Review

TRENDS in Ecology and Evolution Vol.22 No.10

Individual recognition: it is good to be different

Elizabeth A. Tibbetts[1] **and James Dale**[2]

[1] Department of Ecology and Evolutionary Biology, University of Michigan, 830 N. University, Ann Arbor, MI 48109-1048, USA
[2] Department of Behavioural Ecology & Evolutionary Genetics, Max Planck Institute for Ornithology, PO Box 1564, D-82305 Starnberg (Seewiesen), Germany

Individual recognition (IR) behavior has been widely studied, uncovering spectacular recognition abilities across a range of taxa and modalities. Most studies of IR focus on the recognizer (receiver). These studies typically explore whether a species is capable of IR, the cues that are used for recognition and the specializations that receivers use to facilitate recognition. However, relatively little research has explored the other half of the communication equation: the individual being recognized (signaler). Provided there is a benefit to being accurately identified, signalers are expected to actively broadcast their identity with distinctive cues. Considering the prevalence of IR, there are probably widespread benefits associated with distinctiveness. As a result, selection for traits that reveal individual identity might represent an important and underappreciated selective force contributing to the evolution and maintenance of genetic polymorphisms.

Individual recognition as communication

Recognition is required for almost all social behavior. Recognition ranges across a wide spectrum, including self, kin, mate, gender, neighbor, rival, friend, species, predator and prey [1]. Individual recognition (IR) refers to a subset of recognition that occurs when one organism identifies another according to its individually distinctive characteristics [2]. Although IR is the most precise form of recognition, it is always associated with some other form of recognition. Depending on the context in which an individual's identity is learned, IR can be used to discriminate a mate, offspring, sibling, friend or rival. During IR, the signaler is recognized by unique recognition cues, and the receiver learns the cues and uses them to identify the signaler during future interactions.

Here, we provide a cohesive review of IR from both the receiver's and the signaler's perspective. Both perspectives are crucial, because selection can act on receivers and signalers separately. For example, receivers who are capable of IR might be selectively favored regardless of whether signalers benefit from being recognized. Although the signaler's perspective has received less attention, selection on signalers to be memorably different might provide an underappreciated selective mechanism that increases phenotypic variability. IR is frequently considered a relatively complex form of communication, so there has been extensive interest in the diversity and sophistication of receiver behavior in many different taxa. Here, we provide a holistic framework for understanding IR and suggest areas where future research will be most profitable.

The receiver's perspective: individual recognition

Temperate-breeding hooded warblers, *Wilsonia citrina*, can remember their specific neighbors from the previous breeding season even after over wintering in the tropics [3]. King penguins, *Aptenodytes patagonicus*, can find their chick from within a crèche of thousands of potential candidates after months of separation [4]. *Polistes* paper wasps can identify individual nestmates in the same way we humans recognize our own companions – by unique facial features [5]. In these three examples of IR, the receiver learns the individually specific cues of another individual and associates the cues with other important, fitness-related information (i.e. neighbor, offspring, dominance). Later, the receiver uses the cues to identify the individual. Decades of creative research have uncovered many more examples of IR in different social contexts.

How to test individual recognition

IR behavior can seem obvious, and there are numerous anecdotal observations of animals reacting strongly to unknown individuals [6]. However, experimental tests are needed to evaluate whether animals are performing IR rather than other forms of recognition (e.g. familiar versus unfamiliar; Box 1) and to identify the specific cues they are using.

Three methodologies can be used to demonstrate IR. First, researchers can set up behavioral interactions between individuals under controlled circumstances. For example, Karavanich and Atema [7] set up sequential boxing matches among lobsters, *Homarus americanus*. They observed that lobsters retreat from familiar dominants but fight with unfamiliar dominants, suggesting that lobsters learn their previous opponents individually. The second method for testing IR involves presenting the putative cue used for IR and observing receiver responses. Insley used this method to demonstrate that northern fur seals, *Callorhinus ursinus*, learn the individually distinctive calls of their pups. Seals are attracted to speakers playing the call of their pup, but ignore speakers playing calls of other pups. Remarkably, seals responded to their pup's call even after a four-year separation [8]. The third

---

Corresponding author: Tibbetts, E.A. (tibbetts@umich.edu).

www.sciencedirect.com 0169-5347/$ – see front matter © 2007 Elsevier Ltd. All rights reserved. doi:10.1016/j.tree.2007.09.001

Box 1. 'True' individual recognition or recognition of different classes?

The difference between true IR and class-level recognition has been a source of much controversy in the IR literature [13,79,80]. In 'true' IR the receiver learns the signaler's individually distinctive characteristics and associates those characteristics with individual-specific information about the signaler. Class-level recognition falls into two categories: (i) receivers learn the signaler's individually distinctive characteristics and associate these characteristics with inferred class-specific information about the signaler; and (ii) receivers match the signaler's phenotype to an internal template associated with different classes [1]. It is often difficult to distinguish between IR and the first form of class level recognition, as the only difference between the two is the specificity of the information that the receiver learns about the signaler. As a result, most true IR experiments have been done in the few contexts where it is relatively straightforward to test whether the receiver has learned individual-specific information about the signaler (i.e. relative dominance rank or residency in a specific territory) [3,13,80]. The issue of true IR is particularly important for cognitive sciences, because true IR is thought to be a sophisticated process [31] that might require specific cognitive adaptations.

From the signaler's perspective, the selective outcome between true IR and the first type of class-level recognition is not as important. In both cases, receivers learn the individually distinctive phenotype of the signaler, so signalers are selected to be distinctive relative to the rest of the population. By contrast, class-level recognition involving phenotype matching is expected to favor signals that are distinctive relative to the overall population but uniform relative to other individuals within the class.

method for testing IR involves observing receiver responses to cues that have been experimentally manipulated. Signal alteration can be high tech (e.g. using recombinant DNA technology to produce odiferous mouse proteins [9]), medium tech (digitally modifying penguin calls before playback [10]) or low tech (using modeler's paint to experimentally alter the appearance of wasp facial patterns [5]). Regardless of how it is done, experimental signal alteration is a good way to assess the cues used for recognition and the behavioral contexts in which recognition occurs.

