Note

Enhanced Kin Recognition through Population Estimation

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abstract: Kin recognition systems enable organisms to predict genetic relatedness. In so doing, they help to maximize the fitness consequences of social actions. Recognition based on phenotypic similarity—a process known as phenotype matching—is thought to depend upon information about one's own phenotype and the phenotypes of one's partners. We provide a simple model of genetic relatedness conditioned upon phenotypic information, however, that demonstrates that individuals additionally require estimates of the distributions of phenotypes and genotypes in the population. Following the results of our model, we develop an expanded concept of phenotype matching that brings relatedness judgments closer in line with relatedness as it is currently understood and provides a heuristic mechanism by which individuals can discriminate positive from negative relatives, thereby increasing opportunities for the evolution of altruism and spite. Finally, we propose ways in which organisms might acquire population estimates and identify research that supports their use in phenotype matching.

Keywords: kin recognition, phenotype matching, genetic relatedness, population estimates, similarity.

Introduction

Kin recognition systems have been tailored by selection to make de facto inferences about the genetic relatedness of conspecifics. Several such systems rely on a process known as phenotype matching, whereby an evaluator (a potential actor) assesses the similarity of the phenotypes of partners (potential recipients) to information associated with its own phenotype and, by consequence, its genetic identity. Our understanding of the mechanisms that facilitate an organism's acquisition of information about its phenotype has improved rapidly (reviewed in Waldman 1987; Hepper 1991; Sherman et al. 1997; Hauber and Sherman 2001; Krupp et al. 2011), but the particulars of the cognitive machinery underlying phenotype matching have been taken for granted.

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Apart from information about the evaluator's phenotype and that of its potential partner, we argue here that phenotype matching requires evaluators to have information about the distributions of (1) phenotypes and (2) genotypes in the population. These arguments may strike theoreticians as fairly elementary. However, in some 30-odd years of published research on kin recognition, we cannot locate evidence that they have been given serious consideration in either the published descriptions of phenotype matching processes or the empirical tests thereof. There appears to be a substantial gap between how phenotype matching is conceived to operate and how it likely does operate.

Genotypic and Phenotypic Similarity

Genetic relatedness can be conceptualized as a measure of differences in genetic similarity, representing the probability, beyond chance, that partners share copies of a focal allele causing individuals to perform a social action (Hamilton 1970; Grafen 1985; Queller 1994; Gardner and West 2004). If we measure genetic similarity by the coefficient of consanguinity, G—the probability that a partner shares a randomly selected allele identical by descent with an evaluator—then relatedness of the evaluator to its partner is (Rousset and Billiard 2000; Taylor et al. 2000)

$$r = \frac{G - \overline{G}}{1 - \overline{G}}, \tag{1}$$

where $\overline{G}$ is the average coefficient of consanguinity in the evaluator's "interaction neighborhood," or local population. Here, we use Queller's (1994) formulation of relatedness, which automatically accounts for local secondary effects (West and Gardner 2010) of any primary effect of the interaction. The relatedness of an evaluator to a partner is positive when the partner is more likely than chance to share copies of the allele ($r > 0$) and negative when the partner is less likely than chance to share copies of it ($r < 0$). That genetic relatedness can take on both positive and negative values has profound implications for social

evolution, as an individual's indirect fitness can thusly be increased by helping positive relatives or by harming negatively related ones. At the extreme, this can result in the evolution of altruism and spite, respectively (Hamilton 1970; Gardner and West 2004).

In theoretical models, partner choice is often conditioned upon demography. That is, population structure dictates partner assortment, as when a partner is chosen at random from the evaluator's interaction neighborhood (e.g., Frank 1986; Taylor 1992*a*,1992*b*; West and Buckling 2003; Foster 2004; Grafen 2007; Taylor et al. 2007; El Mouden and Gardner 2008). However, numerous animal species routinely regulate their behavior as a function of partner information—as in decisions regarding colony defense, inbreeding avoidance, and parental investment—and such is the express purpose of kin recognition systems. Thus, relatedness may also be conditioned upon other information that predicts genotype (Seger 1983), such as phenotype.

