1. INTRODUCTION

When deciding with whom to mate, where to forage or when to abandon a resource patch, many species rely not only on their own personal information, but also on social information provided by the decisions or performances of conspecifics [1,2]. The use of social information is expected to be advantageous because it allows individuals to acquire more information, especially when the acquisition of personal information is costly, and so leads to more appropriate decisions [3,4]. Conversely, when the acquisition or exploitation of social information is costly [5–8] or its information is outdated or inappropriate [9,10], animals should prefer personal information. So we expect that animals should be capable of adjusting the weight they give to personal and social information according to circumstances. Supporting this expectation, van Bergen et al. [11] reported that nine-spined sticklebacks (Pungitius pungitius) flexibly adjust their decision-making to exploit the most reliable information available, when personal and social information conflict. Also, a number of studies have demonstrated that reliance on public information increases as the cost of acquiring accurate personal information increases (reviewed by Kendal et al. [6]). However, despite their ability to alter the relative weight of social and asocial information, individuals generally differ consistently in their tendency to weight one source of information against the other [12–14], as well as in their ability to adjust their behaviour to local conditions [15]. The most commonly invoked hypotheses to account for such individual differences of tactic use and behavioural plasticity call for intrinsic differences in terms of genetic quality [16], metabolic needs [17,18] or related personality traits [19], that would constrain individuals to use one strategy at the expense of the others and/or prevent them from modifying their behaviour when conditions change. Observations that individuals which rely preferentially on social information are also either shyer (barnacle geese: [20]), more exploratory (three-spined sticklebacks: [21]), or faster at exploring (great tits: [12]) all provide support for such a hypothesis. But, even though the correlation between personality and social information use seems well established, we know next to nothing about its cause.

One potential causal explanation is that individuals with different physiological or behavioural characteristics differ in their ability to collect social or personal information. For instance, shy individuals have a stronger tendency to remain close to conspecifics [22–24] and this could facilitate the acquisition of social information. Conversely, as bold individuals tend to explore more quickly but also more superficially [25], they may be at a disadvantage in terms of assessing their environment reliably from personal information and so may use socially acquired information instead. So, in both cases, the decision to use personal or social information maximizes payoffs, subject to the individual’s ability to acquire either type of information.

**Keywords:** individual differences; social information use; frequency-dependence; sequential decision-making; producer–scrounger game; personality

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We propose a novel explanation for the consistent correlation between social information use and personality which assumes (i) that the gains associated with each behavioural alternative are frequency-dependent and so depend on the choices of others and (ii) that individuals choose options sequentially such that the degrees of freedom of choice decline with the order of choice. Depending on the system, sequential decisions could be enforced, say, by birth order, or differences in time to reach sexual maturity, or arrival at nesting sites or any event that sets off a cascade of choices all influenced by the initial order of the triggering event. One case in which these assumptions apply repeatedly is when animal groups move through space such that they arrive in a habitat sequentially. If, as has been suggested by a number of published studies of group-living animals, the order in which individuals move between locations remains consistent over time and across contexts say because it is related to individual characteristics, such as dominance [26], exploration [27,28] or boldness [29,30], then an individual’s sequence of arrival may constrain its choice of options leading to the emergence of correlated behaviours. This correlation would be a simple by-product of the sequential decision-making process in a frequency-dependent context.

To test this new explanation, we developed an individual-based model of sequential frequency-dependent choice set in the context of a group moving through habitats while socially exploiting resources as a producer–scrounger (PS) game [31,32]. In this model, individuals at any given time can employ either the producer tactic and search for unexploited resources, thereby relying on personal information, or use the scrounger tactic and search for opportunities to join resources uncovered by any other group members, thereby relying on social information. So we will use producer and scrounger foraging tactics as indicators of an individual’s reliance of personal or social information, respectively. We assume, as is commonly the case, that producing and scrounging are incompatible search modes and the payoffs associated with both tactics are negatively frequency-dependent [33]. We show that the order in which animals enter a foraging area influences both their use of personal or social information, the extent to which they exhibit plasticity and more importantly, that individuals remain consistent in their use of personal versus social information over time and across conditions.