Social contexts of recognition

The ability to recognize individuals can be a valuable social skill whenever there are repeated interactions among multiple individuals with differing intentions. Although IR is likely to be important in a range of social contexts, the vast majority of IR research has focused on three main situations: territoriality, aggressive competition and parental care.

Much of the earliest IR research examined recognition of territorial neighbors (originally termed 'dear enemy' recognition). For example, playback experiments demonstrated that hooded warblers know both the identity and position of each of their neighbors. Males largely ignored playbacks of neighbor songs positioned on the correct territorial boundary, but responded aggressively to playbacks of neighbor songs positioned on the incorrect territorial boundary and to playbacks of stranger songs [3]. IR is thought to reduce the energetic costs of territorial defense by enabling territory holders to focus their aggressive efforts on non-territorial floaters instead of their less threatening neighbors [11]. In some species, territory holders might actually increase aggression towards familiar, but untrustworthy, neighbors [12]. Whether they are treated more or less aggressively, recognition of territorial neighbors is widespread and has been found in many taxa, including birds [3,13,14], mammals [15], lizards [16], frogs [17], fish [18] and aquatic invertebrates [19]. Leks are one context where territorial IR might be common, because multiple males defend small territories in close proximity to each other. Continued research will undoubtedly uncover many more cases of territorial IR.

There has also been a strong focus on IR in aggressive competition, because IR can reduce the costs associated with agonistic competition and stabilize dominance hierarchies [20]. Empirical work indicates that IR has an important role in dominance interactions in a range of species, including insects [5,21], aquatic invertebrates [7,22,23], fish [24] and mammals [25,26]. Learning the individual identity and relative competitive ability of conspecifics provides a precise, non-cheatable method of assessing individual agonistic qualities. Therefore, IR is likely to be an important aspect of dominance whenever there are repeated aggressive interactions between small numbers of individuals. In larger groups, individuals can use transitive inference to gauge relative dominance of unfamiliar individuals observed interacting with familiar ones [27], a skill that obviously requires acute IR capabilities. In extremely large or unstable groups, where repeated interactions between familiar individuals are uncommon, status signaling and/or winner–loser effects can stabilize dominance interactions [28–30]. Although receiver responses to status signals and identity signals are similar, the two types of communication can be distinguished by observing receiver responses to unfamiliar signalers. Status signals convey information about agonistic abilities of unfamiliar individuals, whereas identity signals only convey information about the agonistic abilities of known individuals.

The third main focus of IR research has been in the context of parent/offspring recognition. For example, emperor penguins, *Aptenodytes forsteri*, find their chick from among thousands of unrelated individuals after returning from week-long foraging trips [10]. Although the sight of a mother and chick reunion within a teeming rookery is truly remarkable, this is sometimes considered a relatively simple form of IR. Some think true IR requires receivers who can individually discriminate many individuals [31].

Recognition of parents and offspring using individual-specific cues is especially likely to occur in organisms that breed in large, high-density colonies with synchronous nesting, and reduced recognition potential based on positional information. Well known examples include seabirds [10,32], pinnipeds [33] and bats [34]. Seabirds can even individually identify their eggs (Figure 1 and [32,35]). Individual parent/offspring recognition also occurs in sheep (*Ovis aries*) [36] and is probably ubiquitous in herd-living animals.

An important direction for future research is assessing whether multiple parents and/or offspring can be individually identified. In species with biparental care, can offspring discriminate between mom and dad, and associate different information with each? In species with multiple offspring, do parents use identity information to discrimi-

Figure 1. Pictures of eight putative identity signals. We can only get a sense of what visually based individual identity signals 'look' like. However, the selection pressure on olfactory and acoustic identity cues should produce similar signal properties: various independently assorting characteristics that collectively contribute to providing the receiver an overall unique signature. From the top: brown paper wasps (*Polistes fuscatus*), fiddler crabs (*Uca capricornis*), ruffs (*Philomachus pugnax*), red-billed queleas (*Quelea quelea*), cliff swallow chicks (*Petrochelidon pyrrhonota*), common murre eggs (*Uria aalge*), wild dogs (*Lycaon pictus*), humans (*Homo sapiens*). In humans, even among celebrities with a reputation for looking similar, facial differences provide surfeit information for individual identification (from left to right: Kevin Costner, Dennis Quaid, Matt Damon, Patrick Swayze, David Beckham). Photo credits: E.A. Tibbetts, T. Detto, D. Lank, M. Holdt, P. Stoddard, J. Dale, K. Wolhuter, D. Henry Jr, M. Cavanugh, T. Harms and A. Light.

nate between individual offspring? Interesting work in black redstarts, *Phoenicurus ochruros*, suggests such complex recognition might occur because parents use individually distinctive calls to recognize and preferentially feed their 'favorite' chicks [37].

Social contexts of recognition requiring additional study

Relatively little research has examined IR in contexts other than those described above. For example, many models of social interactions have IR as a crucial assumption (e.g. delayed reciprocity [38] and image-scoring or reputations [39]), although recognition has not been tested in these contexts. In addition, few experiments have directly tested individual mate recognition, although the occurrence of stable, long-term biparental care suggests many, if not most, organisms can individually identify their mates. There have been a few experiments examining mate recognition in socially monogamous species, such as Magellanic penguins (*Spheniscus magellanicus*) [40], spectacled parrotlets (*Forpus conspicillatus*) [41] and cleaner shrimp (*Lysmata debelius*) [42]. Interestingly, individual mate recognition even occurs in some polygynous species lacking biparental care [43,44]. Simpler mechanisms, such as positional information, might enable monogamy without IR [45], so targeted experiments are needed to assess the occurrence of individual mate recognition.

