

Research



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**Author for correspondence:**

Hannah M. Scharf  
e-mail: [hscharf2@illinois.edu](mailto:hscharf2@illinois.edu)

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# The evolution of conspecific acceptance threshold models

Hannah M. Scharf<sup>1</sup>, Andrew V. Suarez<sup>1</sup>, H. Kern Reeve<sup>2</sup> and Mark E. Hauber<sup>1</sup>

<sup>1</sup>Department of Evolution, Ecology, and Behavior, School of Integrative Biology, University of Illinois, Urbana-Champaign, IL 61801, USA

<sup>2</sup>Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, USA

HMS, 0000-0002-4385-3850; MEH, 0000-0003-2014-4928

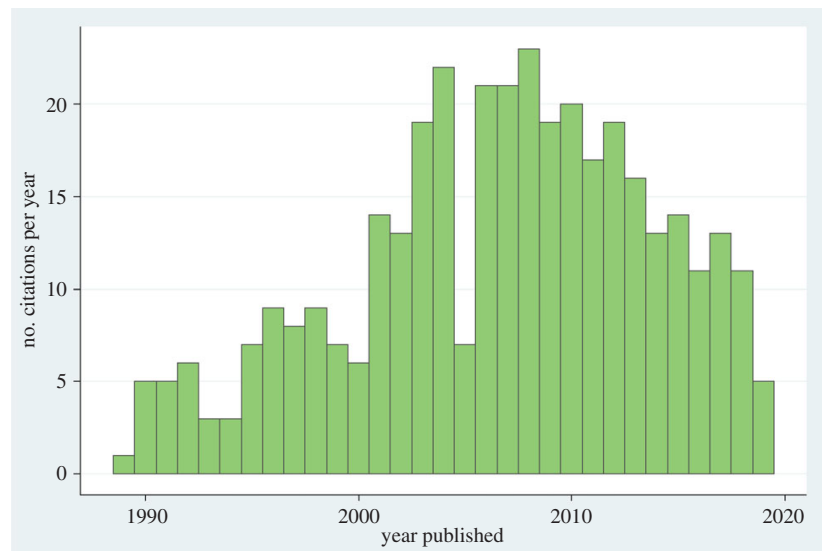
How do organisms balance different types of recognition errors when cues associated with desirable and undesirable individuals or resources overlap? This is a fundamental question of signal detection theory (SDT). As applied in sociobiology, SDT is not limited to a single context or animal taxon, therefore its application can span what may be considered dissimilar systems. One of the applications of SDT is the suite of acceptance threshold models proposed by Reeve (1989), which analysed how individuals should balance acceptance and rejection errors in social discrimination decisions across a variety of recognition contexts, distinguished by how these costs and benefits relatively combine. We conducted a literature review to evaluate whether these models' specific predictions have been upheld. By examining over 350 research papers, we quantify how Reeve's models (Reeve 1989 *Am. Nat.* **133**, 407–435 (doi:10.1086/284926)) have influenced the field of ecological and behavioural recognition systems research. We found overall empirical support for the predictions of the specific models proposed by Reeve, and argue for further expansion of their applications into more diverse taxonomic and additional recognition contexts.

This article is part of the theme issue 'Signal detection theory in recognition systems: from evolving models to experimental tests'.

## 1. Introduction to signal detection theory

Recognition systems, wherein an organism must discriminate between a desirable and undesirable recipient of a costly action, play critical roles in a variety of socio-ecological contexts. Some of the most frequently studied ecological recognition systems include allorecognition (i.e. self versus non-self) [1], kin recognition [2,3], mate recognition [4,5] and conspecific (species) recognition [6]. Yet, the discrimination of desirable from undesirable individuals (or, more generally, resources) can be difficult when their suite of phenotypic traits overlap because recognition cues may not cleanly separate these classes of potential partners (recipients). This overlap generates the possibility of both acceptance errors (acceptance of undesirable recipients) and rejection errors (rejection of desirable recipients), each of which can decrease or altogether eliminate any fitness advantage for an individual (hereafter: the discriminator) attempting discrimination between the different classes of recipients.

The decision-making process to discriminate between desirable and undesirable individuals has been described and modelled extensively by applications of signal detection theory (SDT) [7–9]. First developed for differentiating between information of interest and random patterns from noisy communication systems [10], SDT has been adapted for bio-behavioural research and used for over 50 years. Traditionally, SDT in an ecological context has been used to describe a single decision made by an individual deciding between two choices based on the information available [9]. An explicitly evolutionary application of SDT is Reeve's [7] set of acceptance threshold models, which have been applied to a diverse range of cellular and behavioural recognition contexts and cited over 300 times (table 1 and figure 1).



