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Signal detection, acceptance thresholds and the evolution of animal recognition systems

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Introduction

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One contribution of 22 to a theme issue 'Signal detection theory in recognition systems: from evolving models to experimental tests'.

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Nearly every biological interaction requires some kind of recognition. Even the major transitions in life, from independent replicators joining together into chromosomes, through the formation of the first multicellular organisms, to the evolution of eusociality, depended on the ability of a unit (e.g. molecule, cell or organism) to discriminate among individuals with whom to cooperate, and those to reject [1]. Recognition systems, therefore, play critical roles in discriminating among beneficial and detrimental actors in diverse ecological and evolutionary contexts, including self, species, mates, kin, predator–prey and host–parasite interactions, and even habitat selection. Evolution should select for stringent recognition when mistakes are costly. Yet, both acceptance errors (e.g. accepting a parasitic cuckoo's mimetic egg) and rejection errors (eliminating your own egg instead of the parasite's), which may severely reduce or altogether eliminate fitness of the erring discriminator, are common in many recognition systems.

To examine how individuals can balance these error-costs, Reeve [2] applied a quantitative signal detection theory (SDT) framework and introduced conspecific acceptance threshold theory. Reeve characterized several conceptual models in which the acceptance threshold marks the point below which individuals are accepted, and above which individuals are rejected. Thresholds can be evolutionarily and/or developmentally labile and are defined by the extent of the phenotypic dissimilarity between the discriminator's template of an acceptable individual and the potential partner's actual phenotype. Thus, the acceptance threshold can shift adaptively in different contexts to minimize summed costs and may be affected by the rate of interaction with desirable versus undesirable individuals as well as the extent of fitness consequences for accepter versus rejecter individuals. Reeve's paper has just passed its 30th anniversary and has been cited repeatedly (over 480 times at the time this was written). Since its publication, these models have been applied, adopted and adapted across diverse taxa and ecological contexts and in a variety of recognition systems. How these models have brought signal detection frameworks into the everyday workings of behavioural ecology to influence the field of recognition systems research, and whether their specific predictions have been upheld across quantitative experiments, have not been systematically synthesized.

It is not common that theoretical models are able to function at multiple levels of analysis; however, a strength of SDT and its applications is that it can inform research and hypotheses for both proximate (e.g. developmental and sensory processes) and ultimate (fitness-informed and evolutionary shifts) perspectives [3]. As such, the central aim of our special issue was to bring together diverse biological perspectives, research themes and participants to highlight accomplishments, to underline shortcomings and to point towards future work in threshold-based concepts of recognition system theory and data. We apologize to those not represented in this issue, as the field is ever-active and continues to be productive and transformative.

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The first set of five contributions in this special issue introduce new theory and focus on model development. Sheehan & Reeve [4] ask why recognition systems vary so much in their accuracy (e.g. the ability to discriminate between desirable and undesirable targets). They develop a game theory model where both signallers and receivers can vary investment into outcomes, revealing how recognition systems can evolve based on relative payoff structures. Sumner & Sumner [5] return to the source and advocate the use of SDT in behavioural ecology and comparative psychology, and compare the assumptions and predictions of SDT with Reeve's [2] optimal threshold models. They then apply SDT to guarding behaviour in social insects and develop a model to examine its utility to analysing behavioural data. Shizuka & Lyon [6] present a mathematical model based on intraspecific brood parasitism in American coots (*Fulica americana*) to examine fitness payoffs resulting from recognition errors. Miller *et al*. [7] examine coevolutionary dynamics between sender and receiver traits, presenting a model elucidating the conditions under which signallers and receivers should invest in facilitating recognition. Finally, what happens in systems with multiple sensory modalities and multicomponent cues? Does one override the other e.g. colour versus maculation in parasitic cowbird eggs as in [8]. Tibbetts *et al*. [9] develop an individual-based model which reveals that complex signals can lead to more accurate recognition than simple ones and are more likely to evolve when recognition errors are costly.