Research will continue to uncover diverse contexts in which IR is used. Yellow-bellied marmots (*Marmota flaviventris*) [46] and vervet monkeys (*Chlorocebus pygerythrus*) [47] assess the reliability of alarm calls based on the identity of the caller. Meadow voles, *Microtus pennsylvanicus*, use positional information of individually distinctive odor cues to assess potential mates [48]. Individual mate recognition might provide a non-cheatable method of assessing an individual's value as a mate. Individuals could eavesdrop on mating and competitive interactions between known individuals to make informed mate choice decisions [49].

Perhaps the largest body of recognition literature has focused on kin recognition. Recognition of unfamiliar kin has received most of the attention, although familiar kin might be identified using learned individual-specific cues [1]. For example, long-tailed tits, *Aegithalos caudatus*, learn the individually specific calls of their relatives [50]. Because each tit has a unique call, birds could use these calls for IR as well as kin discrimination. Thus far, there is only one example of a signal that is used for both individual and kin recognition. Chacma baboons, *Papio hamadryas*, associate kinship and dominance information with the calls of group members [51].

The ability to associate multiple kinds of information with individually distinctive cues is not confined to primates. In fact, hermit crabs, *Pagurus longicarpus*, learn the distinctive scents of competitors, and associate an individual's scent with their agonistic abilities and the quality of their shell house [23]. Instead of merely identifying one context in which an identity signal is used, future research should explore whether identity signals function in multiple contexts. For example, how many kinds of fitness-related information do birds associate with each other's individually distinctive songs?

IR and cognitive representations of conspecifics

The idea of animals associating many different kinds of information with an identity signal raises important questions about animals' cognitive representations of each other [52,53]. Many different cognitive mechanisms might be used during IR. For example, baboons might form cognitive associations between identity signals and memories of past experiences, whereas hermit crabs might rely on simpler behavioral decision rules to associate multiple kinds of information with identity signals.

Although behavioral research does not specifically address the cognitive mechanisms underlying recognition behavior, a few studies suggest that animals form relatively complex representations of each other. For example, golden hamsters, *Mesocricetus auratus*, have many different, individually distinctive odors from different parts of their body. A naïve receiver treats the odors as if they are from different individuals. After experience with the live scent donor, receivers treat the odors as if they represent the same individual, suggesting that experience enables hamsters to form multi-component representation of other individuals [52]. Male song sparrows, *Melospiza melodia*, have intricate social communication systems in which they integrate information about the identity and individual song repertoires of each of their neighbors [54]. Although somewhat controversial [55], there is evidence that bottlenose dolphins (*Tursiops truncatus*) [56] and spectacled parrotlets [57] have individually distinctive auditory signatures that are used like names. Individuals use their signatures to announce their identity and others use the signatures to label conspecifics. These examples of IR are very different, but each suggests that animals develop sophisticated, multifaceted internal models of other individuals.

Receiver specialization for recognition

When the ability to recognize individuals is strongly favored by selection, receivers might evolve specializations that help them identify individuals more easily. For example, humans (*Homo sapiens*) [58,59], sheep [60] and macaques (*Macaca mulatta*) [61] have neural specialization for facial IR. Faces are processed in a specific area of the brain and the brain treats faces differently from other objects. A striking consequence of human neural specialization for face recognition is that some humans experience a condition called 'face blindness' during which they cannot recognize individual faces but can still recognize objects [58]. Neural specializations for IR are probably not universal, but they might evolve when there is strong selection for quick and easy identification of many individuals.

Variation in the sensory abilities of penguin chicks illustrates how ecological circumstances can influence the evolution of recognition systems. King penguin chicks have truly remarkable recognition abilities; they can discriminate the call of their parent even when the parental call is seemingly overshadowed by louder calls from multiple other adults. This impressive ability to perceive and extract a parent's call from other sounds has been compared to the way humans notice their name being mentioned from across a noisy room: 'the cocktail party effect' [4]. King penguin chicks need precise recognition abilities because they live in large colonies and must find their parents without the benefit of the positional information that would be provided by a stable nest site. By contrast, Adelie (*Pygoscelis adeliae*) and gentoo (*P. papua*) penguins have stable nest sites and poorer call recognition abilities [62]. Therefore, the degree of receiver specialization will vary; strong selection can give rise to amazing adaptations for recognizing individuals.

Box 2. The benefits (and costs) of identity signaling

There are numerous potential benefits associated with identity signaling, including: decreased harassment by neighbors during territorial interactions, increased altruism from familiar kin, decreased risk of inbreeding, decreased inter- and intraspecific brood parasitism, decreased aggressive competition over status, and increasing stability in reciprocal interactions and cooperative groups. In addition, sexual selection can favor identity signaling whenever being recognizable improves mating success. Sexual selection for distinctiveness might operate through both intrasexual (e.g. reduced aggression received from neighbors within a lek) and intersexual (e.g. female guppies preferring unfamiliar males as mates) processes. Although benefits associated with distinctiveness are likely to be widespread, these benefits have not been experimentally tested.

Identity signaling can also be costly, because it is more difficult for a recognizable individual to cheat. For example, a distinctive chick will get a higher proportion of correctly delivered food from its parents, but it will also receive a lower proportion of food incorrectly delivered by non-related adults. Although distinctiveness might be costly in some contexts, identity signals will spread as long as the benefits associated with distinctiveness outweigh the benefits associated with confusion [2].

The signaler's perspective: signals of individual identity

As described above, a relatively large number of studies have demonstrated that receivers are capable of individually recognizing conspecifics. However, surprisingly little is known about how selection acts on the conspecifics that are recognized. Do they actively signal their individual identity? If being recognized is beneficial (Box 2), selection should favor individuals who actively broadcast information about their identities to facilitate accurate recognition. When being memorably different is favored, distinctive traits will spread via negatively frequency-dependent selection, such that individuals who look, sound or smell unique will be favored. Signals that evolve to facilitate IR are called identity signals [2,63].

