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Animal Personalities: The Advantage of Diversity

Animals do not always perform to the best of their abilities when faced with difficult choices. New findings on foraging honeybees show that co-existing strategies, where some individuals place more emphasis on accuracy and others on speed, can be advantageous to the colony in a variable environment.

Helene Muller and Lars Chittka

For decades, researchers in animal behaviour have been largely concerned with the accuracy, and not the speed, of decision making, and have measured choice percentages when animals faced multiple options in terms of foraging, mates or predation risk. In human psychophysics, however, it has long been known that decision accuracy and speed are interrelated, and accuracy can only be understood in a meaningful way if decision time is also quantified [1,2]. This is because, in noisy or uncertain conditions, accurate decisions require a higher sampling time [3]. In research on nonhuman animals, this interaction has received more attention since two studies in 2003 examined the possibility of speed-accuracy tradeoffs in olfactory discrimination by rats [4] and colour discrimination by bees [5]. Far from simply copying concepts from human psychophysics, behavioural ecologists have since explored several new dimensions of such tradeoffs, including their ecological and evolutionary relevance — for example, in house-hunting ants [6], spatial exploration by passerine birds [7], predators choosing between aposematic prey [8], and predator avoidance behaviour by pollinators [9].

Burns [10] recognized the potential implications for research on animal ‘personality’. Rather than the typical scenario where speed-accuracy tradeoffs are evaluated within subjects,

there might also be consistent *between*-individual differences in terms of whether an animal places greater emphasis on speed or precision [2,5]. Some individuals might consistently be meticulous and slow, while others choose a ‘fast-and-sloppy approach’ — and perhaps such ‘impulsive’ individuals might not be selected against, because despite their high number of errors, their strategy can be advantageous, if the temporal costs of accurate decisions exceed those of errors [10].

One of the major challenges in research on the individuality of animals, from insects to humans, is understanding its adaptive significance [11,12]. How can multiple ‘personalities’ persist, side-by-side, in the same environment, when one might expect that one particular configuration of traits might outperform all others, and should therefore be favoured by selection? One possibility is that variation is selectively neutral [11], but in many cases, spatial and temporal heterogeneity in the environment might play important roles in maintaining diversity [12]. As they report in this issue of *Current Biology*, Burns and Dyer [13] set out to identify the kinds of environmental conditions that might favour ‘fast-and-sloppy’ individuals among honeybees, as well as the conditions that might give ‘slow-and-precise’ individuals an edge.

Bees typically obtain their entire diet — nectar and pollen — from flowers. In doing so, they operate in

a ‘pollination market’, where they must choose adaptively between multiple flower species that differ in reward profitability, handling costs, densities and predation threat — and memorise these features by associating them with flower signals such as colours [9,11]. The complexity of this interaction makes the collection of meaningful data in field conditions difficult, and so Burns and Dyer [13] used artificial flowers with precisely controlled rewards and colours. The authors assessed the ‘personality’ of 12 freely-flying worker bees by evaluating choice precision and times spent in flight between flower visits, and the consistency of these parameters over time and experimental conditions. They then quantified their individual nectar collection rates by testing each bee in two conditions (Figure 1). In both conditions, the bees foraged on a patch containing two ‘flower species’ with two similar colours, with one flower type containing nectar and the other containing water. In condition 1, there were as many rewarding as unrewarding flowers. Therefore, the cost of inaccuracy was relatively low, as bees had a one-in-two chance to find nectar by random choice. In condition 2, however, the rewarding flowers were outnumbered by the similarly coloured unrewarding flowers by a factor of two, so that bees had a 33% chance of finding nectar.

Burns and Dyer [13] found that individuals fell along a continuum from slow-accurate to fast-inaccurate strategies. Moreover, they discovered that, when there were equal numbers of both flower types, fast-inaccurate bees collected slightly more nectar than slow-accurate bees. Conversely, when the accumulating cost of mistakes was higher, slow-accurate bees clearly out-competed the fast-inaccurate bees (Figure 1). Therefore, these findings support a differential advantage for

