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Forum

Considering Complexity: Animal Social Networks and Behavioural Contagions

Josh A. Firth[1,2,@,*]

The spread of behaviours through animal social networks have often been considered as 'simple contagions'. However, research across other disciplines now provides substantial grounding for the 'complex contagion' of behaviours. The study of animal behaviour could benefit greatly from generally expanding to incorporate these new insights.

Current Understanding of Behavioural Transmission in Animal Systems

The transmission of information in animal social systems takes place in many contexts, such as through direct communication or inadvertent social cues, and shapes various aspects of individuals' behaviour, such as foraging or mating [1,2]. Social transmission is dependent on the network of social connections between individuals, and these 'social networks' are increasingly acknowledged as fundamental for understanding social processes[1–3]. Furthermore, these socially informed changes in behaviour have various implications, ranging from affecting individuals' fitness to shaping population-level processes [1,2], and can even feed back to influence the structure of the social system and the subsequent spreading of behaviours [1].

To date, the majority of animal behaviour research examining this dynamic relationship between social networks and the transmission of behaviours has

followed two related and widely ascertained concepts. First, individuals that are more socially connected (i.e., more 'central') are more likely to gain and spread new behaviours [1,2]. Second, adopting a new behaviour may dynamically feed back and increase an individual's social centrality, and this can then positively promote further transmission to others [1].

The Complex Nature of the Social Diffusion of Behaviours

The central assertions above, which are largely representative of the general state of knowledge across animal social network research [1], are underpinned with a simple assumption that is frequently (and sometimes unknowingly) made when considering the spread of behaviours. This is that new behaviours diffuse through social networks based on the 'total amount of social connections'; that is, the 'number of unique connections' for unweighted networks or the 'number and the strength of the connections' for weighted networks [4]. Studies often state that individuals with the most social connections are the most likely to gain, and spread, socially informed behaviours [1,2]. Further, along with the qualitative assertion that increased social connectivity increases the potential for behavioural transmission, the primary quantitative method for assessing the spread of behaviours is Network Based Diffusion Analysis (NBDA). This progressive approach has provided much insight into social systems ranging from captive fish and insects to wild birds and mammals [3,4]. NBDA estimates the influence of a social network on the uptake of a behaviour by generally assuming that the likelihood of adopting the behaviour is related to the total amount of relevant network connections to 'informed' individuals [3,4]. This assumption is known as a 'simple contagion' and is analogous to how a disease may spread through a

network based simply on contacts between individuals [5–7].

The notion of the simple contagion of behaviours was initially formalised in sociology, where it was subsequently enormously influential [5,6]. However, an increasing number of empirical studies, particularly from the growing field of computational sociology, are now consistently demonstrating that behaviours may generally spread as 'complex contagions' (Figure 1 and Box 1). The complex contagion concept contrasts with simple contagions. This alternative notion posits that socially induced behavioural change does not simply depend on an individual's total amount of connections to informed individuals, but instead holds some 'complexity' [5,6]. This complexity, for instance, often comes from considering behavioural change in relation to some function associated with the proportion of individuals' social connections to informed individuals. Therefore, the likelihood of adopting a behaviour often depends on the individual's exposure to both informed and uninformed individuals, instead of the simply the sum of connections to informed individuals (Figure 1).