**Figure 1.** Histogram showing the number of times Reeve [7] was cited each year. Note that the last data point represents citations from January up to August 2019 only. Data collected from Web of Science. (Online version in colour).

**Table 1.** Non-exhaustive, representative studies investigating discrimination in a range of taxa and recognition contexts.

species	recognition context	outcome	reference
<i>Hydractinia symbiolongicarpus</i>	kin	<i>Hydractinia</i> reject colony fusion when the probability of interacting with kin decreases and costs of parasitism increase	Wilson & Grosberg [11]
brown-and-yellow marshbird ( <i>Pseudoleistes virescens</i> ) and shiny cowbird ( <i>Molothrus bonariensis</i> )	conspecific	marshbirds reject mimetic cowbird eggs more often in the presence of non-mimetic cowbird eggs when their perceived risk of parasitism is high	Mermoz <i>et al.</i> [12]
honeybee ( <i>Apis mellifera</i> )	sibling	honeybees accept nest-mates and non-nest-mates more often when nectar conditions improve and cost of robbing decreases	Downs <i>et al.</i> [13]
swordtail fish ( <i>Xiphophorus nezahualcoyotl</i> )	mate	males do not attack false-brood spot (female-mimic) males when the probability of encountering a desirable individual (female) is high and the probability of encountering an undesirable individual (female-mimic) is low	Rios-Cardenas <i>et al.</i> [14]
nematode ( <i>Steinernema longicaudum</i> )	kin	male mortality rates from fighting are lower when relatedness is high	Kapranas <i>et al.</i> [15]
coral snake ( <i>Micrurus fulvius</i> ) and scarlet kingsnake ( <i>Lampropeltis elapsoides</i> )	predator–prey	predators attack intermediate mimics less in areas where encountering an undesirable individual is high, and attack intermediate mimics more in areas where encountering undesirable individuals is low	Kikuchi & Pfennig [16]

## 2. The optimal acceptance threshold

The central problem in optimal acceptance threshold theory is to determine what acceptance threshold optimally balances the inversely related probabilities of acceptance errors and rejection errors [7]. This optimal threshold maximizes expected net fitness, and depends critically on contextual parameters such as the rates of an individual's interaction with

desirable and undesirable individuals, the fitness consequences of accepting or rejecting different types of recipients, and how the latter fitness consequences combine [7]. The theory solves generally for how acceptance thresholds should shift across different recognition and social interaction contexts regardless of cue distributions for desirable and undesirable recipients. Using the latter approach, Reeve considers six models that are applicable to a variety of social

and behavioural contexts, categorized either as 'guard' versus 'search' models that are either frequency-independent or frequency-dependent. These include a frequency-dependent and a frequency-independent 'guard' model (e.g. accepting or rejecting encountered individuals that may be nest-mates or non-nest-mates), 'search-and-settle' (e.g. a female searching for a single mate), 'repeated search' (e.g. a male searching for female mates repeatedly), a frequency-dependent robber-competitor context (e.g. a guard protecting a resource), and a non-additive costs and benefits context (e.g. undesirable recipients are usurpers or cannibals).

Because SDT and its derived models, such as the acceptance threshold model set, are widely used in the behavioural sciences, reviewing and updating these intellectual frameworks and evaluating the realized usefulness of these predictions across taxa in the literature are critical to ensure that they remain relevant, current, and open to ongoing experimentation and empirical tests. The extent to which acceptance threshold models have influenced the field of ecological and behavioural recognition systems research and evolutionary decision making, and whether their specific predictions have been upheld across quantitative experiments, have not yet been systematically reviewed in the 30 years since the publication of the theory and its predictions. Therefore, here we assess what fields Reeve's acceptance threshold models are most commonly used in, what recognition contexts they are applied to, whether these models are actively being used in forming predictions and hypotheses, and the degree to which these predictions are upheld.