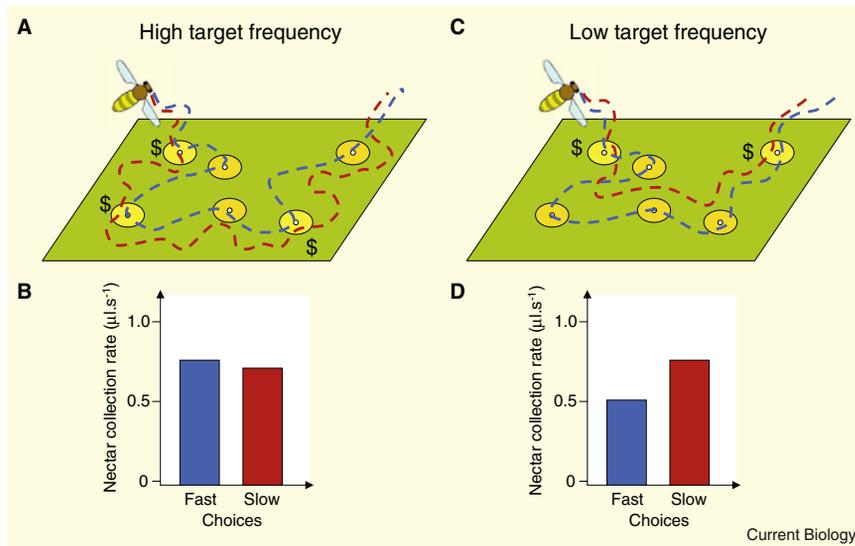


Figure 1. Different bee personalities prevail in different foraging environments.

Burns and Dyer [13] tested individual foragers in artificial flower meadows where one ‘species’ of artificial flower contained sucrose rewards (indicated here by \$ symbols) and the other, similarly coloured species did not. The two test situations differed in the percentage of unrewarding and rewarding flowers — in one condition there were equally as many (A,B), whereas in the other condition, there were twice as many unrewarding flowers as those that contained sugar solution (C,D). The colour red exemplifies the strategy of a ‘careful’, slow and accurate forager, and the colour blue corresponds to the performance of a fast, inaccurate ‘impulsive’ forager. In conditions with fewer unrewarding flowers (A,B), a slow and careful strategy does not pay off: the temporal costs of correct decisions are too high, whereas the temporal costs of erroneous probing of unrewarding flowers are low. Therefore, under such conditions the foraging rate of a careful forager does not exceed that of a ‘sloppy’ forager (B). Conversely, under conditions where rewarding flowers are scarcer, a careful strategy prevails (D).

each ‘personality’: when discrimination is difficult because flowers are similar, but costs of errors are low, it is advantageous (or at least, not detrimental) to be fast and inaccurate — perhaps a reason why rewardless orchids are able to persist in the pollination market [14]. But when a highly rewarding flower species is far outnumbered by poorly rewarding ones, a slow-accurate bee will bring back more nectar to the hive.

Burns and Dyer [13] propose that such intra-colony variability is essential to colony survival in that it enables the colony to respond flexibly to environmental variation. Indeed, the array of available flower species will vary with season and, within a flower species, the availability of nectar varies across time [15–17]. During the foraging season, or indeed in meadows simultaneously available within a hive’s flight range, a colony is likely to encounter conditions resulting in selection pressure maintaining both personality types.

Burns and Dyer’s [13] findings open up several promising avenues for future research. For example, for

how long does an individual retain its strategy — is there indeed lifetime repeatability in speed-accuracy strategies? In honeybees, the genetic architecture, and the physiology, underlying individual differences is especially well researched [18], but we do not yet know the genetic basis (if any) of psychological dimensions such as those under investigation here, or possibly any individual differences in sensory performance. Indeed, genetically diverse honeybee colonies, where workers all stem from the same queen but multiple fathers, harvest nectar more efficiently than colonies where all workers share the same father and mother [19]. However, the mechanism by which such diversity promotes foraging performance has not yet been identified. It would be interesting to compare the range of foraging strategies (including speed accuracy tradeoffs) displayed by foragers from colonies that vary in genetic diversity (i.e. where the tested colonies differ in the number of males that the queen has mated with).

And what is the ultimate reason that each individual does not have

the full flexibility to switch from a fast-and-inaccurate approach to a slow-and-precise one? While some (limited) flexibility to adjust speed and accuracy has already been demonstrated [5,13], perhaps the colony functions best if each individual is pre-programmed to be flexible only over a limited range of conditions, where it becomes a specialist in a given strategy [16] — but this hypothesis, too, requires empirical support.

Moreover, the diversity of personalities in a bee colony means that some individuals will perform better in some patches/meadows, while other individuals will be better in other environmental conditions (as shown by the target article). Because each bee can decide where to forage depending on its ‘personal’ experience of foraging success, a prediction is that workers should distribute themselves adaptively across foraging locations that differ in reward variability. Does each personality choose patches or meadows where its personality works best?

