their
242 observed sociability metrics compared to what is expected under that general network
243 structure). Quantifying social structure in such ways, for different but closely related species
244 for example, could allow for the investigation of possible differences in social structure that
245 may be associated with differing levels of complexity in individual recognition.

246

247 In a study of human subjects, Parkinson et al. [59] used functional magnetic resonance
248 imaging (fMRI) in conjunction with social network analysis to show that network positions
249 (information about how well connected individuals are to others in the network) are
250 perceived accurately, encoded, and activated in the presence of familiar others. In human
251 studies like this one, it seems obvious that individual recognition is necessary to keep track of
252 numerous individuals and how they are related to the self and to one another. However, it is
253 possible that complex social network phenotypes are actually represented by simple
254 behaviours [60], which other individuals can then recognise. In other words, some complex
255 population-level patterns found in social networks can be explained by simple social
256 differences (in general sociability and tendencies to re-associate with within-group or out-
257 group members) at the dyadic level. Future studies can use simulations in combination with

258 real social networks to consider how individuals identify network positions of others and how
259 differences in individual recognition abilities may lead to different types of social structure.

260

261 Social transmission and individual recognition

262

263 The ability to identify individuals can also have an influence on the way information flows
264 through different populations. While social network connections provide the substrate for
265 information to potentially diffuse through a system, social learning strategies (based on
266 choosing which individuals to learn from, or when to learn) may govern how behaviours
267 actually spread [61]. Indeed, by recognizing the identity of others, individuals can assess the
268 reliability of information that they receive and subsequently adjust their behaviour
269 accordingly, by deciding whether or not to follow or act on the information provided by
270 particular individuals [62,63]. Dwarf mongooses (*Helogale parvula*) adjust their vigilance
271 behaviour on the basis of the dominance rank of their sentinel [64], fairy wrens (*Malurus*
272 *cyaneus*) are more responsive to the alarm calls of mates and kin than those of unfamiliar
273 individuals [22], and vervet monkeys are more likely to copy solutions from higher ranked
274 individuals [65]. The use of information about individual identity when deciding which
275 information sources are most reliable can feed back and shape social structure [66]. For
276 example, 'homophily' (like-with-like i.e. assortment) in social influence increases behavioural
277 similarity and reinforces strong bonds between similar individuals while further separating
278 those that have distinct behaviour (clustering).

279

280 However, it is also important to keep in mind that there may be similar effects on
281 information flow in the absence of the recognition of *who* is producing the information. For

282 example, modelling has demonstrated that information can flow, and collective decisions can
283 be made, in the absence of individual recognition and without accounting for how informed
284 or reliable the individual that provided the information is [67]. Seemingly “complex” actions
285 or decisions can be taken on the basis of very simple principles or mechanisms. Developing
286 methods to tease apart the various mechanisms that allow for social information flow in
287 different populations is a vital part of our understanding of the relationship between
288 individual recognition and how social information spreads [68,69].

289

290 One instance where understanding the influence of individual recognition may be particularly
291 important is in cases of conformist social learning (learning behavioural options that are
292 favoured in the local population, even though alternative options are available) that may
293 have implications for animal culture [70,71]. How we expect conformist transmission to occur
294 may depend on whether individuals recognise others; do individuals conform to the
295 behaviour that is being performed by the majority of *individuals* (*a larger proportion of*
296 *individuals perform a behaviour*), or do they simply conform to the behaviour that they
297 observe in the majority of *instances* (*the behaviour is performed a larger number of times, but*
298 *not necessarily by a higher proportion of individuals*) [72–74]. Understanding which of these
299 approaches to establishing the majority is taken is vital to interpreting how socially-learnt
300 behaviours influence and interact with social transmission and cultural evolution. More
301 generally, do more “complex” mechanisms allow animals (including humans) to identify, keep
302 track of, and learn from others, or is the appearance of complexity being maintained by
303 several, simpler processes? One potential way to explore these questions may be to
304 manipulate the cues that allow for individual recognition and examine resultant changes (or
305 the lack of) in the way information, and emerging behaviours, spreads.

306

307 Cooperation and individual recognition

308

309 Finally, the presence or absence and even the complexity of individual recognition abilities

310 may have major implications for the emergence and spread of cooperation, especially when

311 the processes proposed to enable this cooperation assume that unique individuals and their

312 behaviours can be tracked and recalled by others over time [e.g. image-scoring or reciprocity

313 75]. Tibbetts & Dale [1] note that individual recognition is particularly important when “there

314 are repeated interactions among multiple individuals with differing intentions” which is

315 exactly the case in most settings where cooperation arises; cooperation (especially among

316 non-kin) is most likely to occur when there are stable social structures and heterogenous

317 interactions [76–78].