For instance, animals may judge genetic relatedness by assessing the phenotypic similarity of partners to themselves (reviewed in Waldman 1987; Hepper 1991; Krupp et al. 2011). Phenotype matching is a common and versatile category of kin recognition systems wherein an evaluator matches elements of the phenotypes of social partners to an internal representation derived from information associated with the evaluator's own phenotype (Holmes and Sherman 1982; Lacy and Sherman 1983; Waldman 1987; Hepper 1991; Sherman et al. 1997; Hauber and Sherman 2001; Krupp et al. 2011). In keeping with convention, we will refer to this representation as the "kin template" (though it need not represent kin per se; Waldman 1987). To perform phenotype matching, it is commonly assumed that the evaluator needs information only about two objects: (1) its own phenotype, as instantiated by the kin template, and (2) its partner's phenotype. These are insufficient, however, for reasons that will shortly become clear.

Consider an evaluator x attempting to assess the similarity of a partner y to itself on the basis of a continuous phenotypic label. The evaluator knows only its own value (inferred from its kin template) and that of y—say 0.35 and 0.45 units, respectively. As determined by a phenotype matching mechanism, x's relatedness to y should reflect the similarity between their label values. But how similar are they?

As figure 1 illustrates, this question cannot be answered unless the label values are properly contextualized by the phenotypic "space" of the population. If x and y lie on the same side of the mean phenotype, as in the dashed distribution of figure 1*A*, then they can be said to be similar. However, if they lie on opposite sides of the mean, as in the distribution represented by the solid line, they are dissimilar. Likewise, the relative similarity of x and y changes in concert with the variability of the phenotypic space surrounding them, as can be seen by comparing the dashed (more variable) and solid (less variable) distributions of figure 1*B*: with increasing variance comes concomitant increases in both the phenotypic range and the frequency of extreme phenotypes. Finally, the evaluator must also have some means of connecting phenotypic similarity to genetic similarity, or there is little point in relying on phenotypic information. Hence, evaluators cannot determine genetic relatedness solely on the basis of information about their own and their partners' phenotypes.

Population Estimation and Kin Recognition

To determine what is required of a recognition system that conditions relatedness upon phenotypic similarity, we work with a simple, additive genotype-phenotype model. We take a large number N of loci, each with two alleles that assume values 0 and 1. The individual phenotypic label L is then taken to be the average of the N genic values (and thus has a value between 0 and 1). We focus attention on an evaluator with phenotype L_0, in a population with mean phenotype $\overline{L}$, who wishes to estimate its coefficient of consanguinity G with a partner with observed phenotype L. The evaluator would like to know $P(G|L)$, the probability distribution of G given L. While our phenotypic model does not give us a direct expression for $P(G|L)$, we show below that it does provide a simple formula for $P(L|G)$, the probability distribution of L given G, and these two conditional probabilities are connected through Bayes's formula:

$$P(G|L) = \frac{P(L|G)P(G)}{P(L)}. \tag{2}$$

We now provide a model for $P(L|G)$. An individual with a coefficient of consanguinity G with the evaluator will be identical by descent to the evaluator at GN loci and will select alleles at the remaining $(1 - G)N$ loci at random from the local population. The resulting phenotype will have a value $L = J + K$, where J is the phenotypic average of GN loci sampled from the evaluator without replacement with mean L_0 and K is the phenotypic average of $(1 - G)N$ loci sampled independently with mean $\overline{L}$. This gives J a hypergeometric distribution with mean GL_0 and variance $G(1 - G)L_0(1 - L_0)/N$ and gives K a binomial distribution with mean $(1 - G)\overline{L}$ and variance $(1 - G)\overline{L}(1 - \overline{L})/N$. Since J and K are independent, the mean and variance of L will be the sum of the means and variances of J and K. For large N the distribution of L will be close to normal, and we make this assumption in our calculations and figures below.