Signals that convey different information are theoretically expected to have different properties [64] (Table 1, Box 3). Identity signals are expected to evolve via negatively frequency-dependent selection because individuals with rare phenotypes are more distinctive and less likely to be confused with others [2]. Negatively frequency-dependent selection will result in identity signals that are (i) variable and (ii) have polymodal frequency distributions [65] of trait variance. In addition, the signals will be (iii) cheap (i.e. not condition-dependent) because costly phenotypes will not rise to an appreciable frequency in the population [2]. At equilibrium, signal variants are expected to have (iv) equal fitness [2]. The components of identity signals are expected to (v) assort independently [2,31] and the signal phenotype should be relatively fixed or inflexible over an animal's lifetime. Finally, (vi) high degrees of genetic determination provide a simple developmental

Table 1. The expected properties of seven different signal types (adapted from Ref. [64])

Signal[a]	Selection	Variability[b]	Modality[c]	Continuity[d]
Quality	Directional	Moderate	Unimodal	Continuous
Fisherian attractiveness	Directional	Low	Unimodal	Continuous
Strategy	Disruptive	Low[e]	Bimodal	Discrete
Genetic compatibility	Disruptive	Moderate	Multimodal	Discrete
Kinship	Negatively frequency dependent	High	Multimodal	Continuous
Individual identity	Negatively frequency dependent	High	Multimodal	Continuous
Presence	Stabilizing	Low	Unimodal	Continuous

[a] See above text for descriptions of the information that could be broadcast by a signal trait.
[b] Relative degree of phenotypic variability observed in a putative signal.
[c] Number of modes observed in frequency distributions of trait variance.
[d] Whether trait variance is continuously or discretely variable.
[e] Within strategies.

mechanism to produce fixed, independently assorting traits, so variance in identity signals will often be genetically based [2,66] (although environmentally determined traits that are relatively fixed can also function as identity signals e.g. [56,57]). The expected properties of identity signals are compared with the properties of other types of signals in Box 3. For example, red-billed quelea, *Quelea quelea*, plumage variation (a putative identity signal) is dramatically more variable and complex than analogous variability in coloration of male northern cardinals, *Cardinalis cardinalis* (a putative quality signal) (Figure 2) [64].

How to test identity signaling

Selection might favor receivers who can recognize individuals regardless of whether the signalers benefit from being recognized [2,63]. As a result, phenotypic variability might be used for IR even if the variability has not especially evolved to signal identity. For example, the timbre of a human's voice can be used for IR even though the variability might be a by-product of sound production [67]. Three approaches can be used to test whether traits evolved as identity signals.

First, do variable traits used for IR have the expected characteristics of identity signals? If so, the traits might have evolved via negatively frequency-dependent selection for distinctiveness. A brief survey of traits used for IR shows that signal properties match those expected for identity signals (Table 2). Therefore, identity signaling (i.e. selection for distinctiveness) might be a more widespread explanation of phenotypic variability than previously recognized. Although analyzing signal properties is the easiest method to find a putative identity signal, it is also the least conclusive.

A second approach for studying identity signals is comparing traits across taxa to assess the social and ecological factors that favor identity signal evolution. For example, Medvin and colleagues [68] looked at the degree of variability in nestling calls across a range of swallow species (Hirundinidae). Species that nest in larger colonies have more variable nestling calls than species that nest in smaller colonies, suggesting that chicks have been selected to provide variable, distinctive cues in circumstances where parents could potentially confuse their own offspring with other nestlings [68,69]. A similar pattern has been found in penguin nestling calls [62]. Additionally, intraspecific egg color variability tends to be higher in passerine species more vulnerable to interspecific brood parasitism [70]. In paper wasps (*Polistes*), only species with complex social interactions have the type of variable markings necessary for IR, suggesting that complex social behavior selects for distinctiveness [71]. Whitfield [30] pointed out the power of the comparative approach, suggesting that species comparisons could be used to assess the factors favoring the evolution of variable avian plumage ornaments used for IR. For example, the highly polymorphic plumage color variability in hawks, eagles and falcons (Falconidae) are a promising taxon [64]. Twenty years after Whitfield's suggestion, the power of the comparative approach for understanding identity signal evolution has remained largely untapped.

The third, and most conclusive, approach to studying identity signaling is to test the fundamental assumption of identity signaling. Do individuals who have rare signal phenotypes (more individually recognizable) experience a selective advantage over those who have more common signal phenotypes (less individually recognizable)? Such a selective advantage for distinctiveness has yet to be shown

Box 3. Signal properties and signal information

Signals that evolve to reveal different information are theoretically expected to have different properties [64]. As a result, it should be possible to 'reverse-engineer' observed signal design to get clues about the function of a putative signal. Any signal can potentially reveal at least seven different types of information about the broadcaster including: (i) quality (traits that reflect relative overall genetic and phenotypic constitution); (ii) Fisherian attractiveness (traits that define attractiveness independent of quality and arise from Fisherian runaway selection); (iii) behavioral strategy (traits that reveal the behavioral strategy pursued, e.g. signals of gender); (iv) genetic compatibility (traits that reflect genetic compatibility for mate choice, e.g. species isolation signals and signals of genetic similarity); (v) kinship (traits which facilitate discrimination of unfamiliar kin); (vi) individual identity ('name tags' that increase individual recognizability); and (vii) presence (traits which either reveal or conceal an individual's physical location to receivers).

There are three fundamental properties of a signal's variance: degree of variability, modality and continuity. In terms of these properties, what should a signal of individual identity look (or sound or smell) like? Dale [64] recently summarized the expected signal properties for the above seven different kinds of signals, and predicted that only signals of kinship and identity are expected to be highly variable, multimodal and continuously variable (Table 1). Signals of identity and kinship differ substantially from each other even though both are expected to have similar properties and both can be used for kin recognition. Identity signals can only be used to identify familiar kin because the recognition template is based on the signaler [2,66]. By contrast, signals of kinship can be used to identify unfamiliar kin using a recognition-template based on self or another known relative [1,66].