318

319 It is also possible that individual recognition allows for more fine-tuned cooperation (through

320 direct and indirect reciprocity) while other populations rely on more simple, conditional rules

321 (e.g. generalized reciprocity). For example, guppies (*Poecilia reticulata*) have been shown to

322 behave consistently with the use of the “walk-away” heuristic, where they keep their partner

323 after experiencing cooperation but switch partners after experiencing defection – regardless

324 of the identity of the individual [79]. Are species lacking individual recognition abilities more

325 likely to engage in generalized reciprocity? Does this translate to differences in social

326 structure? A better understanding of individual recognition is crucial to uncovering the

327 mechanisms that allow for cooperation in different populations.

328

329 Individual recognition and the ability to track the cooperative or un-cooperative behaviours
330 of others can help to maintain group cohesion and prevent “cheating” [“a trait that is
331 beneficial to a cheat and costly to a cooperator in terms of inclusive fitness (ii) when these
332 benefits and costs arise from the actor directing a cooperative behavior toward the cheat,
333 rather than the intended recipient”; 66]. Social eavesdropping has significant implications for
334 how cooperation spreads, as the presence of a bystander can increase the benefit that is
335 received (by the actor) by engaging in a cooperative behaviour as their signal will be
336 perceived by not only the recipient of the behaviour but also the bystander, potentially
337 increasing the possibility of future cooperation by either party [81]. This selective pressure
338 that comes with the presence of bystanders, and social eavesdropping, is only possible if
339 individual recognition is involved.

340

341 Although the dear-enemy effect is taken advantage of in studies of both cooperation and
342 individual recognition, the link between them is rarely ever explicitly acknowledged.

343 Assortment is often considered important for cooperation to be maintained: if individuals are
344 assorted by cooperativeness in social or physical space, it is more likely that cooperators will
345 interact with other cooperators, increasing the benefits of being a cooperator in that
346 population [76,82]. With the dear enemy effect, it is possible that cooperators are clustered
347 in physical space simply because of this phenomenon – individuals may not be cooperative in
348 other contexts, but establish and maintain this mutualism with their familiar neighbours on
349 the basis of individual recognition. But do individuals really recognise their dear enemies, or
350 do they associate particular cues with particular locations? How does this translate into
351 relationships within social space? New advances are now needed to determine whether dear
352 enemies are better connected to each other than to unfamiliar others (in the case of

individual recognition) or whether they are no more likely to have strong ties with familiar neighbours than with unfamiliar conspecifics (in the absence of individual recognition; see Figure 2).

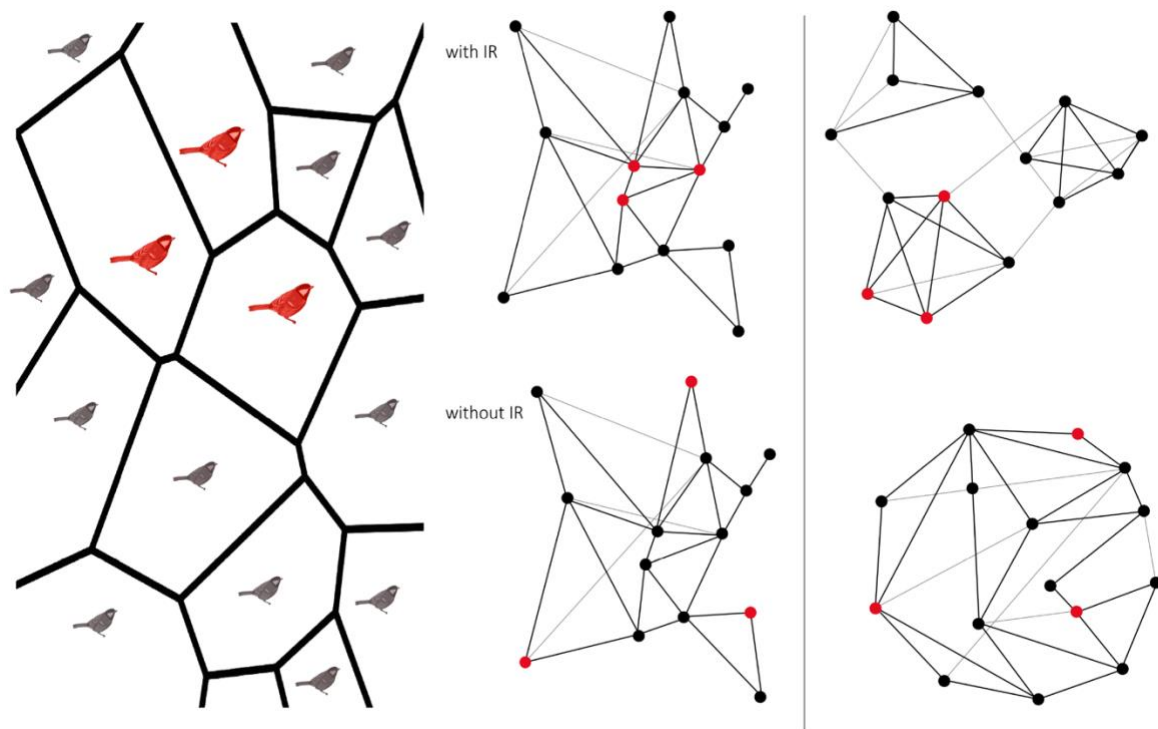


Figure 2 - A hypothetical illustration of the dear-enemy effect in territorial breeding birds (here exemplified as a great tit – *Parus major*), with breeding territories on the left and expected social associations and cooperative social structure for the subsequent non-territorial season on the right. Although the dear enemy effect may be maintained in the absence of individual recognition during the breeding season, whether or not individuals are using individual recognition or simple associative learning may have an impact on how those individuals are associated and interact in the non-territorial season. Using data from real populations, these relationships can be tested.

