

Review

# Personality in the context of social networks

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There is great interest in environmental effects on the development and evolution of animal personality traits. An important component of an individual's environment is its social environment. However, few studies look beyond dyadic relationships and try to place the personality of individuals in the context of a social network. Social network analysis provides us with many new metrics to characterize the social fine-structure of populations and, therefore, with an opportunity to gain an understanding of the role that different personalities play in groups, communities and populations regarding information or disease transmission or in terms of cooperation and policing of social conflicts. The network position of an individual's experiences (especially in the case of juveniles) and therefore can influence the way in which it interacts with others in future. Finally, over evolutionary time, the social fine-structure of animal populations (as quantified by social network analysis) can have important consequences for the evolution of personalities—an approach that goes beyond the conventional game-theoretic analyses that assumed random mixing of individuals in populations.

Keywords: social networks; personality; social behaviour; cooperation

## **1. INTRODUCTION**

# (a) Why look at personalities in the context of social networks?

Animal personalities are usually defined as withinindividual and between-individual consistency in behaviour (Sih & Bell 2008). For instance, an individual is perceived to be consistently more (or less) cooperative or aggressive than other individuals in most of its interactions. However, behavioural assessments that are based on dyadic interactions only represent a snapshot of the more complex social fabric of which an individual is part (Krause et al. 2007, 2009a,b; Wey et al. 2008; Sih et al. 2009). For a complete understanding of the ecology and evolution of personalities, it might be useful to consider not just the immediate interaction with partners of individuals or the groups that they are members of but also to include indirect relationships (i.e. who is connected to whom via intermediates) and view personalities in the context of the whole population. This is possible through a social network approach that allows us to study individual-level interactions as well as population-level social structures (Croft et al. 2008). The importance of indirect connections is easily understood from the perspective of how information is transmitted through populations or how infectious diseases are passed on between individuals (see also Barber & Dingemanse 2010). Regarding sexually transmitted diseases, for instance, the probability of an individual being infected is not only dependent on its direct sexual contacts but also on those of its immediate partners (via whom it could pick up infections; Krause et al. 2007; Croft et al. 2008). However, the study of transmission processes is only one type of investigation that is facilitated using networks. We can also use networks to study evolutionary processes such as frequency-dependent selection. The network structure selects for the behavioural traits of its constituent members, which means that the network perspective is also important when we want to better understand the evolution of behavioural strategies and personalities.

## (b) Aims of review

The main aim of this review is to provide an introduction to the concept of social networks (to those with a primary interest in personality) and to explain how this concept can be used to better understand the ecology and evolution of personalities and behavioural strategies in general. We will first discuss the fact that some individuals play a much more important role in transmission processes (information or disease) than others and relate these differences to the structure of social networks and the positions that individuals occupy in them. In the following section, we will

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explain how network positions can be statistically characterized, which lays the foundation for relating personalities to influential network positions. We will then ask the question of how social networks develop over multiple generations to gain an insight into the evolution of personalities.

Although our emphasis will be on the discussion of personalities in the context of networks, we will take a somewhat broader perspective throughout this review. Network structures and network positions of individuals can be related to both genotypic and phenotypic differences of individuals and regarding the latter to behavioural characteristics (be they behavioural strategies or personalities) and morphological ones (such as size, sex, body colour, etc.). There are two reasons for this broader perspective. First of all, most of the currently available network literature pertains to morphological traits and behavioural strategies and very little work has been conducted on personalities in animal social networks. Second, the studies using morphological traits and behavioural strategies can be used as templates for work on personalities because the methodological approach is very similar.

#### 2. ROLE OF KEY INDIVIDUALS

Some individuals play an important role in social networks because of the sheer number of their contacts (virtual or real) and others because they interconnect others (Newman 2003; Croft et al. 2008). For the study of disease transmission and for vaccination purposes it can be of vital importance to identify such individuals because they potentially lead to rapid outbreaks in a population or increase the probability of a global outbreak, respectively (Watts & Strogatz 1998). These principles are also used in the world of advertising where celebrities are targeted because of their perceived central role in social networks. The fact that celebrities have a virtual link to their fans (and other people who know them) through the films that they appear in and sports clubs they play for means that any products with which they are associated may be in greater demand. Likewise younger scientists may choose to publish with senior ones to try and use the latter's contact and relationship network for a better distribution of their own ideas. In summary, how individuals are placed in networks can be of a crucial importance depending on the transmission processes that we are interested in.