The second set of contributions consist of empirical papers that are categorized by the sensory system examined. Focusing on visual cues, Russell *et al*. [10] ask how imperfect mimicry fits into SDT. They examine learning in a bumblebee (*Bombus impatiens*) in relation to imperfect Batesian mimicry within a floral community. In contrast with expectations, they find support that imperfect mimicry can be adaptive. Hämäläinen & Thorogood [11] use SDT to examine the role of personal and social information in the evolution of aversion to aposematic prey in great tits (*Parus major*). Using chemical cues, Briard *et al*. [12] examine responses of slime moulds to conspecifics (from stressed or unstressed clone-mates), while experiencing biotic or abiotic stresses themselves. Cappa *et al*. [13] subjected *Polistes* wasps to olfactory cues at different life stages to demonstrate that the social environment, even late in life, shapes recognition abilities. The final set of empirical papers generates insights into recognition from auditory systems. Römer & Holderied [14] examine the coevolution of signal production and detection between predatory bats and their cricket prey. Tegtman & Magrath [15] examine variation in alarm calls of superb fairywrens (*Malurus cyaneus*) to test whether predator-specific calls can be discriminated despite high overlap in their acoustic features. Finally, Leedale *et al*. [16] use a social pedigree in long-tailed tits (*Aegithalos caudatus*) to show that vocal cues can be used for kin discrimination.

The special issue ends with a series of papers that integrate, review and synthesize the literature. Scharf *et al*. [17] kick off this section with a literature review evaluating the impact of Reeve's [2] models over the last 30 years. Shizuka & Hudson [18] then apply Reeve's optimal threshold model to species recognition. They focus on premating isolating mechanisms, particularly considering the costs of hybridization. They suggest that restrictive acceptance thresholds could result in the rejection of conspecific mates in favour of heterospecifics, a pattern recently supported by empirical data in American spadefoot toads (*Spea* spp.) [19]. Lichtenberg *et al*. [20] use SDT to examine how recognition errors (e.g. rejecting flowers with rewards or visiting flowers without rewards) shape forager decision-making of nectivores in floral communities. Carlson *et al*. [21] review the literature on individual vocal recognition, including how it is measured, its associated costs and the contexts in which it is most often used. Rossi & Derégnaucourt [22] also examine auditory individual recognition in birds and compare the mechanisms underlying recognition with chemical nest-mate recognition in social Hymenoptera. Focusing on species recognition, Adams & Tsutsui [23] examine chemically mediated species recognition in insects, highlighting the results of a few well-studied taxa. Ruiz-Raya & Soler [24] apply SDT and optimal threshold models to foreign egg rejection behaviour in avian brood parasites. Galloway *et al*. [25] overview and discuss how different mechanisms of visual camouflage evolve in response to predator vision and cognition. Finally, Avilés [26] reviews the literature on egg and nestling colour detection to ask whether visual models, specifically, receptor-noise limited avian-perceptual models, are effective at capturing the complex reality of visual perception.

Collectively, we hope these articles provide both a synthesis of current knowledge and a roadmap for future research including model application to more applied areas such as conservation, epidemiology and bio-inspired design. For example, acceptance threshold models can be used to generate and test predictions of how population bottlenecks can influence recognition systems following a loss of genetic diversity at loci responsible for cues used for recognition, as Starks [27] demonstrated with genetic and behavioural patterns from ant invasions. Thresholds can also change based on encounter frequency, the identity of conspecifics or maturation of the recognition system itself (e.g. [28,29]). Subsequently, long-term studies coupling behavioural responses with underlying neural and genomic data will be particularly important for teasing apart innate versus learned components of recognition systems. This approach will also promote the utility of SDT, and its subset of acceptance threshold models, for determining the decision rules an animal uses to respond to a signal or cue. Answering such questions requires insight into the neural mechanisms (e.g. template formation and comparison) underlying recognition systems (e.g. self-referencing [30]). Advances in this area will promote the application of SDT and acceptance threshold models in the development of computationally based recognition systems to be applied in bio- and public security. Finally, as we are writing this introduction while in quarantine during the Covid-19 outbreak, this special issue may be particularly timely given the epidemiological applications of threshold models to understanding immunity and disease transmission.