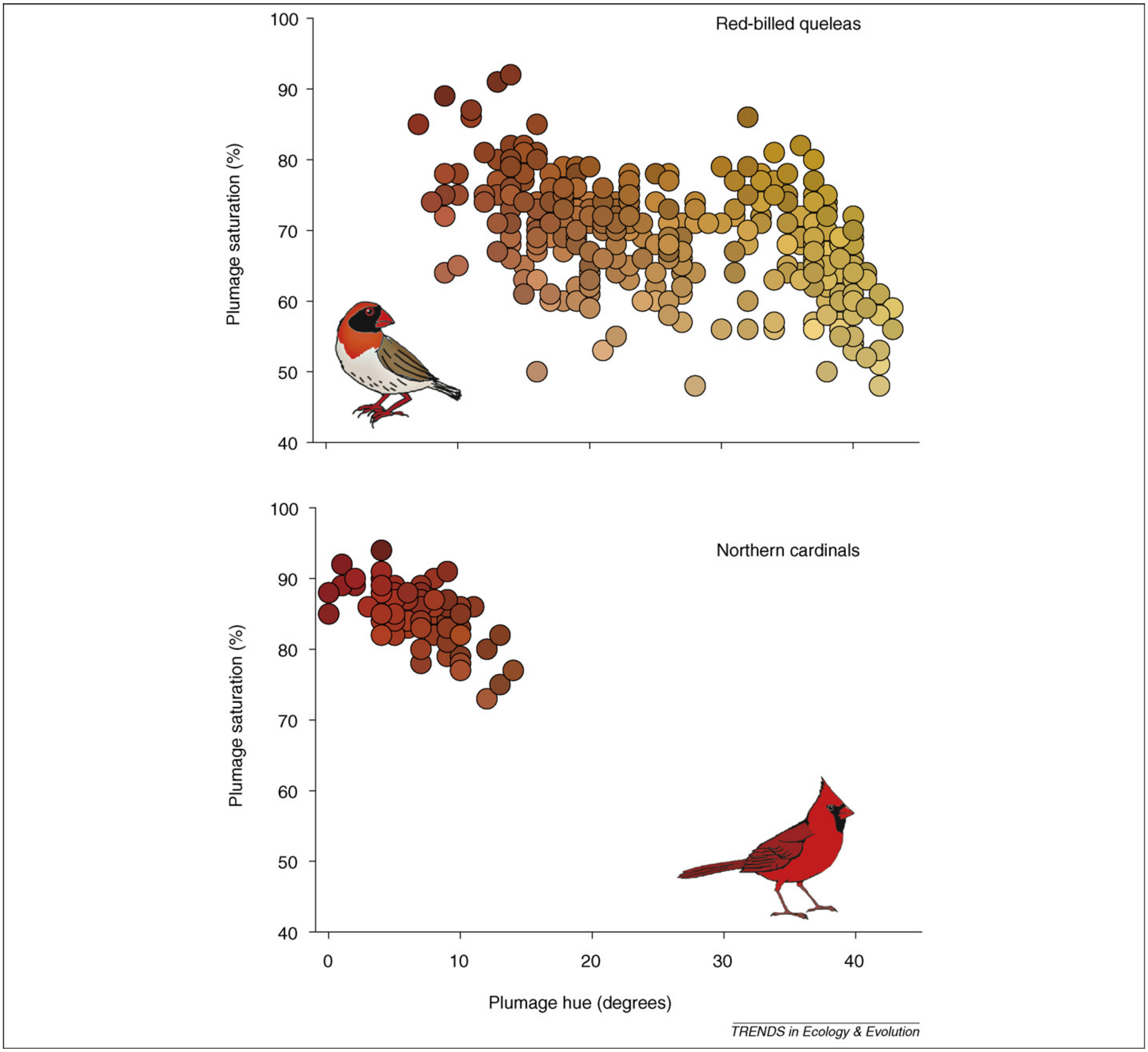

Figure 2. Saturation versus hue in male breast coloration of red-billed queleas and northern cardinals. Quelea plumage is hypothesized to signal individual identity whereas cardinal plumage is thought to signal quality [64]. Plotted on similarly scaled axes, quelea plumage demonstrates higher and more complex (i.e. bimodal) variability than cardinal plumage. Color of data points approximates the actual color of the individual birds measured. Saturation is analogous to chroma, whereas hue is analogous to the peak reflected wavelength. Adapted from data in [2,64].

for any putative identity signal in any communication medium in any taxon. Attempts to demonstrate the benefits associated with recognizability should thus be an important focus for future studies of IR [64]. A promising example is that female guppies, *Poecilia reticulata*, prefer to mate with males that have rare (i.e. distinctive) color patterns [72]. One explanation for this is that females adopt a strategy of mating with multiple males and they use visual identity signals to identify previous mates [72], thereby providing a sexually selected benefit for distinctiveness.

Social context of identity signaling

Under what circumstances should selection favor the evolution of distinctive signals of individual identity? Identity signals will spread when there is the possibility of costly confusion between the signaler and another individual. Generally, the same selection pressures that favor receivers who are good at recognizing individuals will favor signalers who display their identity with conspicuous, distinctive signals. However, it is worth noting that signaler and receiver interests are not always aligned. If being correctly recognized is costly, individuals will be selected to actively conceal their identity by reducing phenotypic variability. Selection is expected to favor identity signals only when facilitating recognition among receivers is advantageous [63].