### 3. Methodology of the literature review

Using Web of Science (<http://www.webofknowledge.com>), we identified 361 papers that cited Reeve [7] from February 1990 until August 2019 (see the electronic supplementary material). For each paper, we determined the study species and the recognition system(s) investigated. Examples included parent-offspring recognition, mate recognition, and the recognition of conspecifics, among others. We categorized each paper according to (1) with which of the six conspecific acceptance threshold models [7] the study aligned, (2) if the recognition context was between conspecifics, heterospecifics, or both, (3) if the study investigated kin recognition in particular, and (4) the socioecological context in which the theory was cited. If one of these questions was not applicable, such as those that cited the original work but were reviews, it was recorded as N/A and not included. Naturally, some of these recognition categories overlap and are not mutually exclusive, so papers were categorized where they fitted most directly. Some papers investigated more than one recognition context, so to simplify the analysis, the most prominent (data-rich) category was chosen. We note that ours is not a formal meta-analysis as the sample sizes for each of the diverse recognition context categories are too small to conduct quantitative tests.

For studies that used one or more models from Reeve [7] in a predictive way, additional information was recorded. Each of these papers was read to determine (1) whether the theory's and particular model's predictions generated were supported, partly accepted, or rejected, (2) what the fitness consequence of discrimination was for the study species, (3) what the consequence of an incorrect acceptance

was, (4) what the consequence of an incorrect rejection was, and (5) if the change in acceptance versus rejection was due to a shift in the acceptance threshold, a change in cues, or both.

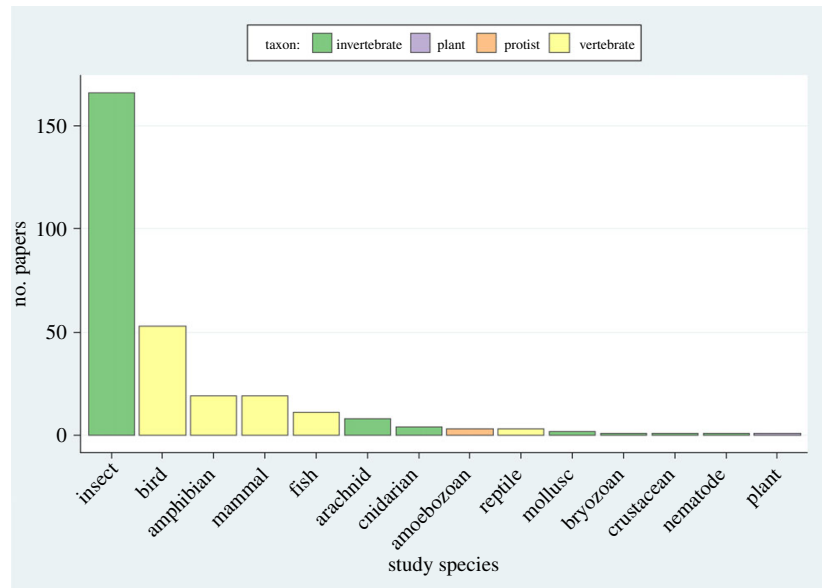
### 4. Report on the literature review

We found that Reeve [7] was cited mostly in original data-driven articles (72.8% of 361 total papers) but was also prominently used in a variety of other paper types, including reviews and follow-up model creations. The original research articles used a broad range of experimental study species, from taxonomic groups including plants, protists, amoebozoans, invertebrates and vertebrates (figure 2). While there was a large breadth in the study taxa used, over half (56.8%) of the 292 data-driven papers that cited Reeve [7] used insects, with the most common study species being honeybees (*Apis mellifera*), paper wasps (*Polistes dominula*), and Argentine ants (*Linepithema humile*). Birds were the second most commonly used lineage, consisting of 18.2% of the experimental study species involved. The most common bird species used were brown-headed cowbirds (*Molothrus ater*), common cuckoos (*Cuculus canorus*) and great reed warblers (*Acrocephalus arundinaceus*). All other taxa were used in fewer than 10% of all articles.