### 2. THE MODEL

The model simulates a group of $G$ identical individuals (all parameters are listed in table 1) searching for food in a foraging area that can be represented as a matrix of $(N \times N)$ patches, among which only $n_F$ randomly chosen patches, contain $F$ indivisible food items. A simulation proceeds by time steps $t$, and ends after $T$ time steps. In the course of the first $T G$ time steps each of the $G$ individuals enters one at a time (i.e. only one new individual is introduced at every time step) in the foraging area. Once in the area they can choose at each step $t$ whether to play producer (use personal information) or scrounger (rely on social information). The following sequential procedure is used at each $t$: we consider successively all the individuals that have been in the foraging area for at least one $t$ and if $t < G$, we add a new individual. For simplicity, we assume that during a single time step a forager cannot eat more than one food item and a producer cannot assess the quality of more than a single unexploited patch.

<table>
<thead>
<tr>
<th>symbol</th>
<th>meaning</th>
</tr>
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<tbody>
<tr>
<td>$G$</td>
<td>number of individuals (i.e. foragers within the group); default value: 10</td>
</tr>
<tr>
<td>$N \times N$</td>
<td>dimension of the foraging area (i.e. number of patches); default value: 100</td>
</tr>
<tr>
<td>$n_F$</td>
<td>number of food patches; tested values: 10 and 20</td>
</tr>
<tr>
<td>$F$</td>
<td>value of food patches; tested starting values: 5, 10, 15, 20, 25, 30</td>
</tr>
<tr>
<td>$T$</td>
<td>number of time steps per simulation; tested values: 40, 60</td>
</tr>
<tr>
<td>$x$</td>
<td>number of consecutive time steps with no reward at which individuals switch from producer to scrounger; tested values: 5 and 10</td>
</tr>
<tr>
<td>patch_value ($j, t$)</td>
<td>value of the patch $j$ at time $t$ (from 0 to $F$)</td>
</tr>
<tr>
<td>patch_state ($j, t$)</td>
<td>state of the patch $j$ at time $t$: 0 if no competitors and 1 if at least one competitor</td>
</tr>
<tr>
<td>position ($i, t$)</td>
<td>location of the individual $i$ at time $t$</td>
</tr>
<tr>
<td>tactic ($i, t$)</td>
<td>tactic adopted by individual $i$ at time $t$; the variable takes value 0 if the individual plays scrounger or value 1 if it plays producer</td>
</tr>
<tr>
<td>success ($i, t$)</td>
<td>variable defining the state of the individual $i$ at time $t$ (0 if it has no access to food and 1 if it has access)</td>
</tr>
<tr>
<td>payoff ($i, t$)</td>
<td>cumulative payoff for the individual $i$ at time $t$</td>
</tr>
<tr>
<td>failure ($i, t$)</td>
<td>number of consecutive attempts at time $t$ in which the individual $i$ failed at finding food as a producer</td>
</tr>
<tr>
<td>duration ($i, t$)</td>
<td>number of steps from the beginning of the simulation during which the individual $i$ was present in the network at time $t$</td>
</tr>
</tbody>
</table>

### (a) Decision rules of the newly arriving individuals

When the simulation model adds a new individual into the foraging area, its spatial location is selected randomly among all currently unattended empty patches. We assume that all newly arriving individuals first start by using social information and so deciding to play scrounger, and as a result assess the availability of joining opportunities, that is whether at least one competitor is currently exploiting an undepleted patch. When playing scrounger, individuals can detect without error all joining opportunities, whatever their distance, and will always join the closest one and obtain one food item. However, if no joining opportunity is available they get no food and will switch to the producer tactic at the next time step. Thus, at the end of the first step, a newly arriving individual can be in one of two possible states: $SF$ (it played scrounger and
got one food item) or SN (it played scrounger but obtained no food because there were no joining opportunities).

(b) Subsequent time steps
For each of the subsequent time steps, all individuals already present on the foraging area for at least one time step, one after the other, make a decision. In order to ensure that behavioural differences among individuals did not result from their decision order but only because they differed in their initial arrival order, the order at which they made a decision was randomly assigned at each step. Each individual’s behaviour is determined by the success of the tactic it adopted in the previous time step (figure 1). Specifically, if they obtained food in the previous time step, either as a producer or as a scrounger, they keep the same tactic. If no food was obtained as a scrounger in the previous step they switch to producing and search for their own food. Finally, if they were unsuccessful as producers for $x$ consecutive attempts during the previous steps they switch to the scrounger tactic, or otherwise keep playing producer (figure 1).