Data accessibility. This article has additional data.

Authors' contributions. The authors contributed equally to this article.

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References

1. Maynard Smith J, Szathmary E. 1995 *The major transitions in evolution*. Oxford, UK: Freeman.
2. Reeve HK. 1989 The evolution of conspecific acceptance thresholds. *Am. Nat.* **133**, 407–435. (doi:10.1086/284926)
3. Tinbergen N. 1963 On aims and methods in ethology. *Z. Tierpsychol.* **20**, 410–433. (doi:10.1111/j.1439-0310.1963.tb01161.x)
4. Sheehan MJ, Reeve HK. 2020 Evolutionarily stable investments in recognition systems explain patterns of discrimination failure and success. *Phil. Trans. R. Soc. B* **375**, 20190465. (doi:10.1098/rstb.2019.0465)
5. Sumner CJ, Sumner S. 2020 Signal detection: applying analysis methods from psychology to animal behaviour. *Phil. Trans. R. Soc. B* **375**, 20190480. (doi:10.1098/rstb.2019.0480)
6. Shizuka D, Lyon BE. 2020 How to learn to recognize conspecific brood parasitic offspring. *Phil. Trans. R. Soc. B* **375**, 20190472. (doi:10.1098/rstb.2019.0472)
7. Miller SE, Sheehan MJ, Reeve HK. 2020 Coevolution of cognitive abilities and identity signals in individual recognition systems. *Phil. Trans. R. Soc. B* **375**, 20190467. (doi:10.1098/rstb.2019.0467)
8. Hanley D, Lopez AV, Fiorini VD, Reboreda JC, Grim T, Hauber ME. 2019 Variation in multicomponent recognition cues alters egg rejection decisions: a test of the optimal acceptance threshold hypothesis. *Phil. Trans. R. Soc. B* **374**, 20180195. (doi:10.1098/rstb.2018.0195)
9. Tibbetts EA, Liu M, Laub EC, Shen S-F. 2020 Complex signals alter recognition accuracy and conspecific acceptance thresholds. *Phil. Trans. R. Soc. B* **375**, 20190482. (doi:10.1098/rstb.2019.0482)
10. Russell AL, Kikuchi DW, Giebink NW, Papaj DR. 2020 Sensory bias and signal detection trade-offs maintain intersexual floral mimicry. *Phil. Trans. R. Soc. B* **375**, 20190469. (doi:10.1098/rstb.2019.0469)
11. Hämäläinen L, Thorogood R. 2020 The signal detection problem of aposematic prey revisited: integrating prior social and personal experience. *Phil. Trans. R. Soc. B* **375**, 20190473. (doi:10.1098/rstb.2019.0473)
12. Briard L, Goujarde C, Bousquet C, Dussutour A. 2020 Stress signalling in acellular slime moulds and its detection by conspecifics. *Phil. Trans. R. Soc. B* **375**, 20190470. (doi:10.1098/rstb.2019.0470)
13. Cappa F, Cini A, Signorotti L, Cervo R. 2020 Rethinking recognition: social context in adult life rather than early experience shapes recognition in a social wasp. *Phil. Trans. R. Soc. B* **375**, 20190468. (doi:10.1098/rstb.2019.0468)
14. Römer H, Holderied M. 2020 Decision making in the face of a deadly predator: high-amplitude behavioural thresholds can be adaptive for rainforest crickets under high background noise levels. *Phil. Trans. R. Soc. B* **375**, 20190471. (doi:10.1098/rstb.2019.0471)
15. Tegtman NT, Magrath RD. 2020 Discriminating between similar alarm calls of contrasting function. *Phil. Trans. R. Soc. B* **375**, 20190474. (doi:10.1098/rstb.2019.0474)