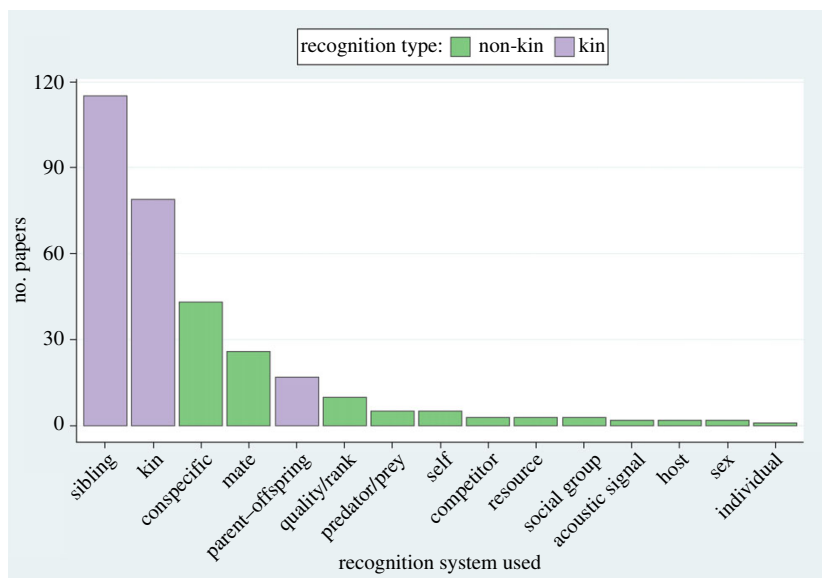
For the 316 papers that investigated a clearly stated recognition context, the majority (66.8%) were kin recognition contexts (figure 3). By far the most common form of kin recognition investigated was sibling recognition (54.5%). The bulk of sibling recognition studies examined nest-mate recognition in social insects (95.7%)—over 100 papers on nest-mate recognition alone have cited Reeve [7]. Following sibling recognition, general kin recognition (the recognition of any type of kin) made up 37.4% of these papers, followed by parent-offspring recognition at 8.1%. The most common non-kin recognition context was the recognition of conspecifics from heterospecifics (41.0%), followed by mate recognition (24.8%). All other contexts were used in fewer than 10% of all articles.

Within the citing literature, 294 papers had tests that could be further divided into one of the six specific acceptance threshold models that Reeve [7] proposed. The model that most commonly aligned with the study system was the frequency-independent guard model (66.7%), followed by the frequency-dependent guard model with pair-wise kin interactions (20.1%). All other contexts were used in fewer than 10% of all articles.

Forty-five (12.5%) out of the 361 papers we reviewed directly formed a hypothesis from one or more of the predictions made by Reeve's acceptance threshold models [7]. Out of those 45, 79.5% found results that agreed with the predictions made from the acceptance threshold model, 9.1% of them found results that disagreed, and 11.4% of them found results that partially agreed with the predictions made. In turn, 77.3% of the 45 papers made predictions aligning with the frequency-independent guard model context. All other models with the exception of the repeated search model (not used), including the frequency-dependent guard model with pair-wise kin interactions, the frequency-dependent robber-competitor guard model, the non-additive costs and benefits model, and the search-and-settle model, were used in the remaining 22.7% of the 45 papers. Of these 45 papers, 43.2% had both a shift in the acceptance threshold of the organism



**Figure 2.** Categories of study species used in research articles citing Reeve [7]. If more than one study species was used, the most prominent (data-rich) one was chosen. (Online version in colour).



**Figure 3.** Categories of recognition context used in research articles citing Reeve [7]. Recognition contexts are further separated into whether they represent kin recognition or non-kin recognition. Papers that investigated more than one recognition system were categorized according to which category was most prominently discussed in the paper. (Online version in colour).

in question, and a shift in the cues to which the organism responded. Conversely, 40.9% had a shift in the threshold only, without a change in cues present. The remaining 15.9% had neither or this categorization was not applicable.

## 5. The impact of the acceptance threshold models

We found that the conspecific acceptance threshold models formulated by Reeve [7] have produced predictions for

recognition systems across multiple taxa, the results of which have been largely aligned with predictions and conclusions made by these original models. In addition, the models proposed by Reeve [7] have been used in explaining the foci and/or results of 300+ papers. For studies in which the predictions of the acceptance threshold models were not supported, a common cause was a directional shift in the threshold not resulting in the predicted change of increased/decreased rejection or acceptance errors. For example, Dalziel & Magrath [17] found that the grey shrike-thrush (*Colluricincla harmonica*) had a context-

dependent signal acceptance threshold and was more discriminating of conspecific song mimicked by the superb lyrebird (*Menura novaehollandiae*) when also presented with a sequence of non-mimetic lyrebird songs. However, they did not find a decrease in shrike-thrush rejection errors even with increased acceptance errors, although they acknowledge that further experiments are needed to explore this. Similarly, Jones *et al.* [18] did not find a decrease in acceptance errors even when they found an increase in rejection errors, nor a decrease in rejection errors even when they found an increase in acceptance errors, while investigating the effect of transferring resin stores (as a source of recognition) between hives of a stingless bee (*Tetragonisca angustula*). However, there was also a large amount of variation in acceptance rates between the six hives studied, which may indicate another, unexplained factor influencing discrimination in this context.