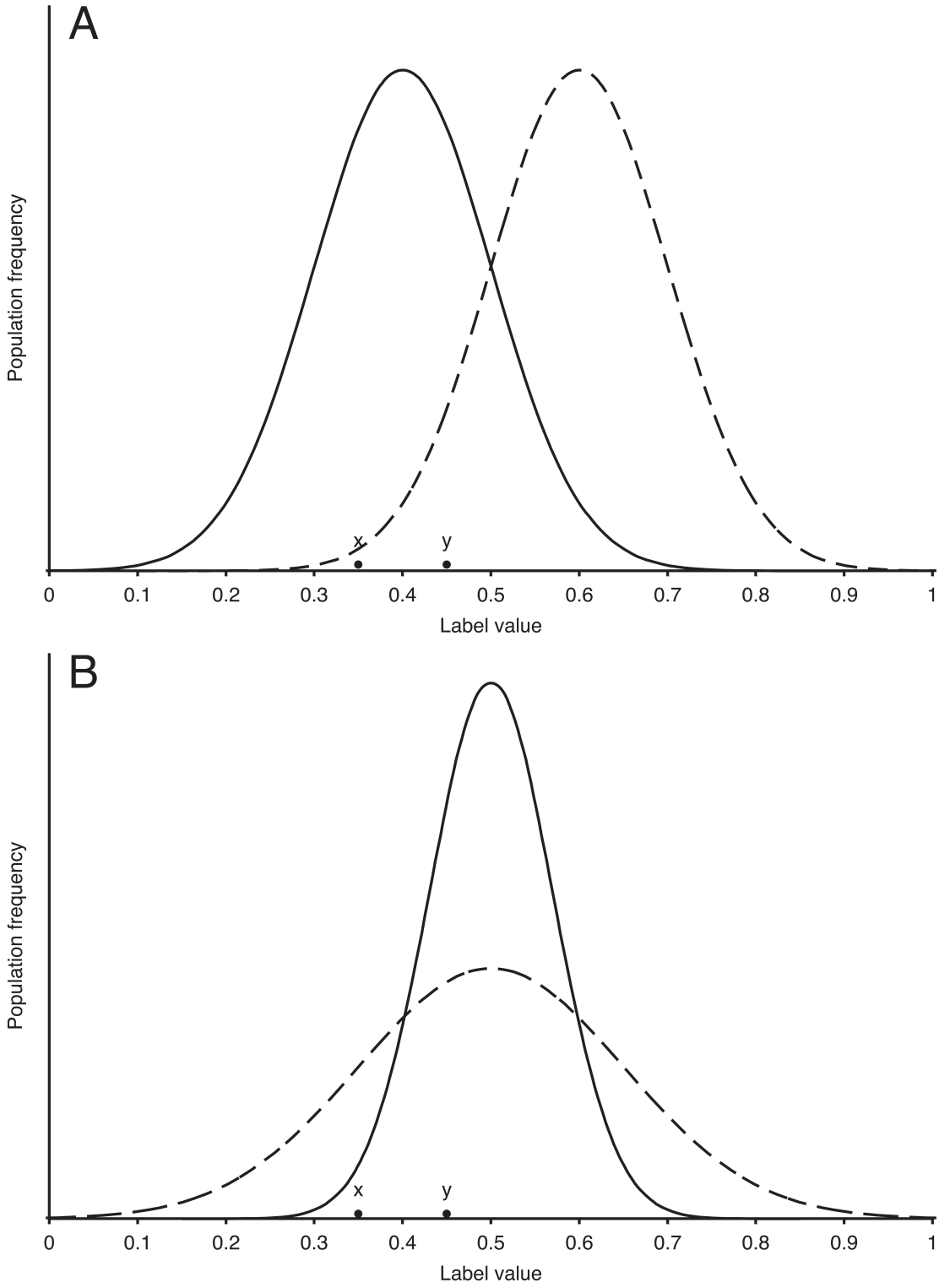

Figure 1: Hypothetical population distributions of a phenotypic label with different means (*A*) and different variances (*B*). Points *x* and *y* represent the label values of the evaluator and its partner, respectively.