Concluding remarks and future directions

Existing studies of if and how individuals recognise others have focused on the effects of individual recognition on contests, territoriality, parent-offspring recognition and mate selection, revealing fundamental differences in the way different species recognise and react to their social partners. New experiments can offer especially powerful insights, such as through manipulating the ability of individuals to identify others or removing particular

371 individuals from the population and examining how different manipulations impact social
372 network structure, the rate and mode of social transmission, and cooperation. Further,
373 continuously modifying the appearance of some individuals (making them un-recognizable)
374 and assessing their arising network position, and their ability to form new ties, would provide
375 a deeper understanding of how the maintenance of relationships (edges) in social networks is
376 dependent on individual recognition.

377

378 Social network studies can also now be integrated with cognitive experiments. Traditional
379 methods of studying individual recognition (reviewed Table 2) can be paired with social
380 network analysis to directly answer questions about how complexity of individual recognition
381 is related to social network characteristics. This can be done both within and among
382 populations/species. Specifically, such questions might include considering whether species
383 with more complex individual recognition abilities also have more variation in the edge
384 weight between individuals within their networks, whereby recognition allows bonding over
385 long time periods. If individuals can identify exceptionally high numbers of individuals (in
386 comparison to others in their population), are they also more likely to have a larger number
387 of social connections? Investigating social choices can also provide insights into what
388 information individuals hold about others. Are focals more connected (higher bond strength)
389 to the individuals that they choose in the partner-choice test (described Table 2)?

390

391 Another potential approach would be observing changes in social structure and individual
392 recognition in response to anthropogenic impacts. Human pollutants in aquatic habitats can
393 potentially disrupt the chemosensory abilities that fish use for recognition [83]. Similarly,
394 noise pollutants may impact individual recognition abilities in terrestrial species that rely on

395 auditory cues for communication. Studying populations of the same species with varying
396 degrees of exposure to potentially disruptive anthropogenic impacts can allow for a deeper
397 understanding of how individual recognition is influenced by changes in the surrounding
398 environment, and how this may have carry-over effects for individuals' social behaviour and
399 the arising social network structure and social processes which depend on this structure.

400

401 Aside from experiments and empirical observational research, it is becoming apparent that
402 modelling [similar to 36] may also aid in elucidating how the absence/presence or
403 multiplicity/specificity/temporality of individual recognition influences the three proposed
404 areas (social structure, social transmission/learning, and cooperation) under different
405 circumstances. This more detailed investigation could help tease apart effects of other
406 external (season, climate, resource availability, etc.) and internal (emotional reactivity,
407 reproductive status, etc.) characteristics on the outcomes of individual recognition
408 investigations [84]. A focus on the relationship between individual recognition and social
409 networks would allow for the study of individual and group-level differences in individual
410 recognition and their influences on how social structures are established, how information
411 and behaviours spread through the population, and how cooperation is maintained – as well
412 as how these aspects of sociality may feedback and shape recognition (see Outstanding
413 Questions).

414

Outstanding Questions

How does individual recognition shape the ties and social bonds that make up social networks, and what patterns of social connectivity do we expect under different forms of recognition?

What is the relationship between individual recognition complexity and the formation and maintenance of social preferences?

How does the complexity of individual recognition impact the social and physical characteristics of different species?

What is the relationship between individual recognition abilities and overall social architecture, as well as individuals positions within the structure?

How might individual recognition shape social learning strategies, and how might this then affect the transmission of social information and the spread of socially-informed behaviours?

What is the relationship between individual recognition complexity and the mechanisms that maintain cooperation in different societies? Do populations lacking individual recognition mechanisms rely solely on conditional cooperation rules?

Does individual recognition shape how individuals within social systems respond to disruptions of social structure or social processes?

Are there stable individual differences in individual recognition abilities? If so, what factors shape these differences (genetic, environmental?) and how do these interact with individuals' social network positions and roles within the society?

415

416

417 **Acknowledgements:** We thank three anonymous reviewers, Andrea Stephens, Christopher

418 Pull and Melanie Ghoul for helpful feedback and discussion on this work and Ferhat Yesilada

419 for help with producing the figures. JAF was supported by BBSRC (BB/S009752/1) and funding

420 from NERC (NE/S010335/1).

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