Complex behavioural states could also be the reason that several studies did not find results predicted by the conspecific acceptance threshold models. Murata *et al.* [19] found that workers of two species of ant (*Brachyponera chinensis*, *Brachyponera nakasujii*) were not aggressive towards non-nest-mates in the same population, but did have differential non-aggressive responses such as antennation and trophallaxis towards non-nest-mates, proposing that discrimination may be more subtle. In a study on common waxbills (*Estrilda astrild*), the host of brood-parasitic pin-tailed whydahs (*Vidua macroura*), Schuetz [20] expected to find that when parents were constrained by clipped wings, they would be more discriminating against the colour-manipulated gape(s) of at least one nestling, but found no significant differences in survival of nestlings with manipulated versus unmanipulated gapes. Because the parents were manipulated rather than the composition of food supplied to them, however, this result may have been caused by an increased investment in the current reproductive output if the parents perceived a decreased probability of future survival. Thus, the predicted outcomes of shifting acceptance thresholds can vary depending on how organisms are manipulated and the intricacies of their behaviour. Finally, Lorenzi [21] found a pattern contrary to the prediction that paper wasps (*Polistes biglumis*) parasitized by the congeneric wasp *Polistes atrimandibularis* should be less permissive towards intruders because they encounter more non-kin. Instead, these wasps actually made more acceptance errors and rejection errors, suggesting that the discrimination systems of the worker wasps may be manipulated by the presence of parasites. The latter possibility suggests that acceptance threshold models should be extended to incorporate manipulation and counter-manipulation by all interactants in a recognition context [22].

The majority of the research papers citing Reeve [7] focused on nest-mate recognition in social insects. Nevertheless, although Reeve [7] was rarely cited in studies on taxa outside of insects or birds, a breadth of taxa were still represented by the 300+ papers examined here, showing that the predictions generated by Reeve's models can be still useful when applied to such systems. For example, in their study on the hydrozoan *Hydractinia symbiolongicarpus*, Wilson & Grosberg [11] showed that the acceptance rates of *Hydractinia* when fusing decline as the probability of interacting with kin decreases and the costs of parasitism

increase (table 1). Thus, overall, the data indicate that SDT and its related biological models, such as those developed in Reeve [7], are useful in explaining variation in biological recognition systems and should be tested more deeply in a wider variety of taxa. Study systems, such as non-arthropod invertebrates and unicellular organisms, could benefit from future tests of acceptance threshold theory, and this could also be extended to other recognition contexts within organisms, such as neural and immune systems or microbiomes.

Mismatches between SDT predictions and the actual properties of recognition systems could point the way to novel and important extensions to the existing theory. For example, it is possible that acceptance thresholds are dynamically flexible within a single recognition context according to the actual sequence of interactions experienced by a discriminator (i.e. that acceptance thresholds are continuously subject to Bayesian updating). Encountering by chance a series of undesirable recipients could yield a revised upward computation of the expected future rate of interaction with undesirable recipients, in turn leading to a progressively more restrictive acceptance threshold.

In addition, more research is needed in the quantification of model components, including the distribution and variation of cues among individuals or the dissimilarity between cues, rather than a qualitative categorization of cues. For example, Hanley *et al.* [23] investigated the role of avian-perceived spectral reflectance of model eggs on chalk-browed mockingbirds' (*Mimus saturninus*) egg rejection thresholds, and found that, as predicted, mockingbirds tolerated spotted eggs more than unspotted eggs, but contrary to predictions, rejected browner eggs more than bluer eggs. This type of analysis in other systems could also open the way towards new insights into acceptance thresholds by generating information that is more specific and comparable across recognition events and individuals.

The conclusions reached by our review show that the ideas presented by SDT are broadly applicable in recognition and discrimination contexts within and among species, and thus connect seemingly disparate systems within a single theoretical framework. Because SDT and its derived models are widely used in the behavioural sciences, reviewing and updating these intellectual frameworks and evaluating the usefulness of these predictions across animal taxa are critical for deepening our understanding of all recognition systems and opening the door for new and better extensions to the existing theory. Future works should focus on extending SDT to underrepresented systems, identifying current limitations of acceptance threshold models, and evaluating the perception of cues in new ways.

**Data accessibility.** The data are available as electronic supplementary material.

**Authors' contributions.** M.E.H., A.V.S. and H.K.R. conceived the idea. H.M.S. performed the review and analysis, wrote the first draft and created the figures and tables. M.E.H., A.V.S. and H.K.R. gave comments and H.M.S. revised the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed herein.

**Competing interests.** We declare we have no competing interests.

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