Note that at each step the food value of a patch differs among individuals on that patch, depending on the order of their decision, and each individual makes a decision based on the current value of the patch. Thus, if an individual obtained food on the previous step as a scrounger (i.e. SF at $t-1$), it remains in the same patch and gets one food item provided that the value of the patch, at the moment it makes a decision, is larger than zero (i.e. SF at $t$). If, on the other hand, the patch is depleted, it continues to search as a producer by moving to the closest unoccupied patch to assess its quality, and gets either a food item if the assessed patch contains $F$ food items (i.e. PF at $t$), or no food if it is empty (i.e. PN at $t$).

At the end of the second and subsequent time steps, each individual can then be in one of four possible states (figure 1): SF (it played scrounger and got one food item); SN (it played scrounger and got no food); PF (it played producer and got one food item and PN (it played producer and got no food). Once a food patch was depleted it was replaced by a new patch containing $F$ food items and whose position was randomly selected among all unoccupied (with no competitor) and empty (with no food) patches. In our analyses, we only consider this simple decision rule because the advantage of using one particular decision rule rather than any other rules is less important in small group sizes compared with larger groups. Indeed, Hamblin & Giraldeau [34] demonstrated from an agent-based model that the relative payoff sum (RPS) decision rule evolved to fixation more frequently compared with the two other competing rules (i.e. linear operator (OP) and perfect memory (PM) decision rules). However, the predominance of the RPS rule was more pronounced in large group sizes, compared with small groups of 10 or less, for which any of the three
learning rules ought to be expected. Furthermore, at all group sizes, the residual value associated with the producer tactic was larger than the residual value associated with the scrounger tactic. This means that individuals should never give up the producer strategy even when it temporarily fails to provide rewards, while it can pay to stop scrounging when current payoffs are low. Thus, based on this prediction, we assumed in our model that producers were more persistent in their tactic use compared with scroungers.

(c) Definition of the state variables
Each individual is characterized by a set of state variables (table 1):

— its location at each time step (i.e. position),
— a tactic variable that takes value 0 or 1 if it plays scrounger or producer, respectively, at each time step,
— a failure variable that represents the number of consecutive attempts in which the animal failed at finding food as a producer,
— a strategy variable that corresponds to the number of steps during which it has played producer from the beginning of the simulation,
— a success variable that takes value 0 or 1, depending on whether it succeeds or fails to find one food item at every time step,
— a payoff variable that represents the cumulated number of food items obtained by an individual among the successive time steps of a simulation, and
— a duration variable that represents the number of time steps during which it was present in the area from the moment of its arrival. Given that the individuals enter sequentially, each exploits the foraging area for a different number of time steps and this variable is used to estimate the mean payoff obtained per time step by each individual as well as the frequency at which it has played the producer tactic by the end of the simulation.

The patches are defined by two state variables that reflect their value and whether or not they are occupied by at least one competitor at every time step.

(d) Procedure and analyses
To ensure comparability across simulations, we fixed G at 10, the total number of patches at 100 and the number of successive failures producers had to experience before switching to the scrounger tactic (x) at 10, and varied the number of food patches (nF), the values of the food patches (F) as well as the number of consecutive time steps in each simulation (T). In total, the simulations inspected 24 different conditions, and each was run 20 consecutive times. For each condition, we could then calculate the mean frequency at which the producer tactic was used by each individual and the level of individual behavioural plasticity measured as the variance around each mean.