Recent support for the complex contagion of behaviour comes from contexts as varied as human health, technological innovations, political movements, and even social media. Importantly, these empirical examinations of the spread of behaviours have often directly contradicted the patterns anticipated from simple contagions (i.e., simply that increased social connections will increase an individuals' propensity to gain and transmit new behaviours) [5–8] and have shown that 'disease spread' is a flawed metaphor for behavioural transmission [5]. A particularly compelling example comes from disease science itself; the spread of viruses (e.g., influenza, HIV) can be explained relatively
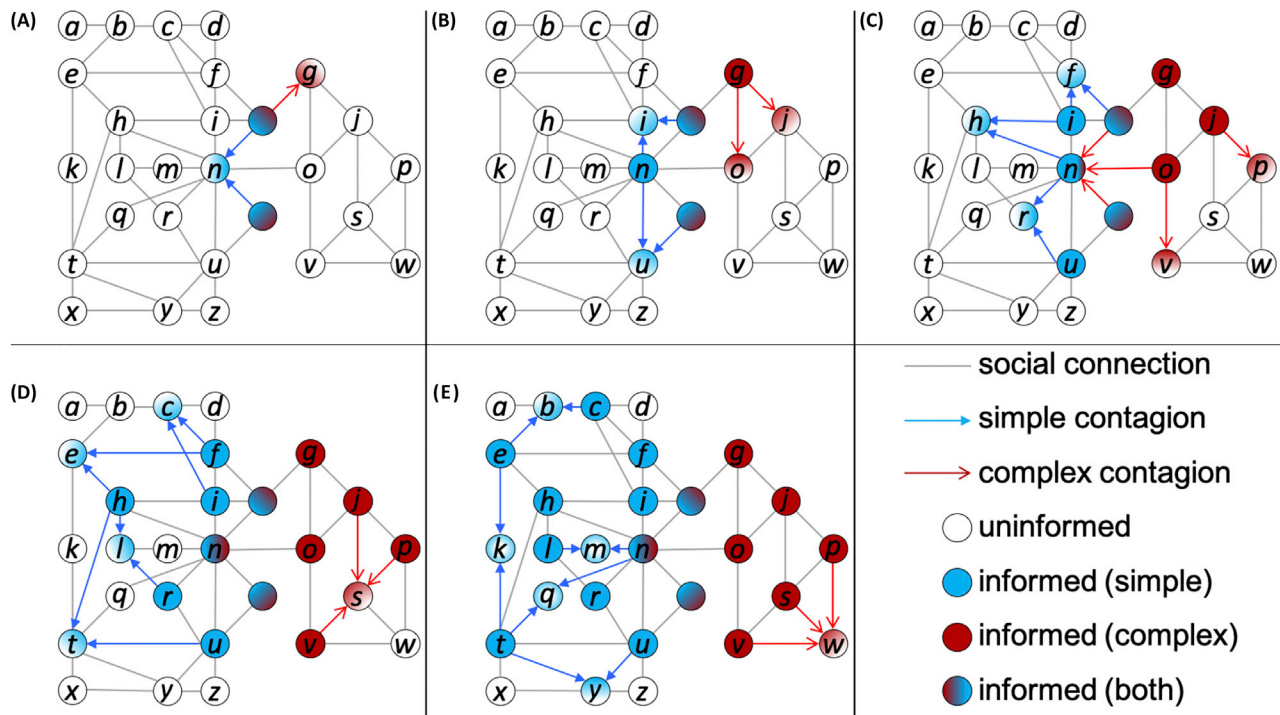
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Figure 1. Simple and Complex Contagions on Social Networks.
Examples (A–E) using undirected unweighted social networks to show how simple contagions can differ from complex contagions. The likelihood of taking up the simple contagion behaviour (S, blue) is based simply on the total amount of social ties to 'informed' individuals (most ties = most likely). The likelihood of taking up this complex contagion behaviour example (C, red) is based on the proportion of ties to informed individuals (highest proportion = most likely). Here, these independent contagions are based entirely on these rules alone, so S spreads primarily through the highly connected individuals (left in each panel) and C spreads through the clustered individuals (right), demonstrating interesting differences. (A) Beginning with two 'starting individuals' (the red/blue individuals holding S and C), individual n (the most 'central', with most connections) has the most connections to the starting individuals and is therefore most likely to take up S, while individual g is most likely to take up C due to having the highest proportion (1/3) of connections to the starting individuals (despite fewer overall connections to them). (B) S is most likely to spread from the starting individuals, or individual n, to the other relatively central individuals i and u, while the more peripheral individuals j and o are most likely to take up C due to higher proportions of connections to C-informed individuals. (C) Only now does n (the most central individual) become one of the most likely to take up C (n, p, and s all have a third of their connections to C-informed individuals). (D) n is not highly influential in spreading C (unlike n was with S), as n's associates are relatively central so only a relatively low proportion of their connections are C informed, and C instead is most likely to spread to the more clustered individual s. (E) Most relatively central individuals are S informed and only peripheral individuals remain unlikely to take up S, while C becomes more established within cliques (e.g., all of w's connections are C informed). Thus, in (A–E), the two independent contagions differ in which individuals are likely to take up the behaviours and subsequently influence their spread.