In most cases, the interaction dynamics of an individual will create its network position which may be influenced by an individual's personality type. However, it is also possible and indeed likely that an individual's personality is also influenced at least partially by its network position. The social environment is a powerful selective force and social experiences may continue to shape the way in which an individual interacts with others. Probably the best examples of how personality can be changed in the longer term by social experiences come from studies on early development (Stamps & Groothuis 2010). In animal contests, it is a well-known effect that cumulative wins affect the initiation and/or outcome of subsequent contests in many species (Hsu *et al.* 2006).



Figure 1. Example of a social network where nodes symbolize individuals (squares denote females and circles males) and edges (lines) social connections between them. This fictitious network comprises 15 individuals (labelled A-O). The size of each symbol indicates an individual's score on a notional personality variable; these and selected individual-based measures are listed in table 1.

Therefore, it might be fair to say that, as winnerand loser-effects are usually demonstrated by showing that prior experience affects an individual's agonistic behaviour against an otherwise equally matched opponent (Chase *et al.* 1994), any standard assay of aggressiveness performed at the beginning of a history of consecutive wins or losses, versus afterwards, could produce rather different scores on this personality trait.

# (a) What can we measure about individuals in networks?

Networks usually consist of individuals (which are represented as nodes) and their interactions (which are represented as lines) (figure 1). Networks can be constructed from any kind of interaction that is of interest, be it spatial (association patterns), aggressive, cooperative, sexual or otherwise. In addition, we can include information on the frequency or intensity of such interactions, their direction (who initiates or who receives) and the order in which they took place (Croft *et al.* 2008). The observation of interactions between animals that are individually identifiable produces information that is stored in matrices from where it can be graphically displayed and used for further processing.

In figure 1, we have created such a graph using a fictitious dataset for illustrative purposes. Let us say that this interaction network is based on the gambit of the group (i.e. individuals that were found together in the same group are connected to each other in the graph; Croft *et al.* 2004). We added attributes of the individuals such as sex and personality type, which enable us to look for correlations between such attributes of individuals and their network position. In the section above we spoke of individuals that interconnect communities or ones that have many social contacts. Network statistics provide many quantitative measures of such individual properties. We could also look at the more global level (of the entire network) for assortative

node/individual	personality score	node degree	path length (to/from a node)	clustering coefficient	node betweenness
A	1	1	4	_	0
В	2	4	3.071	0.333	13.5
С	3	3	3.143	0.333	2.5
D	2	4	2.5	0.5	14
Е	1	3	2.571	0.667	9
F	3	2	2.714	0	4.5
G	2	4	2.071	0.167	49.5
Н	2	4	2	0.333	49.333
I	3	4	2.429	0.5	7
J	2	4	2.429	0.5	11
K	2	6	2.286	0.467	17
L	3	3	3	0.667	0.333
М	4	5	2.857	0.5	2.333
Ν	4	3	3	0.667	0.333
0	3	4	2.929	0.5	1.667
mean values	2.467	3.6	2.733	0.438	12.13

Table 1. Some individual-based measures for the network in figure 1. See text for a definition of measures. In the case of the path length we have calculated the mean distance of nodes to and from a particular node, sometimes called farness.

tendencies and ask the question of whether individuals with similar attributes are connected to each other (Newman 2003; Croft *et al.* 2005). In the following, we will provide a list of network statistics that are useful in describing individual positions or global network patterns and discuss studies that used them. This should enable readers to apply these descriptors to their own datasets. The advanced reader may want to consult Croft *et al.* (2008) for further details and additional network statistics and their use.

The network in figure 1 reveals a number of basic properties at the individual and the global level that can be calculated (table 1). For example, we can calculate for each individual in the network its degree (number of immediate neighbours), cluster coefficient (the degree to which an individual's immediate neighbours are connected), path length (number of connections on the shortest path between two individuals) and node betweenness (the number of shortest paths between pairs of individuals that pass through a particular individual; see Croft et al. 2008 for details). These statistics (which are just a small proportion of those already available from the social sciences literature) can be averaged over all individuals in the network to give an idea of the local and global properties of the network.

