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Different bacterial strategies for organizing microcolonies during early stages of biofilm formation

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Bacterial biofilms are surface-associated, multicellular, morphologically complex microbial communities. Biofilm-forming bacteria are phenotypically distinct from their free-swimming, planktonic counterparts. Much work has focused on factors impacting surface adhesion and it is known that the opportunistic pathogen *P. aeruginosa* secretes the Psl exopolysaccharide (EPS), which promotes surface attachment by acting as a 'molecular glue'. However, how individual surface-attached bacteria self-organize into microcolonies, the first step in communal biofilm organization, is not well understood. Here, we elucidate the social role of EPS in early biofilm development using a massively parallel cell-tracking algorithm to extract the motility history of every cell on a newly colonized surface. By combining these techniques with fluorescent Psl staining and computer simulations, we show that *P. aeruginosa* deposits a trail of Psl as it moves on a surface, which influences the surface motility of subsequent cells that encounter these trails and thus generate positive feedback. Both experiments and simulations indicate that the web of secreted Psl controls the distribution of surface visit frequencies, which can be approximated by a power law. This Zipf's Law indicates that the bacterial community self-organizes in a manner analogous to a capitalist economic system, a 'rich-get-richer' mechanism of Psl accumulation that results in a small number of 'elite' cells extremely enriched in communally produced Psl. Using engineered strains with inducible Psl production, we show that local Psl levels determine post-division cell fates and that high local Psl levels ultimately allow 'elite' cells to serve as the founding population for initial microcolony development. The biofilm behavior of *P. aeruginosa* will be contrasted with those of other species.

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