16. Leedale AE, Lachlan RF, Robinson EJH, Hatchwell BJ. 2020 Helping decisions and kin recognition in long-tailed tits: is call similarity used to direct help towards kin? *Phil. Trans. R. Soc. B* **375**, 20190565. (doi:10.1098/rstb.2019.0565)
17. Scharf HM, Suarez AV, Reeve HK, Hauber ME. 2020 The evolution of conspecific acceptance threshold models. *Phil. Trans. R. Soc. B* **375**, 20190475. (doi:10.1098/rstb.2019.0475)
18. Shizuka D, Hudson EJ. 2020 To accept or reject heterospecific mates: behavioural decisions underlying premating isolation. *Phil. Trans. R. Soc. B* **375**, 20190484. (doi:10.1098/rstb.2019.0484)
19. Chen C, Pfennig KS. 2020 Female toads engaging in adaptive hybridization prefer high-quality heterospecifics as mates. *Science* **367**, 1377–1379. (doi:10.1126/science.aaz5109)
20. Lichtenberg EM, Heiling JM, Bronstein JL, Barker JL. 2020 Noisy communities and signal detection: why do foragers visit rewardless flowers? *Phil. Trans. R. Soc. B* **375**, 20190486. (doi:10.1098/rstb.2019.0486)
21. Carlson NV, Kelly EMK, Couzin I. 2020 Individual vocal recognition across taxa: a review of the literature and a look into the future. *Phil. Trans. R. Soc. B* **375**, 20190479. (doi:10.1098/rstb.2019.0479)
22. Rossi N, Derégnaucourt S. 2020 Mechanisms of recognition in birds and social Hymenoptera: from detection to information processing. *Phil. Trans. R. Soc. B* **375**, 20190483. (doi:10.1098/rstb.2019.0483)
23. Adams SA, Tsutsui ND. 2020 The evolution of species recognition labels in insects. *Phil. Trans. R. Soc. B* **375**, 20190476. (doi:10.1098/rstb.2019.0476)
24. Ruiz-Raya F, Soler M. 2020 Signal detection and optimal acceptance thresholds in avian brood parasite–host systems: implications for egg rejection. *Phil. Trans. R. Soc. B* **375**, 20190477. (doi:10.1098/rstb.2019.0477)
25. Galloway JAM, Green SD, Stevens M, Kelley LA. 2020 Finding a signal hidden among noise: how can predators overcome camouflage strategies? *Phil. Trans. R. Soc. B* **375**, 20190478. (doi:10.1098/rstb.2019.0478)
26. Avilés JM. 2020 Avian egg and nestling detection in the wild: should we rely on visual models or behavioural experiments? *Phil. Trans. R. Soc. B* **375**, 20190485. (doi:10.1098/rstb.2019.0485)
27. Starks PT. 2003 Selection for uniformity: xenophobia and invasion success. *Trends Ecol. Evol.* **18**, 159–162. (doi:10.1016/S0169-5347(03)00038-7)
28. Gamboa JG, Grudzien TA, Espelie KE, Bura EA. 1981 Kin recognition pheromones in social wasps: combining chemical and behavioural evidence. *Anim. Behav.* **51**, 625–629. (doi:10.1006/anbe.1996.0067)
29. Wilson ACC, Grosberg RK. 2004 Ontogenetic shifts in fusion–rejection thresholds in a colonial marine hydrozoan, *Hydractinia symbiolongicarpus*. *Behav. Ecol. Sociobiol.* **57**, 40–49. (doi:10.1007/s00265-004-0831-4)
30. Hauber ME, Sherman PW. 2001 Self-referent phenotype matching: theoretical possibilities and empirical tests. *Trends Neurosci.* **24**, 609–616. (doi:10.1016/S0166-2236(00)01916-0)