The toy network in figure 1 also illustrates other structural features that may be explored via network analysis. Nodes A-G and H-O form clusters of nodes (so-called communities) that are more densely connected among themselves than to others. Many methods for detecting such communities have been developed, and these too have been used in the animal sciences to find layers of social structure in the largely unexplored scale between the group and the population. In our toy network, we could now analyse the extent to which the communities are assorted by personality type or by sex (and whether sex and personality type are correlated). It is also possible, of course, to look at assortment by personality type in the network more generally (regardless of community structure). An example of community analysis for a

figure 2 (see also Wolf *et al.*'s (2007) work on sealions, *Zalophus wollebaeki*). Many of the above network statistics and others can

population of guppies (Poecilia reticulata) is given in

Many of the above network statistics and others can be calculated using the social sciences package UCINET (Borgatti *et al.* 2002; see also Croft *et al.* 2008), which is available from the Internet.

One of the first studies (in the animal behaviour literature) to highlight the position of individuals in social networks was Lusseau & Newman's (2004) work on the social structure of bottlenose dolphins (Tursiops spp.). They used social network analysis to characterize communities and to identify individuals that interconnected these communities, which was indicated by their high betweenness. They suggested that individuals that interconnect communities might be acting as social brokers. Such a suggestion raises interesting questions about the individual differences between dolphins, but without replication, manipulation or indeed a detailed quantification of personality traits of the animals (individual differences were inferred from differences in their network statistics—an interesting point to which we will return later) remains rather speculative.

A study by Flack *et al.* (2006) went a step further and tested the role of high-ranking pig-tailed macaques (*Macaca nemestrina*) for group cohesion. Removal of these individuals from the group demonstrated the expected social fragmentation and supported the idea that dominant individuals socially police other group members thus reducing social conflict. Social network analysis was used to predict the effects of the absence and presence of policing on the social structure of pig-tailed macaques. In the absence of policing, networks for grooming, play and association were smaller and more numerous and the group was characterized by a smaller mean degree and increased social clustering (measured using C, the clustering coefficient) and assortativity.

Another study that used network analysis not only for descriptive purposes but also to make predictions is that by McDonald (2007) on the lekking behaviour



Figure 2. A social network of a guppy population (n = 197) in Trinidad. Guppies from two interconnected pools were marked, released and recaptured daily over the next two weeks. Fish that belonged to the same shoal were connected in the network. Each circle represents an individual male fish and each square an individual female and the size of the symbol is indicative of the body length of the fish. Individuals interconnected by lines were found at least twice together. Five distinct communities (indicated by different colours) were identified in the guppy network. The yellow and green communities belong to the lower pool whereas the grey, blue and orange communities were located in the upper pool. Individuals that interconnect pools are potentially of high betweenness.

of long-tailed manakins (Chiroxiphia linearis). McDonald (2007) showed that the centrality of young males in social networks was a good predictor of social status and mating success in later life (i.e. 4.8 years later). Interestingly, males that had already reached high status did not show particularly high centrality values in their adult social networks, which indicated that this factor only mattered in the early life of these birds. McDonald (2007) used information centrality-which is a measure similar to betweenness but in addition to the shortest path lengths also takes indirect paths into account—as a predictor of status.

Three recent studies made a link between behavioural type and network characteristics in freshwater fishes (Pike et al. 2008; Croft et al. 2009: guppies, Poecilia reticulata; Schürch et al. 2010: cichlid Neolamprologus pulcher). Pike et al. (2008) assessed differences in boldness and shyness in individually marked sticklebacks (Gasterosteus aculeatus) and investigated their network metrics. They found that bold fish had fewer connections (low value of node degree) that were more evenly spread (low value of C) whereas shy fish interacted with fewer fish but more frequently. Croft et al. (2009) found strong assortment by behavioural type, in this case prior predator inspection tendency, in a network of guppies after the individuals assayed had been returned to the wild. This suggests that fish strengthen or cut social ties according to their previous social experiences with conspecifics. In some cases, individuals may have particular habitat preferences and this would not allow full mixing of all individuals resulting in

strong network connections between individuals simply because they prefer the same area (but not necessarily each other). Such habitat preferences need to be taken into account to avoid misinterpreting the results. The work by Krause *et al.* (2009*b*) provides an example of this type of problem. The spotted eagle rays (*Aetobatus narinari*) around Bimini showed strong site fidelity, and a network analysis that does not take this into account could provide misleading results.