Burns and Dyer’s [13] results might also help explain the controversy surrounding ‘risk-sensitivity’ in bees. Several researchers have confronted bees with choices between two flower types equal in average rewards, but differing in the variance of rewards: for example, flower type A might consistently offer one unit of reward, while flower type B contains two unit rewards in every other flower, the other ones being empty [15,17,20]. So far, scientists have not reached a consensus about whether pollinators are more typically risk-averse (preferring flower type A) or risk-prone (choosing flower type B). However, one reason for the contradictory results might be that individuals with different personalities were tested, or colonies where one or the other personality type predominates.

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Plant Signaling: Brassinosteroids, Immunity and Effectors Are BAK !

Plants use the same set of co-receptors to mediate distinct responses to external signals. Brassinosteroid signaling serves as a test case to unravel the mechanisms of receptor-co-receptor activation and initiation of a specific signaling cascade.

Grégory Vert

Plant growth and development are driven by a complex network of internal signals, including brassinosteroids (BRs), the polyhydroxylated steroid hormones of plants. Over the past decade, genetic and biochemical approaches have provided a wealth of information on BR perception and signaling, but the precise molecular mechanisms driving receptor complex activation and signal transduction to downstream ‘actors’ are still not fully understood [1]. Recent reports have elucidated how BR perception leads to sequential activation of the receptor-co-receptor complex and have identified new BR signaling components acting directly downstream of the receptor.

Unlike animal steroid hormones, which are mostly perceived by the nuclear receptor family of transcription factors, BRs bind directly to the extracellular domain of BRI1, a leucine-rich repeat receptor-like kinase (LRR-RLK) that is localized to the plasma membrane [2]. Binding of BRs to pre-existing BRI1 homo-oligomers leads to BRI1 autophosphorylation and to transphosphorylation of the LRR-RLK

BAK1/SERK3 [3–6]. Unexpectedly, BAK1, together with other homologs of the SERK subfamily, was recently shown to regulate cell death and to function in multiple pathogen-associated molecular pattern (PAMP) responses, including responses to flagellin, EF-Tu, bacterial cold-shock protein, and oomycete elicitor INF1, that serve as the first line of defense against pathogens [7–10]. Analogous to its interaction with BRI1, BAK1 was shown to rapidly associate with the LRR-RLK flagellin-binding receptor FLS2 shortly after ligand stimulation [7]. However, BAK1 binds neither BRs nor flagellin [6,7]. Instead, BAK1 appears to act as a general co-receptor of the main ligand-binding receptor, together likely forming a signaling-competent hetero-oligomer. Interestingly, BAK1 has also been shown to promote BRI1 and FLS2 internalization into endosomes [11,12], reminiscent of ligand-induced activation, multimerization and internalization of animal single-pass transmembrane receptors. Therefore, it is unclear whether BAK1’s main function is to activate the ligand-binding receptor, to bridge the receptor with downstream components, or to promote receptor endocytosis.

To crack the code of BR receptor complex activation, Wang and colleagues [13] thoroughly dissected, *in vitro* and *in vivo*, the sequential mechanisms leading to BRI1 and BAK1 phosphorylation, and how differential receptor activation correlates with signaling. This interesting study revealed that BRI1 acts independently of its co-receptor BAK1 to bind its ligand, to initiate kinase activation and to sustain basal BR signaling and responses, as visualized by the elongation of the hypocotyl (the plant embryonic stem). However, full BR responses arise from the association between activated BRI1 and BAK1 and subsequent transphosphorylation of BAK1’s activation loop residues. Activated BAK1, in turn, transphosphorylates BRI1 in the juxtamembrane and carboxy-terminal domains, leading to enhanced BRI1 kinase activity and BR signaling (Figure 1A). More importantly, the authors provide the first framework for grasping how differential phosphorylation of BAK1 by associated ligand-binding receptor kinases likely explains its participation in different signaling pathways. Notably, BAK1 residue T450 is phosphorylated by BRI1 *in vitro* and, presumably, *in vivo*, but mutation of the corresponding residue does not affect the various BAK1-dependent signaling pathways to the same extent. Indeed, phenotypic analysis of plants expressing a T450A non-phosphorylatable BAK1 mutant version revealed that phosphorylation at this BAK1 residue may be important to activate BRI1 and