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Personality composition alters the transmission of cuticular bacteria in social groups

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The initial stages of a disease outbreak can determine the magnitude of the ensuing epidemic. Though rarely tested in unison, two factors with important consequences for the transmission dynamics of infectious agents are the collective traits of the susceptible population and the individual traits of the index case (i.e. 'patient zero'). Here, we test whether the personality composition of a social group can explain horizontal transmission dynamics of cuticular bacteria using the social spider *Stegodyphus dumicola*. We exposed focal spiders of known behavioural phenotypes with a GFP-transformed cuticular bacterium (*Pantoea* sp.) and placed them in groups of 10 susceptible individuals (i.e. those with no experience with this bacterium). We measured bacterial transmission to groups composed of either all shy spiders, 10% bold spiders or 40% bold spiders. We found that colonies with 40% bold spiders experienced over twice the incidence of transmission compared to colonies with just 10% bold individuals after only 24 h of interaction. Colonies of all shy spiders experienced an intermediate degree of transmission. Interestingly, we did not detect an effect of the traits of the index case on transmission. These data suggest that the phenotypic composition of the susceptible population can have a greater influence on the degree of early transmission events than the traits of the index case.

1. Introduction

The transmission of microbial agents from exposed to susceptible hosts represents one of the central forces regulating infectious disease dynamics. It has long been recognized that hosts vary in their likelihood of acquiring and transmitting infectious agents in both human and wildlife diseases [1,2]. Recently, variation among hosts in their behavioural traits and social tendencies have emerged as potential explanations for heterogeneity in disease susceptibility and transmission potential [3,4]. Few studies, though, link the behavioural traits of infected and susceptible individuals to identify combinations that may facilitate the transmission of microbes.

A posteriori studies using molecular tools or theoretical modelling have identified that the actions of one or a few infected individuals are often important in the early stages of epidemics [5–7]. Likewise, populations harbouring a greater diversity of genotypes [8], behavioural phenotypes [9] and patterns of social interactions [10,11] can reduce the spread of infectious agents. However, few studies have compared the relative influence of the individual traits of the index case versus the collective traits of the susceptible population (i.e. its phenotypic composition) in determining the degree of transmission.

Table 1. Summary for statistical models predicting (a) colony-wide bacterial transmission and (b) contacts with the index case while resting. Significant effects in italic.

effect	F-value	d.f.	p-value
(a) colony-wide bacterial transmission			
boldness of index case	0.60	1, 41	0.44
colony composition	*6.93*	*2, 41*	*0.003*
colony composition × index boldness	0.85	2, 41	0.44
body condition of index case	2.97	1, 41	0.09
colony mean body condition	2.66	1, 41	0.11

effect	χ^2	d.f.	p-value
(b) contact with index case			
boldness of index case	0.31	1	0.58
colony composition	*7.65*	*2*	*0.02*
colony composition × index boldness	2.48	2	0.29
body condition of index case	0.09	1	0.77
colony mean body condition	2.87	1	0.09

Here, we use the social spider *Stegodyphus dumicola* as a model to test how the behavioural composition of a social group affects the transmission of a fluorescent cuticular bacterium from the first exposed individual. Previous work demonstrated that cuticular bacterial transmission between two individuals is more likely from bolder to shyer spiders and to individuals in better body condition [12]. Thus, we hypothesize that (i) groups composed of a mixture of personality types and body conditions will exhibit a greater incidence of bacterial transmission and (ii) that bacterial transmission will be greater when a bolder spider is the index case.

2. Material and methods

Stegodyphus dumicola is a southwestern African social spider that lives in colonies of several hundred individuals that cooperate in collective foraging, web-building, and reproduction [13]. We collected 11 colonies along roadside *Acacia* trees in the Northern Cape of South Africa in October 2015. Colonies were transported to the University of Pittsburgh and fed domestic crickets *ad libitum*. Individual adult *S. dumicola* females were isolated into 30 ml plastic housing cups before the onset of behavioural assays.

'Boldness' is a repeatable behavioural trait (i.e. 'personality type', repeatability ≈0.63; [14]) which impacts colonies' ability to attack prey effectively [15]. We measured boldness by placing a spider in a clear plastic arena and administering two rapid puffs of air atop the spider using an infant nose-cleaning bulb, after a 30 s acclimation period. Spiders then halt movement and their latency to resume activity estimates their boldness. Here, we identify bold individuals as those that resume movement within 1–200 s and shy individuals as those that take 600 s or more to resume activity (similar to [15]). We measured spiders' mass and prosoma width to estimate their body conditions using the residuals of a linear regression of body mass and body size [16].

To examine bacterial transmission dynamics, we constructed 53 colonies of 10 spiders each in one of three personality compositions: all shy ($n = 18$), 10% bold ($n = 18$) or 40% bold ($n = 17$). Spiders originated from seven different source colonies, and we did not mix spiders from different source colonies. Colonies were housed in plastic containers with a wire substrate to facilitate web-building. After 24 h, we added to each colony a spider to serve as the 'index case', i.e. a spider of known behavioural type ($n = 26$ bold; $n = 27$ shy) which had been topically exposed to a cuticular bacterium, *Pantoea* sp., that had been transformed via electroporation with a plasmid containing the reporter genes for green fluorescent protein and ampicillin resistance (methods described in [12,17]). We exposed the index case to the bacterium by submerging it in a liquid bacterial solution (approx. 10^9 CFU ml^{-1} in phosphate-buffered saline) for 3 s and leaving it to dry for 24 h before transferring it to a colony. After 20 h, we noted whether or not the index case was in body contact with any susceptible individuals in the social group. After a further 4 h (24 h total interaction time), we tested for the presence of the transformed *Pantoea* on each of the susceptible spiders' cuticles. We vortexed each spider separately in 1 ml of sterile-selective LB broth (100 μg ml^{-1} ampicillin, 20% arabinose) for 10 s and incubated the solution for 20 h at 30°C. Green fluorescence in this solution indicates the presence of the transformed *Pantoea* on the spider's cuticle. Group-wide bacterial transmission was quantified as the proportion of individuals on which we identified the transformed bacteria, not including the index case.