The influence of these three parameters (nF, F, T) as well as their interactions, on the mean producer tactic use, were assessed by conducting a three-factor analysis of variance (ANOVA). We performed this analysis in order to ensure that the decision rule we used generated realistic predictions. More precisely, we verified that the mean expected frequency of producers decreased when both the value of the food patches [35] and their density [36] increased. Also, we tested whether the order of arrival of the individuals was correlated with their mean frequency of using the producer tactic, their average individual level of plasticity and their payoffs. To do that, we conducted linear regression analyses for each of the 24 conditions, and then compared the mean coefficients of correlation with zero using t-tests. To allow comparisons across simulations, the cumulative payoff of each individual was expressed in percentage of food obtained, by comparison to the most successful individual in every simulation. Furthermore, to assess the extent to which our conclusion about how the time spent by the animals on the foraging area affected the link between arrival order and both mean tactic use and individual level of plasticity, we conducted the analyses on the data pooled over the two simulation lengths and then for each simulation length separately. Finally, to determine whether the order of arrival consistently affected the behaviour of the individuals among conditions, we assessed for each given pair of conditions (i,j), the correlation between the relative rate at which the individuals (defined by their order of arrival) played the producer tactic in condition (i) and in condition (j). Then we tested whether the mean correlation coefficient estimated from the 276 pair-wise comparisons significantly differed from zero using a r-test. All statistical analyses were performed with SPSS v. 16.0 for PC.

(e) Assuming that unsuccessful producers are less persistent
To assess the extent to which our conclusion on the effect of arrival order on tactic use and individual level of behavioural plasticity was affected by the number of successive failures producers had to experience before switching to the scrounger tactic, we ran additional simulations for the 24 same conditions as mentioned earlier, but with a number of consecutive attempts with no reward (x) equal to five.

3. RESULTS
(a) Mean tactic use
The number of available food patches (nF) as well as their value (F) affected the mean proportion of producers at equilibrium (figure 2). The producer tactic is used less when the number of food patches (three-factor ANOVA: F_{2,216} = 33.49, p < 0.001) and their value (F_{5,216} = 87.41; p < 0.001) are increased. Conversely, the frequency of the producer tactic was not affected by T (i.e. the time spent by the individuals on the foraging area; F_{2,216} = 2.57, p = 0.110) and there was no interaction between the simulation length (T), the number of food patches (F_{1,216} = 3.31, p = 0.069) nor their value (F_{5,216} = 0.30, p = 0.915).

(b) Inter-individual variation in tactic use, payoffs, plasticity and consistency
The arrival order of individuals was negatively correlated with the mean frequency at which they chose to play the producer tactic (mean correlation coefficient r = −0.80, t_{23} = −39.16, p < 0.001; figure 3a), but positively related to the mean level of individual behavioural plasticity (mean correlation coefficient r = 0.66, t_{23} = 14.68, p < 0.001; figure 3b). So, individuals that arrived first chose...
to play producer more frequently and their choice remained consistent over time. Furthermore, the effect of arrival order on the mean tactic use did not differ between the two simulation lengths ($T = 40$; $r = -0.080$, $T = 60$; $r = -0.79$; $t_{23} = 0.16$, $p = 0.874$). Similarly, the effect of arrival order on the individual level of behavioural plasticity was high whether individuals play 40 ($r = 0.71$) or 60 consecutive steps ($r = 0.61$) and the difference between the two estimates of correlation is not significant ($t_{23} = 1.11$, $p = 0.278$). The order of arrival of an individual on the foraging area also strongly and positively affected its average payoff per time step (mean correlation coefficient $r = 0.80$, $t_{23} = 25.14$, $p < 0.001$; figure 4a) as well as its payoff over the whole simulation (mean correlation coefficient $r = 0.60$, $t_{23} = 9.33$, $p < 0.001$; figure 4b). Thus, the individuals that arrived first relied more on the producer tactic, exhibited less plasticity and were less efficient at obtaining food at each time step, compared with later arriving individuals.

The individuals’ order of arrival affected their mean tactic use similarly in almost all conditions. The average between-condition correlation coefficient in the frequency of the producer tactic for the 276 pair-wise comparisons was 0.63 and highly significant ($t_{275} = 61.03$, $p < 0.001$). Thus, between-individual consistency in the order of arrival leads to consistent tactic use across conditions. First arriving individuals relied more on the producer tactic compared with those arriving later, whatever the condition tested.

Finally, the effect of arrival order was reduced when unsuccessful producers persisted less in using a producer tactic (i.e. $x = 5$). However, in these conditions, arrival order kept having a significant effect on both mean tactic use (mean correlation coefficient $r = -0.65$, $t_{23} = -17.69$, $p < 0.001$) and behavioural plasticity (mean correlation coefficient $r = 0.47$, $t_{23} = 8.50$, $p < 0.001$). Thus, even when individuals switch from producing to scrounging more frequently, we predict that individuals arriving first are constrained to use the producer tactic more and are also more consistent in their tactic use from one simulation to the next for a given condition.

as suspected, the lower correlations between arrival order and mean tactic use and plasticity in that condition.