The literature on human behaviour contains some interesting studies regarding the relationship between personality traits and social networks (Burt *et al.* 1998; Schaefer *et al.* 2008). The integrated use of questionnaires and the behaviour of people on social network sites provide good opportunities for studying this relationship. A strong link has been identified between personality traits (such as extraversion, neuroticism and conscientiousness) and the tie formation process. In particular, extraversion was found to be influential, with individuals that had high scores (and therefore an outgoing personality) taking up more central positions in friendship networks (Wehrli 2008).

So far we have looked at the relationship between network position and personality, which might answer the question of whether particular personality types occupy particular positions. We also explored the use of network analysis to find out whether animals of similar personality type are connected with each other in networks. Another use of the network approach is to use the network metrics themselves to look for assortativity and to identify potential personality traits. As mentioned earlier, we can easily measure

the degree of individuals in networks to distinguish between those that have many connections and those that do not. Interestingly, most social networks that have been studied to date show positive degree correlations, meaning that individuals with many connections are connected with others that have many connections (Newman 2003)-a fact that can have important consequences for transmission processes on networks. Croft et al. (2005) reported a positive degree correlation in social networks of guppies in the context of association networks that are based on shoal membership. It is important to note that degree is not simply the same as a grouping tendency in this context because a high grouping tendency per se does not necessarily imply many different social contacts. This example shows that we can use high betweenness or degree as our attribute because it is a property of individuals and correlate it with other known traits. Little is known about whether individuals that show high betweenness or degree in one network will generally show this property in all networks that they form part of. The latter is a necessary requirement if these attributes are to be regarded as varying consistently between individuals and thus potential personality traits. By comparing a social network to a randomization we can find out whether there is real and consistent variation between individuals or whether differences in network positions (between individuals) are just noise (Croft et al. 2009). Whether and to what degree individuals consistently occupy particular network positions is something that can be evaluated through repeated measurements and comparisons of observed and randomized network structures by developing appropriate test statistics. For example, it would be possible to rank individuals according to their connectedness each time the network structure is measured and to use the sum of the square sums of these ranks, which is compared with the same test statistic from matching randomisations. If individuals consistently have high and low connectedness, then the observed test statistic would be significantly greater than randomized ones. An additional approach could be to transfer individuals between networks to test whether network positions of individuals are context-invariant and consistent over longer time periods, which could be an interesting project for future studies.

We suggested above that the network position that an individual occupies might in itself be considered as a personality trait. One of the problems that needs to be addressed in this context is that the outcome of an interaction is not always a product of an individual's predisposition alone but in some cases also a result of the behaviour of others towards it (Piyapong et al. 2010). Furthermore, there are questions to be asked about the independence of network positions of different individuals that are part of the same network and the repeatability of such positions being taken up by the same individuals (an issue we already addressed above). Using network position as a personality trait could be relatively straightforward in cases where we see a one-way interaction (e.g. one individual being aggressive towards another). In humans, it has been shown that some social network attributes

(such as centrality and in-degree) are heritable using twin studies (Fowler et al. 2009). It becomes more complicated in cases like cooperation where a link between two individuals in a network can only come about if both of them actually engage in the same behaviour. It might be possible to measure an individual's tendency to be cooperative towards others by using a standard stimulus such as a dummy of a conspecific. Individuals with greater cooperative tendencies should be likely to have more cooperative relationships in networks. This could be tested by taking repeated measurements of individuals' network positions to find out whether there are consistent differences between their positions in this regard. The fact that network positions are not independent of each other can be overcome by comparing the positions of individuals with those in a randomized network (see Croft et al. 2008 for randomization techniques in networks and the technique we describe above).

We would like to finish this section with a note of caution though. From a purely methodological viewpoint it is always risky to give too much importance to the network position of particular individuals, especially if the work was done in the field where cases of mistaken identity are possible or where individuals can be overlooked (James et al. 2009). For instance, if individual G or H got misidentified (figure 1) we might arrive at erroneous conclusions regarding their potential to act as brokers between communities. Such errors can have a dramatic effect on measures of betweenness (Krause et al. 2007) and produce misleading interpretations regarding the role that certain individuals or personality types play in groups or populations. A safer way of collecting or analysing the data is the use of categories or correlations. For example, one could look at the correlation between individual attributes and betweenness rather than focus on the individual with the greatest betweenness and its role in the group or population (see Croft et al. 2008).