We used a generalized linear mixed model (GLMM) to determine how group-wide bacterial transmission was affected by group composition, boldness of the index case, the interaction term between them, body condition of the index case and mean colony body condition. The proportions of individuals exposed to bacteria were arcsine square root transformed to meet model assumptions. We analysed the number of instances where susceptible spiders were observed in contact with the index case using a nominal logistic regression with the same independent variables listed above. Experimental group ID nested in source colony ID was included as a random effect in each model. The experiment was conducted in two consecutive trials, so we also included trial number as a random effect. Data used for all analyses can be found in the Dryad Digital Repository [18].

3. Results and discussion

Groups' behavioural compositions significantly influenced bacterial transmission (GLMM: $F_{2,41} = 6.93$, $p = 0.003$; table 1). Colonies of 40% bold spiders experienced twice the
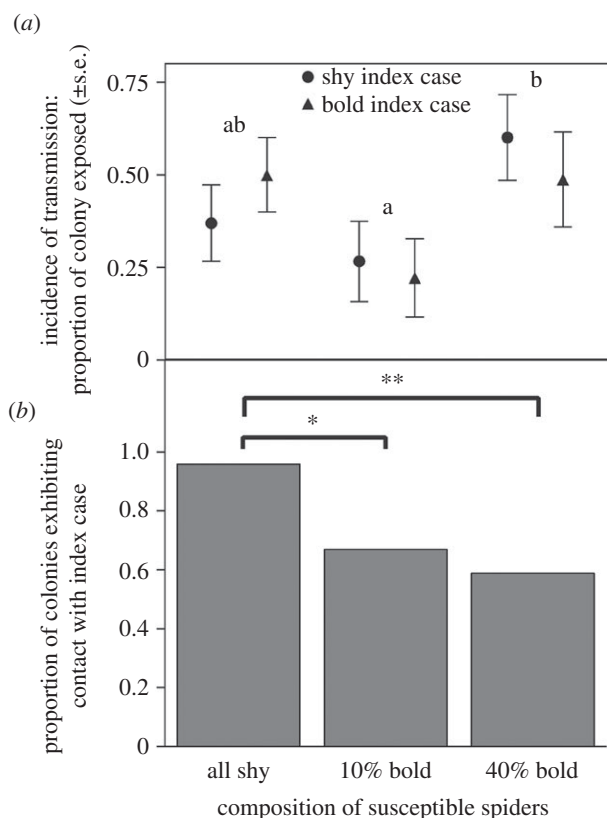
Figure 1. (*a*) Colonies containing 40% bold spiders experienced the greatest incidence of colony-wide bacterial transmission. That is, the proportion of spiders from which fluorescent *Pantoea* was collected was greatest in colonies of 40% bold spiders, regardless of the behavioural type of the index case. Colony compositions with different letter headings denote statistically different values. (*b*) Colonies containing all shy spiders were more likely to be found in physical contact with the index case, $*p < 0.05$, $**p < 0.01$.

incidence of bacterial transmission compared to groups with only 10% bold individuals, while colonies with all shy spiders experienced an intermediate level (Tukey's post-hoc test: $Q = 2.43$, $p < 0.05$; figure 1*a*). However, neither the boldness nor the body condition of the index case significantly influenced bacterial transmission (figure 1*a* and table 1*a*). The index case was more likely to rest in contact with susceptible spiders in colonies of all shy individuals than in the other two group compositions (nominal logistic regression: $\chi^2 = 7.65$, d.f. = 2, $p = 0.02$; figure 1*b*), regardless of whether the index case was bold or shy (table 1*b*).

The actions of just a few key individuals during early stages of an epidemic may have a large influence over its trajectory and magnitude [19]. Here, it appears that group personality composition is more important than the personality of the index case in predicting bacterial transmission. Modelling approaches have demonstrated that the traits of

the index case can influence their infectiousness in a heterogeneous population [20], and that transmission can depend on their social connectedness [21]. We were unable to differentiate transmission events that arose from the index case versus those that arose from secondary or tertiary events from newly exposed spiders. However, it appears that bodily contact with the index case is not the only likely explanation for colony-wide transmission (figure 1). Further, some of the transmission events may have occurred indirectly via the environment (contaminated silk) or via social contacts that we failed to observe [12].

Interestingly, group personality composition may drive trade-offs among ecological challenges. In *S. dumicola*, a greater proportion of bold spiders in the colony facilitates more effective collective foraging [15,22]. Here, a greater number of bold spiders in the group facilitated more widescale transmission of bacteria. Thus, the group compositions that promote success in the context of collective foraging also experience the greatest incidence of bacterial transmission. Such transmission is potentially costly because increased bacterial load on key group members can hinder a group's ability to execute important collective behaviours like foraging and web-building [23]. Natural colonies of *S. dumicola* harbour a small proportion of bold individuals [24]. We reason that having a small proportion of bold individuals, as compared with a large proportion of bold individuals or none at all, may provide benefits to colonies in the context of foraging while imposing the smallest costs with respect to bacterial transmission. Taken together, indirect evidence suggests that group traits like phenotypic composition may drive trade-offs in group performance, ensuring that no group composition experiences superior performance in all contexts/environments [25].

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