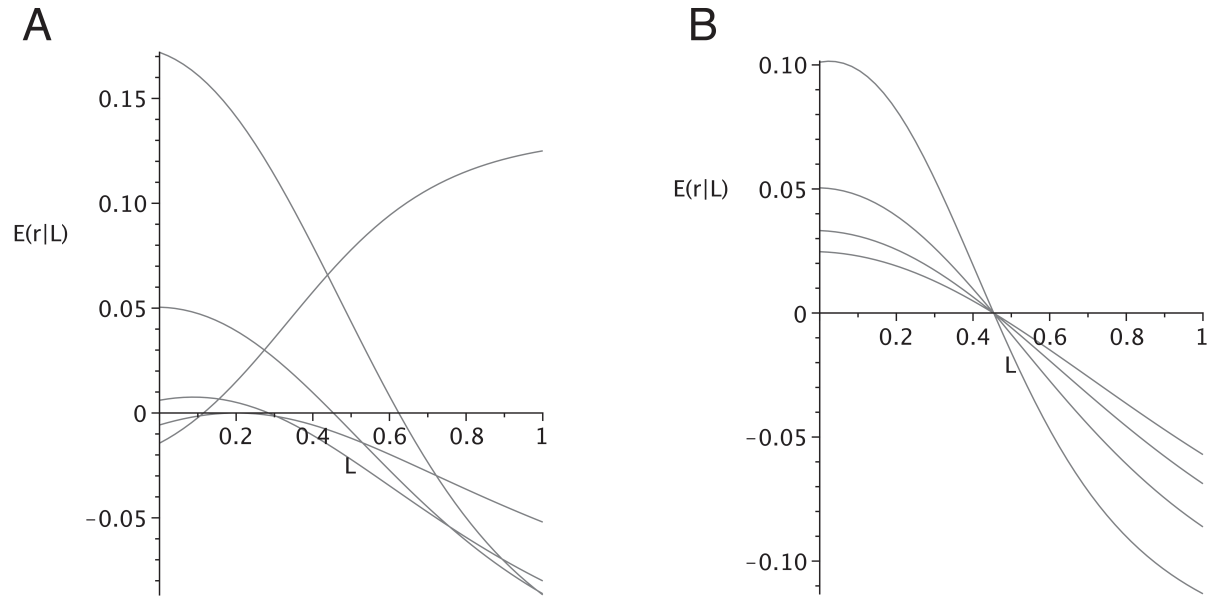

Figure 2: *A*, Expected values of relatedness r given L for an evaluator with phenotype $L_0 = 0.2$ and mean phenotypes (from top to bottom at left) $\overline{L} = 0.7$, 0.5, 0.3, 0.2, and 0.1. *B*, Expected values of relatedness r given L for an evaluator with phenotype $L_0 = 0.2$ and mean phenotype $\overline{L} = 0.5$ with population phenotypic variance multiplied by (from top to bottom at left) 0.5, 1.0, 1.5, and 2.0.

The calculation of $P(G|L)$ from equation (2) still requires knowledge of the distributions of G and L. The distribution $P(G)$ will depend upon the local mating and dispersal structure of the population, but, most importantly, it will also depend upon the evaluator's phenotype. For example, an evaluator with a phenotype close to $\overline{L}$ will be more closely related to others in the local population than will an evaluator with an extreme phenotype, who might well be a recent immigrant. Finally, the probability distribution of L can be obtained by integrating the numerator of equation (2) over G.

Now suppose the evaluator meets a partner y. Assuming that the evaluator has a sense of the probability distribution of G given L_y (found in eq. [2]), what is it to take as its estimate of G_y? We can imagine two possible candidates, the first being the value of G that maximizes $P(G|L_y)$ and the second being the expected value of G given L_y:

$$E(G|L_y) = \int_0^1 GP(G|L_y)dG. \tag{3}$$

The second estimate would seem to us to be more robust and less sensitive to the actual underlying distributions. In fact, these two measures are very close in practice and, as would be expected from the asymmetry of the conditional distribution, which is truncated more severely at $G = 0$ than at $G = 1$, $E(G|L_y)$ is in every case slightly above the value of G that maximizes $P(G|L_y)$. For example, when $L_0 = 0.3$ and $\overline{L} = 0.5$, $E(G|0.5) = 0.21$, whereas $P(G|0.5)$ attains its maximum at 0.19.