Thus far, it seems that colonial breeding, complex social interactions, dominance hierarchies and territoriality might favor identity signaling. The comparative studies

Table 2. The predicted properties of traits specially evolved to signal individual identity and the observed properties in six candidate species with putative visual signals of identity

Species (and trait)	Relative variability[a]	Frequency distribution[b]	Correlation between traits[c]	Condition dependence[d]	Correlation with fitness[e]	Degree of genetic determination	Refs
Expected for identity signals	High	Multimodal	None	No	No	High	[2]
Brown paper wasp *Polistes fuscatus* (face coloration)	High	Multimodal	None	No	-	High (?)	[5,81]
Ruff *Philomachus pugnax* (male coloration)	High	Multimodal	Low	No	No	High	[2,73]
Common murre *Uria aalge* (egg coloration)	High	Multimodal	-[g]	-	-	High (?)	[35,64]
Royal tern *Sterna maxima* (nestling coloration)	High	Multimodal	Low	-	-	High (?)	[32]
Cliff swallow *Petrochelidon pyrrhonota* (nestling calls)	High	Unimodal (?)[f]	Low	-	-	High	[66,68]
Red-billed quelea *Quelea quelea* (male coloration)	High	Bimodal	None	No	No	High	[2]

[a] Refers to observed phenotypic variability as compared to variation typically observed in other close relatives.
[b] Nature of observed frequency distribution of phenotypic variance.
[c] Degree of correlation between different components of signal (e.g. peak wavelength of color patch versus area of color patch).
[d] Relationship between condition and trait variance; used as a proxy of expense of trait development.
[e] Relationship between trait variance and indices of reproductive success.
[f] Question marks indicate that additional data are needed to confirm speculative remarks in references.
[g] Dashes indicate no data currently published.

in swallows and penguins indicate that high-density, colonial breeding might be one of the most important ecological factors favoring identity signaling [68,71]. Complex social interactions can also favor identity signaling, especially when there are repeated social interactions between individuals with differing roles/intentions [71]. Sociality might explain the highly variable olfactory signals in many social mammals, the distinctive contact calls among social birds [68], the complex acoustic signals in many primates [53], and the spectacular color variation among wolves (*Canis lupus*) and African wild dogs (*Lycaon pictus*) (Figure 1). Within-species comparisons suggest identity signals are also important for territoriality. In ruffs (*Philomachus pugnax*) [73] (Figure 1) and blue-headed wrasse (*Thalassoma bifasciatum*) [74], males who defend territories have variable, unique patterns, whereas non-territorial (i.e. satellite) males tend to be much more uniform (i.e. less distinctive) in appearance, suggesting aspects of territorial males' fantastic color patterns are specially evolved identity signals that reduce conflict in territorial contests. Although identity signals are probably widespread in nature, much more data on the benefits of distinctiveness are needed to fully understand the circumstances that favor identity signaling.

Identity signaling in humans

Our faces provide powerful images that are full of multiple messages. Our expressions provide information about current motivational state. Our male-like or female-like facial proportions provide information about gender and hormone-exposure [75,76]. High symmetry and youthfulness signal characteristics associated with attractiveness [77]. In addition, there are countless subtle differences that collectively contribute to our overall distinctiveness (Figure 1): a key aspect of being human.

Is human facial distinctiveness an adaptive signal of individual identity? From a sociobiological perspective, humans seem to have the 'perfect storm' of selection pressures that might favor recognizability. We are extremely social, interacting repeatedly with large numbers of individuals, each with varying roles in our lives. We are extremely cooperative, and we make complex decisions about whether and how much to cooperate based on kinship, friendship and social reputation [39,78]. These behaviors require accurate IR and the cognitive ability to associate complex information with each individual's identity. If human facial variability has evolved to signal individual identity, the properties of human facial variation are expected to be consistent with those expected for identity signals [2] (Box 3). Targeted research is needed to evaluate how well human faces fit the general model. If human faces are identity signals, humans who are difficult to individually distinguish are expected to suffer costs. For example, perhaps career success in the entertainment industry is determined not only by attractiveness and talent, but also by a particularly distinctive appearance?

Conclusions

In this review, we present IR from the perspective of both the recognizer (receiver) and the recognized (signaler). Studies from the receiver's perspective are relatively common and have demonstrated that IR is an extremely widespread phenomenon. Studies from the signaler's perspective are just beginning to gather momentum. Both perspectives are crucial for a complete understanding of IR, because it is the behavioral responses of the receivers that ultimately impose selection pressures on signalers to reveal (or conceal) their identity. Precise quantification of relative selection pressures represent an important area for future IR research.

Understanding high phenotypic variability is of great interest to evolutionary biologists because directional and stabilizing selection tend to reduce genetic (and phenotypic diversity). However, with IR, being memorably different is advantageous. Indeed, positive selection for broadcasting individual identity could represent a widespread explanation for the high levels of phenotypic diversity in social organisms.

Acknowledgements

Thanks to B. Daley, R. Seyfarth, M. Sheehan and two anonymous reviewers for their comments on early drafts of this paper. Financial support was provided to J.D. by the Max Planck Society (Germany).