well by simple models, but the spread of anti-infection behaviours (e.g., vaccinations and HIV-prevention measures, respectively) is not. Instead, adoption of these behaviours is based on more complex social factors, and thus they are likely to be spread as 'complex contagions' [5–7]. This shift in the basic expectations of contagions (from simple to complex) holds important ramifications for considering the spread of behaviours, both in

terms of individuals' adoption of a behaviour and how they may potentially feed back to shape the social structure and subsequent spreading pattern [5–7,9] (Box 1).

Advancing Insights into How Animal Behaviours Spread

Although potentially challenging, many of the separate tools and conceptual

approaches required to develop a general understanding of the contagion of animal behaviours across natural populations already exist. Vast amounts of research on animal Social Learning Strategies (SLSs) [3] have long presented compelling evidence that adopting socially informed behaviours may depend on more than just social connections alone. Animals express various SLSs governing who to learn from and when

Box 1. Altering Expectations: Simple versus Complex Contagions

The interplay between social connections and behavioural transmission [1] is altered when considering complex contagions.

First, the socially central individuals (which hold many dispersed social connections that bridge the network and are not constrained to cliques [2]) are considered particularly important for adopting behaviours and enabling rapid social spreading when the total amount of social connections is considered [1] (i.e., for simple contagions). However, in complex contagions these central individuals can instead be some of the least likely to initially adopt a new behaviour if – for instance – a high proportion of their social connections are directed to those not expressing the behaviour [5,10] (Figure 1A–C). Furthermore, even if these central individuals do adopt the behaviour early, they are less likely to facilitate its spread in a complex contagion if – for instance – behavioural adoption by others depends on multiple social exposures within cliques[5,6,8] (Figure 1D,E).

Second, a dynamic relationship between sociality and behavioural transmission may exist, whereby adopting a behaviour causes individuals to gain new social connections [1]. This feedback would be predicted to promote the spread of behaviour under the expectations of simple contagions. However, changes in social connections that aid simple contagions can hinder complex ones. New sociological research shows that increasing individuals' social connections to non-informed individuals from other social groups can instead decelerate complex contagions [5]. For instance, if newly informed individuals retain their current connections (rather than gaining new connections to non-informed individuals), they have an increased likelihood of: (i) continually expressing the behaviour; and (ii) their group establishing a high prevalence of informed individuals and promoting spread to all members [5]. In this way, maintaining clique-based social organisation can allow complex contagions to become reinforced within local neighbourhoods and ultimately spread the behaviour more effectively [5,8]. This is somewhat comparable with the spread of cooperation, where exposing cooperators to non-cooperators can cause cooperative behaviour to break down [9].

[3,11]. For instance, experiments in wild birds have suggested that SLSs, such as 'conformity' or 'learning from relevant tutors', may influence information diffusion through social networks [11,12]. In this way, SLSs can cause behaviours to spread as complex contagions as transmission is then not just governed by the social network, but also by the specific rule (i.e., the SLS) shaping the uptake of the behaviour from their social connections. Further, the specifics of the SLS will also determine how the spreading pattern differs from that expected from a simple contagion. For example, assessments in captive schooling fish have shown that even the spread of relatively basic behaviours (escape responses) may be markedly better explained by complex, rather than simple, contagions when uptake is based on the proportion, not the sum, of individuals' neighbours expressing the behaviour [10].