To compute relatedness, all that remains is to estimate the average coefficient of consanguinity,

$$E(G) = \int_0^1 GP(G)dG, \tag{4}$$

and to substitute the results of equations (3) and (4) for G and $\overline{G}$ in equation (1). Figure 2*A* presents the results of numerical calculations of the relatedness of an evaluator with a phenotype $L_0 = 0.2$ to partners with phenotype L as a function of the mean phenotype $\overline{L}$. As expected, relatedness between the evaluator and its partner changes in concert with their distance from the mean phenotype. Note that no label value is associated with a particularly high relatedness because in our simulations the evaluator's label value (L_0) was never rare and so the label itself is not terribly predictive of G. Moreover, the shape of $E(r|L)$ is roughly monotonic when L_0 is farther from $\overline{L}$, whereas it is roughly parabolic in form when L_0 and $\overline{L}$ are closer (see the graph corresponding to $\overline{L} = 0.2$). For these reasons, it is worth pointing out that phenotype matching systems are likely to rely on labels that are highly diagnostic of G and on the integration of multiple labels, such that the probability of many close matches on a large number of labels is very small. It should also be noted that label

variation might have to be maintained by selection for functions other than kin recognition, lest label values be driven to fixation by the advantage that individuals bearing common phenotypes enjoy in finding suitably similar cooperative partners (Crozier 1986; Rousset and Roze 2007).

Figure 2*B* presents the relatedness of an evaluator with a phenotype $L_0 = 0.2$ to partners with phenotype L in a population with mean phenotype $\overline{L} = 0.5$ and a population phenotypic variance ranging from half to twice that of the model described above. As can be seen, the slope of the relatedness function increases as the population variance decreases, yielding stronger positive and negative relatedness estimates for the evaluator and its partners at every value of L save when $L = \overline{L}$. This is likely the consequence of two competing forces: (1) the phenotypic range increases with variance, simultaneously increasing the similarity of any two fixed points, and (2) the frequency of extreme phenotypes increases with variance, simultaneously decreasing the similarity of these same two points (with larger effects on phenotypes located toward the tails of the distribution). In our model, the latter force appears to outweigh the former.

An Expanded Concept of Phenotype Matching

A cognitive model can be built upon the results of our analytical model, expanding the concept of phenotype matching to include all the requisite pieces of information. First, we have confirmed that evaluators need information about their own phenotypes and the phenotypes of their partners, so we continue to expect evaluators to acquire kin templates and encode their partners' phenotypes. Second, the graphs depicted in figure 2*A* show that relatedness changes sign approximately at the point at which a partner's phenotype becomes more or less similar to the evaluator's phenotype than is the average phenotype. (Again, this result holds when L_0 significantly differs from $\overline{L}$, as when evaluating highly predictive labels or when numerous labels have been integrated.) Thus, evaluators may use information about the average phenotype as a standard against which to judge the relatedness of a given partner, acquiring an "average" template analogous to the kin template. Third, the graphs depicted in figure 2*B* show that evaluators need to have information about the variability of phenotypes in the population. This information, perhaps in the form of the variance of the distribution, can be used to provide a scale of phenotypic similarity, bounded at 0 (completely different) and 1 (completely identical).

To match phenotypes, the evaluator could locate its kin template, the average template, and a representation of its partner's phenotype along the similarity scale, as depicted in figure 3. Evaluators can then make de facto computations of the effective positions of the average template and the partner's phenotype relative to the kin template (Krupp et al. 2011). To the degree that the partner's phenotype more closely resembles the kin template than does the average template, the evaluator would perceive its partner as positively related. Conversely, to the degree that the average template more closely resembles the kin template than does the partner's phenotype, the evaluator would perceive its partner as negatively related. This heuristic cognitive model describes the first general process by which organisms can distinguish between positive and negative relatives, allowing individuals to optimize their behavior toward altruistic and spiteful ends by regulating partner choice and the direction and magnitude of social actions toward given partners.

Figure 3: Expanded phenotype matching via population estimation. Evaluators define a similarity scale (represented by the length of the lower line) and locate the kin (K) and average (A) templates along this scale. Partners whose phenotypes fall in between the kin and average templates (solid arrow) are perceived as positively related, whereas partners whose phenotypes fall farther from the kin template than does the average template (dashed arrow) are perceived as negatively related.

Information regarding the evaluator's phenotype, the distribution of phenotypes, and the distribution of coefficients of consanguinity may be genetically determined, learned, or acquired by some combination of the two. There is compelling evidence of genetic influence on template design in species recognition and mate choice (e.g., Hoy et al. 1977; Bakker and Pomiankowski 1995; Shaw 2000; Kronforst et al. 2006), but the same cannot be said of kin templates (Waldman 1987; Sherman et al. 1997). This may be because a genetically determined kin template would be unreliable when genes coding for the template and for the label values are not tightly linked or when the label values are partly or wholly environmentally determined (and therefore variable over time and space; Sherman et al. 1997). Linkage may pose fewer complications for the average template and similarity scale, but environmental determination remains problematic, as the average phenotype and scale may shift with a changing environment. Nevertheless, given that genetically determined species recognition templates exist, it is reasonable to hypothesize that average templates and similarity scales are likewise so determined. Indeed, species recognition and average templates may overlap considerably, and the former may even serve as a substitute for the latter.