Figure 2. Mean ($\pm$ s.e.m.) frequency at which the $G$ individuals play the producer tactic in relation to patch richness ($F$). For panels in the first and second column, the number of available food patches ($n_F$) is fixed at 10 and 20, respectively, while the number of time steps per simulation ($T$) is fixed at 40 and 60, for panels in the first and second line, respectively.

Figure 3. Effect of the order at which the individuals are added in the foraging area on: (a) the mean ($\pm$ s.e.m.) frequency at which they rely on the producer tactic and (b) the mean ($\pm$ s.e.m.) level of individual plasticity estimated from 20 repetitions for each condition.
were: despite arrival order having a significant effect on both mean tactic use and behavioural plasticity when producers switched to the scrounger tactic after five or 10 unsuccessful consecutive attempts, the effects were more pronounced when unsuccessful producers persisted more in using the producer tactic. This is because first arriving individuals rely more on personal information during the first time steps, compared with those who are introduced later, because they have less chance to detect a joining opportunity when they arrive. Whether these differences in individuals’ tactic use persist over time, therefore, strongly depends on how many empty patches producers visit before switching to the scrounger tactic. Hence our results suggest that the influence of arrival order might vary depending on the type of the resources, how they are spatially distributed as well as the amount of environmental variability.

Consistent individual differences over time in both tactic use and behavioural plasticity arose in our simulations because individuals maintained a consistent order of arrival from one foraging event to the next. For this to happen, group composition must remain fixed over successive decision episodes so that the first decision order at some earlier time can exert an influence on later first decision orders. Such dependency may arise for at least two different reasons: experience of one decision episode influences the sequence of arrival in the next thereby leading to differences in leadership among the members of a group even in the absence of any variation in state [37,38], or individual arrival sequences depend on intrinsic individual attributes (e.g. dominance rank, activity level, boldness, exploratory tendency or hunger level) [27,28,30,39]. In that later case, we would not only expect that individuals will differ consistently in their tactic use and level of behavioural plasticity, but that those differences will also be correlated with the intrinsic attributes that determine the order of arrival. No study has yet demonstrated that the use of alternative tactics and adjustment in tactic use in a social context are affected by the order in which individuals decide. Some experimental results, however, indicate that such consistency may depend, as we predict, on keeping group compositions unchanged. Morand-Ferron et al. [40] tested nutmeg mannikins (Lonchura punctulata) in a PS game. The birds were exposed to different food distributions and the tests were repeated at a six month interval. They found that the birds showed consistent individual differences in their use of tactics that persisted under different food distributions and over the six month interval when the flock members were reunited with the same flockmates, but not when flock members were different [40]. Other studies suggest that personality traits will exert effects on the sequence of decision opportunities. For instance, Kurvers et al. [30] show that bold barnacle geese (Branta leucopsis) arrive more quickly on food patches. They also show, as we would expect from our simulation, that individuals show consistent differences in foraging tactic use that are related to boldness and so perhaps the order of arrival [41]. A simple way to test whether boldness per se or its consequence, order of arrival, are the cause of increased use of producer would be by experimentally controlling individuals’ order of arrival at a foraging site and testing to see whether boldness still exerts an effect on foraging tactic use.