#### 3. EVOLUTION OF PERSONALITIES

The traditional use of game theory was based on the assumption that individuals mix freely within a population (Maynard Smith 1982). However, empirical data show that this is rarely the case (Krause et al. 2007; Croft et al. 2008). Animal populations exhibit complex social structures with differences between individuals in their degree of connectedness and centrality. Depending on the actual network structure, different evolutionary dynamics are possible and this has reignited interest by modellers in the evolution of behavioural strategies such as cooperation (Ohtsuki et al. 2006; Santos et al. 2006a,b). In a first approach, the evolution of cooperation was investigated on static networks where individuals were not able to change their network position or their interaction partners. They could only evolve a new behavioural strategy (Ohtsuki et al. 2006; Santos et al. 2006a). The main result from this approach was that cooperation could spread in a network if the ratio of benefits to costs (b/c) exceeded the average number of connections of individuals in the network (Ohtsuki et al. 2006).

However, given the high average number of connections in some real-life networks this would require the benefits to exceed the costs by a huge margin, which turned out to be unrealistic. Furthermore, the use of a completely static network also makes assumptions that are unlikely to be met by many biological systems because most animals have some influence over their network position. In a further development, Santos et al. (2006b) introduced a model which allowed individuals some control over their network connections which meant that they could maintain or cut connections. If a connection is cut then a randomly chosen new connection to a local neighbour in the network is established. They introduced a term W that is positively correlated with the rapidity with which individuals respond to defection (in an interaction with a network neighbour) with rewiring. It is the value of W in relation to the average connectivity in the population that determines whether cooperation can flourish in the population. This type of network dynamics allows for a certain degree of assortativity of social connections as well as a change of behavioural strategy and provides a possible explanation for the evolution of cooperative behavioural strategies under more realistic conditions (i.e. cooperators can choose between their local network neighbours to seek out interactions with other cooperators and thereby avoid defectors).

Studies like the ones by Santos *et al.* (2006*b*) provide a fascinating glimpse into the possible evolutionary dynamics of networks. However, it is important to keep in mind that these are highly abstracted models that play out dynamics over many generations. Therefore, this is hardly the kind of work which is amenable to direct empirical testing though the results may inspire empiricists to look for structural signatures in the social networks of their study systems that are compatible with Santos *et al.*'s (2006*a*,*b*) predictions.

Keeping the above note of caution in mind, we investigated the network structure of a free-ranging population of guppies (Croft et al. 2009). In the laboratory, we repeatedly measured the tendency of guppies to leave a shoal and inspect a predator model that provides a proxy of cooperative behaviour. Combining the two variables into one behaviour type we found that between-individual differences were highly consistent. After being returned to the wild, the association network of the guppies was assessed and we found that fish were significantly assorted by behaviour type. Individuals that were deemed more cooperative (according to the behaviour type we defined) had strong repeated interactions primarily with other cooperators and only weak social links with defectors. This result strongly suggests that these fish assort by personality type in the wild and is consistent with the model predictions by Santos et al. (2006b).

Insights into evolutionary processes are also possible from species or population comparisons (Harvey & Pagel 1991; Krebs & Davies 1993; Krause & Ruxton 2002). The costs and benefits of personality types such as shyness and boldness depend on the environment (Réale *et al.* 2010). And the investigation of populations in different ecological conditions can shed light on the occurrence and frequency of different personality types in populations (i.e. proportions of bold and shy individuals). Whether different social network structures are found in different environments and the role that different personality types might play in them could then be studied. In small freshwater fishes such as sticklebacks and guppies such population differences in the context of specific ecological constraints have been well documented and would provide a ready template for this approach (Croft *et al.* 2006; Botham *et al.* 2008).