In contrast to genetic determination, there is ample evidence that learning determines elements of the kin templates of numerous species (reviewed in Waldman 1987; Sherman et al. 1997; Hauber and Sherman 2001; Krupp et al. 2011). The "referents" that serve as the sources of phenotypic information feeding into the kin template may comprise any number of individuals of a kin class, including the evaluator itself ("self-referent phenotype matching") or its parents, siblings, and others assumed to be genetic relatives ("other-referent phenotype matching") as a consequence of the workings of separate kin recognition systems, such as spatiotemporal association mechanisms (Waldman 1987; Krupp et al. 2011). Likewise, sampling the phenotypes of the local population might yield information sufficient to encode the average template and the similarity scale.

There are at least two advantages of learning the phenotypic distribution over inheriting it. First, evaluators will tend to have their strongest effects on those partners that they encounter directly, and secondarily on the partners of their partners (and so forth). Hence, insofar as the local population represents the evaluator's interaction neighborhood (Queller 1994), it appeals as a referent population from which to learn the phenotypic distribution. Second, evaluators who have dynamically updated their perceptions of the phenotypic distribution over the life span—perhaps in a manner not unlike a Bayesian updating process (Frank 1998)—will predict relatedness more accurately than those who have not done so in populations with changing phenotypic distributions (caused, for instance, by migration or shifting environments). Of course, it is also possible that organisms inherit "generic" templates and modify them according to their experience.

We have identified only a few studies that address our cognitive model, but they are suggestive. First, great reed warblers (*Acrocephalus arundinaceus*), hosts to the brood parasitic cuckoo (*Cuculus canorus*), are less likely to reject a nonmimetic artificial egg when the phenotypic variation among their own eggs has been experimentally increased (Moskát et al. 2008; see also Stokke et al. 1999). Second, within-colony phenotypic variability in the Argentine ant (*Linepithema humile*) is negatively associated with aggression toward conspecifics drawn from foreign, less related colonies (Tsutsui et al. 2003). Third, exposure to such foreign conspecifics, or cues thereof, alters levels of social conflict toward other foreigners in *L. humile* (Thomas et al. 2005; Van Wilgenburg et al. 2010) and in the Columbian ground squirrel (*Spermophilus columbianus*; Hare 1994). Fourth, among weaver ants (*Oecophylla smaragdina*), evaluator and colony identity appear to influence aggression toward foreigners independently of one another (Newey et al. 2010). Newey (2011) attributes this result to the simultaneous use of two distinct recognition templates, one representing the evaluator's phenotype prior to the effects of colony mixing and the other representing the mean colony phenotype. Respectively, these putative templates bear a striking resemblance to the (self-referent) kin and average templates proposed here. Finally, a recent experiment suggests that humans can discriminate positive from negative relatives, showing positive preferences for digitally manufactured face images that are more self-resembling than average (and are hence phenotypically similar) and negative preferences for those that are less self-resembling than average (and are hence phenotypically dissimilar; Krupp et al. 2012). In keeping with these findings, another study of humans has shown that repeated exposure to face images of individuals belonging to the same ethnic group causes ethnic categorization thresholds to be adjusted (Webster et al. 2004)—a perceptual shift that may rely on the same similarity assessment processes as those that underlie phenotype matching.