4. DISCUSSION

Our simulation results confirm that consistent individual differences in behaviour both over time and across conditions can arise from frequency-dependent payoffs of sequentially deciding individuals. The results indicate that the order of arrival on a foraging area creates a dynamic process that channels individuals into consistent roles. We show that individuals arriving first on the area tended to play the producer tactic more frequently and so as a consequence relied on personal information to a greater extent. Moreover, they were also more consistent over time in their tactic use, compared with later deciding individuals. These results are robust given that individuals played repeatedly and could switch tactics during a simulation. Furthermore, the same patterns were detected whatever the simulation length and so despite the order at which individuals make their decision at each time step was randomly selected. Finally, predictions from our simulation model not only apply to social information use but also to any other situations where one or more individuals (scroungers) can reduce the costs of obtaining a resource by exploiting the investment of others (producers). Thus, scroungers can benefit from stealing not only social information produced by the behaviour of others, but also food, mating opportunities or parental care [32]. The magnitude of the effects of arrival order, however, depended on how persistent unsuccessful producers
As the order of arrival influences individual's behavioural plasticity in our model, the consequence is a group composed of both plastic and fixed individuals. Behavioural plasticity is generally considered to be beneficial [42,43], given that it allows individuals to adjust their behaviour when local conditions change and hence reduces the risk of responding inappropriately. As a consequence, the lack of behavioural plasticity is often taken as evidence for the costs of plasticity [44,45]; it could increase mortality during information sampling or could impose energetic costs to build and maintain the required sensory machinery. Because of its cost, therefore, behavioural plasticity is expected only in high-quality individuals that can afford it. Our results contradict this commonly accepted interpretation in two ways. First, despite their early arrival tendency within areas, relatively fixed individuals were less efficient at finding food at each time step compared with plastic individuals. Second, our model predicts individual variation in plasticity as a result only of the order of arrival on the foraging grid and does not require assuming a cost of switching from one tactic to the other or among individual differences in the ability of either detecting food patches or scrounging opportunities. Recent models examining the evolution of behavioural plasticity in social foraging games [38,46–48] have demonstrated that frequency-dependent selection may result in a stable polymorphism of plastic and fixed individuals as well. Although frequency-dependence is also one important component that favours individual differences in behavioural plasticity in our model, we predict that the apparent lack of behavioural plasticity of some individuals does not have to reflect their inability to modify behaviour but may simply follow from their early arrival in foraging areas. Therefore, depending on the social context experienced by the individuals, they might be either fixed or plastic over time, and, on average, all group members should demonstrate a similar level of behavioural plasticity. Experimental manipulation of the order of arrival of each individual will offer a way to detect if consistent individual differences in behavioural plasticity reflects either an intrinsic individual feature of tactic use (e.g. genetic or developmental) or the effect of a frequency-dependent process related to the order of arrival.

Our findings have the advantage of providing a simple behavioural explanation for cases of consistent individual differences. Indeed, when personality traits, such as boldness or exploratory tendency influence the order of decision-making, we predict that consistent individual differences in information use and in plasticity of information use will be correlated to these traits. Consistent with our simulation a number of studies have reported that bold individuals are relatively fixed in their behaviour compared with shy individuals that display greater plasticity [49–52]. To date, few studies have explored the link between differences in tactic use, plasticity and personality traits, and those that have consistently refer invoke adaptive rather than proximal explanations [53–56]. For instance, correlations between tactic use and personality traits could exist because they share the same underlying endocrine mechanisms or because of genetic correlation between the genes coding for the two traits (i.e. pleiotropic effects or linkage disequilibrium). In general, it is assumed that selection acting on trait combinations would have led to such correlation. Here, we show that tactic use and its plasticity reflect adaptive solutions to a frequency-dependent choice in response to the order of decisions of individuals arriving on a foraging area. When, on one hand, an intrinsic individual feature (e.g. personality) affects the order of arrival of an individual, an ‘adaptive’ correlation between that feature and tactic use (and its plasticity) arises based on the frequency-dependent processes that are associated with the order of arrival. In other words, our model does not involve any genetic basis for the link between personality and tactic use. When, on the other hand, the order of arrival at the first foraging event is random but has a contingent effect of the order of arrival on a new area in subsequent events (i.e. the first individuals to arrive on an area will be the first to leave that area and to move to another area), spurious intrinsic-like individual consistency in tactic use and plasticity can be generated. In this case, consistency in tactic use is proximal and conditional of the order of arrival and not an intrinsic individual feature. We predict that such behaviourally maintained group-specific individual differences can arise whenever factors promote sequential choice in a frequency-dependent situation. This may occur, for instance, if females arrive sequentially at a mating ground and must decide whether to copy mate choice of others or sample for themselves. It could also apply to males arriving sequentially to breeding territories where early arriving males get choice opportunities that are different from the later arriving ones. If personality or the order of arrival itself affects the order of arrival in the next season, consistent behavioural differences are to be expected. We then strongly encourage others to explore the potential role of order effects in generating spurious, intrinsic-like behavioural differences associated with animal personality in a wide range of behavioural systems.

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