It is now important to move forward from generally just considering socially transmittable behaviours to diffuse as simple contagions through wild animal populations. Instead, the unique opportunities that these natural systems present should be utilised to create an ideal framework for directly examining the factors causally shaping behavioural spread across social networks. Specifically, recent – but largely independent – advances in animal social networks provide the opportunity: (i) to experimentally create specified social network structures [11]; (ii) to observe the fine-scale spread of seeded behaviours [10,12] and (iii) how this feeds back onto social connections [1]; and (iv) to statistically quantify the influence of social structure and specific SLSs [4,12] on the dynamics of contagions. Developing and combining these complementary approaches will allow simultaneous quantification of how different behavioural rules, SLSs, and network architectures contribute to the spread of behaviour (and how this feeds back onto social structure itself) in natural populations.

Integration of the complex contagion concepts into the rapidly developing field of animal social networks and social learning would markedly contribute to our understanding of social processes and diverse kinds of socially transmittable behaviours (e.g., movements, foraging, sexual, antipredatory). This will not just reveal how individual network positions and overall society structure relates to behavioural spread, but also aid in establishing which behaviours diffuse differently/similarly to one another, how contrasting contagions may interact with each other, and the wider consequences of these contagions. Furthermore, other systems examining social contagions (e.g., in sociology) often lack some of the capabilities available within natural animal societies [2], such as being able to conduct real-world experiments or track many individuals in great detail across their lifetime and over many generations. As such, the ability to take such a comprehensive approach to testing behavioural transmission within animal social systems now holds the potential to increase conceptual knowledge of complex contagions more generally across disciplines.

Much progress has recently been made in understanding the dynamic relationship between individuals' social connections and the adoption of behaviours in animal systems [1]. However,

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to build on our understanding of sociality and to potentially advance investigations into contagions generally, we now need to explicitly incorporate the recent advances made in other disciplines [5] into the newly emerging approaches in animal behaviour and consistently consider the potential complexity of behavioural contagions in animal social networks.

¹Department of Zoology, University of Oxford, Oxford OX1 3PS, UK

²Merton College, University of Oxford, Oxford OX1 4JD, UK

@Twitter: @JoshAFirth (J.A. Firth).

*Correspondence:
joshua.firth@zoo.ox.ac.uk

References

1. Kulahci, I.G. and Quinn, J.L. (2019) Dynamic relationships between information transmission and social connections. *Trends Ecol. Evol.* 34, 545–554
2. Kurvers, R.H.J.M. *et al.* (2014) The evolutionary and ecological consequences of animal social networks: emerging issues. *Trends Ecol. Evol.* 29, 326–335
3. Hoppitt, W. and Laland, K.N. (2013) *Social Learning: An Introduction to Mechanisms, Methods, and Models*, Princeton University Press
4. Hoppitt, W. (2017) The conceptual foundations of network-based diffusion analysis: choosing networks and interpreting results. *Philos. Trans. R Soc. Lond. B Biol. Sci.* 372, 20160418
5. Centola, D. (2018) *How Behaviour Spreads: The Science of Complex Contagions*, Princeton University Press
6. Guilbeault, D. *et al.* (2018) Complex contagions: a decade in review. In *Complex Spreading Phenomena in Social Systems* (Lehmann, S. and Ahn, Y.Y. eds), pp. 3–25, Springer
7. Campbell, E. and Salathe, M. (2013) Complex social contagion makes networks more vulnerable to disease outbreaks. *Sci. Rep.* 3, 1905
8. Montanaria, A. and Saberib, A. (2010) The spread of innovations in social networks. *Proc. Natl Acad. Sci. U. S. A.* 107, 20196–20201
9. Rand, D.G. *et al.* (2011) Dynamic social networks promote cooperation in experiments with humans. *Proc. Natl Acad. Sci. U. S. A.* 108, 19193–19198
10. Rosenthal, S.B. *et al.* (2015) Revealing the hidden networks of interaction in mobile animal groups allows prediction of complex behavioral contagion. *Proc. Natl Acad. Sci. U. S. A.* 112, 4690–4695
11. Firth, J.A. *et al.* (2016) Pathways of information transmission among wild songbirds follow experimentally imposed changes in social foraging structure. *Biol. Lett.* 12, 20160144
12. Somveille, M. *et al.* (2018) Movement and conformity interact to establish local behavioural traditions in animal populations. *PLoS Comp. Biol.* 14, e1006647