References

1 Sherman, P.W. *et al.* (1997) Recognition systems. In *Behavioural Ecology: An Evolutionary Approach* (Krebs, J.R. and Davies, N.B., eds), pp. 69–96, Blackwell Science
2 Dale, J. *et al.* (2001) Signaling individual identity versus quality: a model and case studies with ruffs, queleas, and house finches. *Am. Nat.* 158, 75–86
3 Godard, R. (1991) Long-term-memory of individual neighbors in a migratory songbird. *Nature* 350, 228–229
4 Aubin, T. and Jouventin, P. (1998) Cocktail-party effect in king penguin colonies. *Proc. R. Soc. Lond. B Biol. Sci.* 265, 1665–1673
5 Tibbetts, E.A. (2002) Visual signals of individual identity in the wasp *Polistes fuscatus*. *Proc. R. Soc. Lond. B Biol. Sci.* 269, 1423–1428
6 Tinbergen, N. (1958) *Curious Naturalists,* Country Life
7 Karavanich, C. and Atema, J. (1998) Individual recognition and memory in lobster dominance. *Anim. Behav.* 56, 1553–1560
8 Insley, S.J. (2000) Long-term vocal recognition in the northern fur seal. *Nature* 406, 404–405
9 Hurst, J.L. *et al.* (2001) Individual recognition in mice mediated by major urinary proteins. *Nature* 414, 631–634
10 Aubin, T. *et al.* (2000) Penguins use the two-voice system to recognize each other. *Proc. R. Soc. Lond. B Biol. Sci.* 267, 1081–1087
11 Temeles, E.J. (1994) The role of neighbors in territorial systems – when are they dear enemies. *Anim. Behav.* 47, 339–350
12 Olendorf, R. *et al.* (2004) Male red-winged blackbirds distrust unreliable and sexually attractive neighbours. *Proc. R. Soc. Lond. B. Biol. Sci.* 271, 1033–1038
13 Falls, J. (1982) Individual recognition by sound in birds. In *Song Learning and Its Consequences* (Kroodsma, D.E. and Miller, E.H., eds), pp. 237–278, Academic Press
14 Whitfield, D.P. (1986) Plumage variability and territoriality in breeding turnstone *Arenaria interpres* – status signaling or individual recognition. *Anim. Behav.* 34, 1471–1482
15 Johnston, R.E. (2003) Chemical communication in rodents: from pheromones to individual recognition. *J. Mammal.* 84, 1141–1162
16 Husak, J.F. and Fox, S.F. (2003) Adult male collared lizards, *Crotaphytus collaris*, increase aggression towards displaced neighbours. *Anim. Behav.* 65, 391–396
17 Davis, M.S. (1987) Acoustically mediated neighbor recognition in the North-American bullfrog, *Rana catesbeiana*. *Behav. Ecol. Sociobiol.* 21, 185–190
18 Myrberg, A.A. and Riggio, R.J. (1985) Acoustically mediated individual recognition by a coral-reef fish (*Pomacentrus partitus*). *Anim. Behav.* 33, 411–416
19 Detto, T. *et al.* (2006) Visually mediated species and neighbour recognition in fiddler crabs (*Uca mjoebergi* and *Uca capricomis*). *Proc. R. Soc. Lond. B Biol. Sci.* 273, 1661–1666
20 Barnard, C.J. and Burk, T. (1979) Dominance hierarchies and the evolution of individual recognition. *J. Theor. Biol.* 81, 65–73
21 D'Ettorre, P. and Heinze, J. (2005) Individual recognition in ant queens. *Curr. Biol.* 15, 2170–2174
22 Caldwell, R.L. (1985) A test of individual recognition in the stomatopod *Gonodactylus festae*. *Anim. Behav.* 33, 101–106
23 Gherardi, F. *et al.* (2005) Unraveling the nature of individual recognition by odor in hermit crabs. *J. Chem. Ecol.* 31, 2877–2896
24 Johnsson, J.I. (1997) Individual recognition affects aggression and dominance relations in rainbow trout, *Oncorhynchus mykiss*. *Ethology* 103, 267–282
25 Silk, J.B. (1999) Male bonnet macaques use information about third-party rank relationships to recruit allies. *Anim. Behav.* 58, 45–51
26 Cheney, D.L. *et al.* (1995) The responses of female baboons (*Papio cynocephalus ursinus*) to anomalous social interactions – evidence for causal reasoning. *J. Comp. Psychol.* 109, 134–141
27 Grosenick, L. *et al.* (2007) Fish can infer social rank by observation alone. *Nature* 445, 429–432
28 Dugatkin, L.A. and Earley, R.L. (2004) Individual recognition, dominance hierarchies and winner and loser effects. *Proc. R. Soc. Lond. B Biol. Sci.* 271, 1537–1540
29 Tibbetts, E.A. and Dale, J. (2004) A socially enforced signal of quality in a paper wasp. *Nature* 432, 218–222
30 Whitfield, D.P. (1987) Plumage variability, status signaling and individual recognition in avian flocks. *Trends Ecol. Evol.* 2, 13–18
31 Beecher, M.D. (1989) Signaling systems for individual recognition – an information-theory approach. *Anim. Behav.* 38, 248–261
32 Buckley, P.A. and Buckley, F.G. (1972) Individual egg and chick recognition by adult royal terns (*Sterna maxima maxima*). *Anim. Behav.* 20, 457–462
33 Charrier, I. *et al.* (2003) Vocal signature recognition of mothers by fur seal pups. *Anim. Behav.* 65, 543–550
34 Balcombe, J.P. (1990) Vocal recognition of pups by mother Mexican free-tailed bats, *Tadarida brasiliensis mexicana*. *Anim. Behav.* 39, 960–966
35 Gaston, A.J. *et al.* (1993) Egg recognition and egg stealing in murres (*Uria* Spp). *Anim. Behav.* 45, 301–306
36 Searby, A. and Jouventin, P. (2003) Mother-lamb acoustic recognition in sheep: a frequency coding. *Proc. R. Soc. Lond. B. Biol. Sci.* 270, 1765–1771
37 Draganoiu, T.I. *et al.* (2006) In a songbird, the black redstart, parents use acoustic cues to discriminate between their different fledglings. *Anim. Behav.* 71, 1039–1046
38 Trivers, R.L. (1971) Evolution of reciprocal altruism. *Q. Rev. Biol.* 46, 35–57
39 Nowak, M.A. and Sigmund, K. (1998) Evolution of indirect reciprocity by image scoring. *Nature* 393, 573–577
40 Clark, J.A. *et al.* (2006) Name that tune: call discrimination and individual recognition in Magellanic penguins. *Anim. Behav.* 72, 1141–1148
41 Wanker, R. *et al.* (1998) Discrimination of different social companions in spectacled parrotlets (*Forpus conspicillatus*): evidence for individual vocal recognition. *Behav. Ecol. Sociobiol.* 43, 197–202
42 Rufino, M.M. and Jones, D.A. (2001) Binary individual recognition in *Lysmata debelius* (Decapoda: Hippolytidae) under laboratory conditions. *J. Crustacean Biol.* 21, 388–392
43 Caldwell, R.L. (1992) Recognition, signaling and reduced aggression between former mates in a stomatopod. *Anim. Behav.* 44, 11–19
44 Amos, B. *et al.* (1995) Evidence for mate fidelity in the Gray Seal. *Science* 268, 1897–1899
45 Muller, J.K. *et al.* (2003) Nestmate recognition in burying beetles: the "breeder's badge" as a cue used by females to distinguish their mates from male intruders. *Behav. Ecol.* 14, 212–220
46 Blumstein, D.T. *et al.* (2004) Reliability and the adaptive utility of discrimination among alarm callers. *Proc. R. Soc. Lond. B. Biol. Sci.* 271, 1851–1857
47 Cheney, D.L. and Seyfarth, R.M. (1988) Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Anim. Behav.* 36, 477–486
48 Johnston, R.E. *et al.* (1997) Female voles discriminate males' over-marks and prefer top-scent males. *Anim. Behav.* 54, 679–690
49 Mennill, D.J. *et al.* (2002) Female eavesdropping on male song contests in songbirds. *Science* 296, 873
50 Sharp, S.P. *et al.* (2005) Learned kin recognition cues in a social bird. *Nature* 434, 1127–1130
51 Bergman, T.J. *et al.* (2003) Hierarchical classification by rank and kinship in baboons. *Science* 302, 1234–1236