## **4. FUTURE PERSPECTIVES**

The study of personalities in the context of networks is not without its problems and challenges. Network studies require that all individuals are marked and that social contact patterns of entire groups or even populations (or at least large proportions of populations) can be recorded. This is usually not possible without some considerable logistic effort and often requires an entire research team. The possibility of emigration and immigration processes and of course mortality poses further difficulties when assessing social networks in the field. In addition, screening the personalities of large numbers of individuals is a time-consuming exercise, which is fraught with its own problems. Nevertheless, this type of approach that builds up population-level information from individual contact patterns has the potential to provide unparalleled insights into processes that underlie the evolution of personalities and behavioural strategies. We miss out on a wealth of information regarding the rich social fabric of real animal populations when using models that make simplistic assumptions such as random interaction between individuals. Recent models that explore the evolution of behavioural strategies on networks indicate that the social fine-structure of populations (as revealed by networks) is of crucial importance for an understanding of evolutionary processes (Ohtsuki et al. 2006; Santos et al. 2006a,b). More empirical work in this area is urgently needed to increase the realism of future models and to properly integrate empirical and theoretical work.

What can different study systems offer in this context? Work on primates and cetaceans has the advantage of complex social systems and cognitively highly developed individuals with differentiated personality traits (Flack *et al.* 2006). But a price has to be paid in terms of the logistic effort required for their study, which usually results in a lack of replication (and sometimes manipulation and control experiments). Small freshwater fish have become popular systems for the study of social networks (Croft *et al.* 2004; Pike *et al.* 2008) because they allow replication and manipulation and the individuals are sufficiently complex to allow characterization of their personalities.

Little is currently known about the relationships between animal personalities and network position (in contrast to the literature on humans; Schaefer *et al.* 2008). The work by Pike *et al.* (2008) provides insights into how bold and shy individuals differ with regards to their network connections. More studies along these lines are needed to better understand some basic relationships between personalities and networks and we can learn in this area from the psychological literature on human social networks where this is already a well-established topic. Which personality types take up central positions, positions of high betweenness or high connectedness? Are these network positions specific to the network inhabited by this individual or can we generalize across networks? How important is social recognition in this context? To which degree is the network structure a result of experiences that result from past interactions with individually recognized conspecifics? The work by Croft et al. (2009) suggests that the latter could play an important role in structuring networks and placing individuals within them. Furthermore, we need to gain a better understanding of what the population-level consequences are of links between personality types and network positions in the context of social cohesion (this is an area where Flack et al.'s (2006) study provides an excellent template for further experimental work), information transfer, disease transmission and cooperative processes (see Croft et al. (2009)).

Experimental manipulations that are commonplace in other areas of behavioural ecology are still in their infancy in social network studies (partly because of the logistic difficulties discussed above) and this is certainly an area that provides a promising field for future work. Once an individual's position in a network has been characterized, group composition could be changed (while controlling for group size) to assess whether the individual will consistently take up the same network position independently of the particular group composition. In additional experiments, group size could be changed to assess the importance of this factor. It is conceivable that interaction patterns that lead to a particular network position in a small group do not produce the same result in a large group. Such scaling issues are a field of particular interest in network studies (Lehmann & Dunbar 2009) but require careful analysis to detect the biologically relevant information. Likewise removal (or introduction) experiments (Flack et al. 2006) of particular individuals or groups of individuals can provide new insights into the dynamics of networks.

For natural selection to act on the evolution of personality traits there needs to be heritable variation. Previous work looking at personality traits in great tits, *Parus major*, and sticklebacks, *G. aculeatus*, has shown that they are heritable (Dingemanse *et al.* 2007, 2009). An interesting question for future research is the extent to which social network attributes are themselves heritable and thus could be subject to natural selection. While there has been no work in this area on non-human animals, work on humans has demonstrated heritable variation in network measures such as centrality (Fowler *et al.* 2009). Quantifying the heritability of social network attributes in animals provides an exciting area for future research.

The rapid development of new technologies provides interesting opportunities for network studies and may help overcome some of their logistic difficulties discussed above. Many species are large enough to carry pit-tags that allow automatic registration of the individuals within the range of a sensor, which is a cheap way to tag large numbers of individuals. A more expensive but more powerful approach is to fit animals with proximity receivers that can register the presence of others within a certain range that carry the same technology (Guttridge *et al.* 2010). This approach allows the building up of interaction data (frequency, duration, etc.) between individuals that range over large distances and could provide detailed information about the social contact patterns in relation to personality types.

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