52 Johnston, R.E. and Bullock, T.A. (2001) Individual recognition by use of odours in golden hamsters: the nature of individual representations. *Anim. Behav.* 61, 545–557

53 Seyfarth, R.M. and Cheney, D.L. (2003) Signalers and receivers in animal communication. *Annu. Rev. Psychol.* 54, 145–173

54 Beecher, M.D. *et al.* (1996) Repertoire matching between neighbouring song sparrows. *Anim. Behav.* 51, 917–923

55 Barton, R.A. (2006) Animal communication: do dolphins have names? *Curr. Biol.* 16, R598–R599

56 Janik, V.M. *et al.* (2006) Signature whistle shape conveys identity information to bottlenose dolphins. *Proc. Natl. Acad. Sci. U. S. A.* 103, 8293–8297

57 Wanker, R. *et al.* (2005) Vocal labelling of family members in spectacled parrotlets, *Forpus conspicillatus*. *Anim. Behav.* 70, 111–118

58 Kanwisher, N. and Yovel, G. (2006) The fusiform face area: a cortical region specialized for the perception of faces. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 361, 2109–2128

59 Kreiman, G. *et al.* (2000) Category-specific visual responses of single neurons in the human medial temporal lobe. *Nat. Neurosci.* 3, 946–953

60 Kendrick, K.M. and Baldwin, B.A. (1987) Cells in temporal cortex of conscious sheep can respond preferentially to the sight of faces. *Science* 236, 448–450

61 Tsao, D.Y. *et al.* (2006) A cortical region consisting entirely of face-selective cells. *Science* 311, 670–674

62 Jouventin, P. and Aubin, T. (2002) Acoustic systems are adapted to breeding ecologies: individual recognition in nesting penguins. *Anim. Behav.* 64, 747–757

63 Johnstone, R.A. (1997) Recognition and the evolution of distinctive signatures: when does it pay to reveal identity? *Proc. R. Soc. Lond. B. Biol. Sci.* 264, 1547–1553

64 Dale, J. (2006) Intraspecific variation in coloration. In *Bird Coloration, Vol 2: Function and Evolution* (Hill, G.E. and McGraw, K.J., eds), pp. 36–86, Harvard University Press

65 Maynard Smith, J. (1982) *Evolution and the Theory of Games*, Cambridge University Press

66 Beecher, M.D. (1982) Signature systems and kin recognition. *Am. Zool.* 22, 477–490

67 Belin, P. (2006) Voice processing in human and non-human primates. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 361, 2091–2107

68 Medvin, M.B. *et al.* (1993) Signals for parent offspring recognition – a comparative-analysis of the begging calls of cliff swallows and barn swallows. *Anim. Behav.* 45, 841–850

69 Leonard, M.L. *et al.* (1997) Parent-offspring recognition in tree swallows, *Tachycineta bicolor*. *Anim. Behav.* 54, 1107–1116

70 Soler, J.J. and Møller, A.P. (1996) A comparative analysis of the evolution of variation in appearance of eggs of European passerines in relation to brood parasitism. *Behav. Ecol.* 7, 89–94

71 Tibbetts, E.A. (2004) Complex social behaviour can select for variability in visual features: a case study in Polistes wasps. *Proc. R. Soc. Lond. B. Biol. Sci.* 271, 1955–1960

72 Eakley, A.L. and Houde, A.E. (2004) Possible role of female discrimination against 'redundant' males in the evolution of colour pattern polymorphism in guppies. *Proc. R. Soc. Lond. B. Biol. Sci. (Suppl.)* 271, S299–S301

73 Lank, D.B. and Dale, J. (2001) Visual signals for individual identification: the silent "song" of Ruffs. *Auk* 118, 759–765

74 Warner, R.R. (1987) Female choice of sites versus mates in a coral reef fish, *Thalassoma bifasciatum*. *Anim. Behav.* 35, 1470–1478

75 Law-Smith, M.J. *et al.* (2006) Facial appearance is a cue to oestrogen levels in women. *Proc. R. Soc. Lond. B. Biol. Sci.* 273, 135–140

76 Perrett, D.I. *et al.* (1998) Effects of sexual dimorphism on facial attractiveness. *Nature* 394, 884–887

77 Thornhill, R. and Gangestad, S.W. (1993) Human facial beauty – averageness, symmetry, and parasite resistance. *Hum. Nature – Int. Bios.* 4, 237–269

78 Wedekind, C. and Milinski, M. (2000) Cooperation through image scoring in humans. *Science* 288, 850–852

79 Halpin, Z.T. (1986) Individual odors among mammals: origins and functions. *Adv. Stud. Behav.* 16, 39–70

80 Brooks, R.J. and Falls, J.B. (1975) Individual recognition by song in white-throated sparrows.1. discrimination of songs of neighbors and strangers. *Can. J. Zool.* 53, 879–888

81 Tibbetts, E.A. and Curtis, T.R. (2007) Rearing conditions influence quality signals but not individual identity signals in *Polistes* wasps. *Behav. Ecol.* 18, 602–607