Of course, there are numerous alternative interpretations of these results that do not involve sampling-based adjustments to perceptions of genetic relatedness per se but that might instead be associated with other constructs, such as group or colony membership (e.g., Hare 1994; Newey 2011). Thus, a more direct effort to test the cognitive model proposed here is needed. In general, the model generates hypotheses concerning continuous relatedness judgments (rather than binary or threshold ones; see Reeve 1989), the assessment of both positive and negative relatedness, the use of estimates of the phenotypic distribution to improve the accuracy of relatedness judgments, and the effects of these judgments on social behavior (fostering altruistic and mutually beneficial behavior when interacting with phenotypically similar conspecifics and fomenting spiteful and selfish behavior when interacting with phenotypically dissimilar conspecifics). However, two key hypotheses from this model are readily apparent: perceptions of relatedness will vary as a function of manipulations of (1) the average phenotype and (2) the variability among phenotypes. As the average phenotype approaches the evaluator's phenotype, a narrower spectrum of phenotypes will appear positively related and, by corollary, a broader spectrum of phenotypes will appear negatively related. Similarly, as the variability (e.g., variance) among phenotypes increases, the scale of similarity changes and, by consequence, the relatedness of two partners of fixed phenotype will also change. If these hypotheses are correct, they may help to bridge some of the gaps in our understanding of social evolution in general and kin recognition systems in particular.

In summary, evaluators require information about their own phenotypes, the phenotypes of their partners, and the distributions of phenotypes and genotypes in the population to properly perform phenotype matching. They may

assume certain distributions as "priors" by genetic determination, or they may modify them through experience. Having acquired this information, they may then construct representations of their prototypical kin (the kin template), the average phenotype (the average template), their partner's phenotype, and a scale with which to judge their similarity. From this, evaluators can predict the relatedness of a partner and use this prediction to guide their social actions, helping phenotypically similar partners and harming dissimilar ones.

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Literature Cited

Bakker, T. C. M., and A. Pomiankowski. 1995. The genetic basis of female mate preferences. Journal of Evolutionary Biology 8:129–171.

Crozier, R. H. 1986. Genetic clonal recognition abilities in marine invertebrates must be maintained by selection for something else. Evolution 40:1100–1101.

El Mouden, C., and A. Gardner. 2008. Nice natives and mean migrants: the evolution of dispersal-dependent social behaviour in viscous populations. Journal of Evolutionary Biology 21:1480–1491.

Foster, K. R. 2004. Diminishing returns in social evolution: the not-so-tragic commons. Journal of Evolutionary Biology 17:1058–1072.

Frank, S. A. 1986. Dispersal polymorphisms in subdivided populations. Journal of Theoretical Biology 122:303–309.

———. 1998. Foundations of social evolution. Princeton University Press, Princeton, NJ.

Gardner, A., and S. A. West. 2004. Spite and the scale of competition. Journal of Evolutionary Biology 17:1195–1203.

Grafen, A. 1985. A geometric view of relatedness. Oxford Surveys in Evolutionary Biology 2:28–89.

———. 2007. An inclusive fitness analysis of altruism on a cyclical network. Journal of Evolutionary Biology 20:2278–2283.

Hamilton, W. D. 1970. Selfish and spiteful behaviour in an evolutionary model. Nature 228:1218–1220.

Hare, J. F. 1994. Group member discrimination by Columbian ground squirrels via familiarity with substrate-borne chemical cues. Animal Behaviour 47:803–813.

Hauber, M. E., and P. W. Sherman. 2001. Self-referent phenotype matching: theoretical considerations and empirical evidence. Trends in Neurosciences 24:609–616.

Hepper, P. G. 1991. Kin recognition. Cambridge University Press, New York.

Holmes, W. G., and P. W. Sherman. 1982. The ontogeny of kin recognition in two species of ground squirrels. American Zoologist 22:491–517.

Hoy, R. R., J. Hahn, and R. C. Paul. 1977. Hybrid cricket auditory behavior: evidence for genetic coupling in animal communication. Science 195:82–84.

Kronforst, M. R., L. G. Young, D. D. Kapan, C. McNeely, R. J. O'Neill, and L. E. Gilbert. 2006. Linkage of butterfly mate preference and wing color preference cue at the genomic location of wingless. Proceedings of the National Academy of Sciences of the USA 103:6575–6580.

Krupp, D. B., L. M. DeBruine, and B. C. Jones. 2011. Cooperation and conflict in the light of kin recognition systems. Pages 345–364 *in* C. A. Salmon and T. K. Shackelford, eds. The Oxford handbook of evolutionary family psychology. Oxford University Press, New York.

Krupp, D. B., L. M. DeBruine, B. C. Jones, and M. L. Lalumière. 2012. Kin recognition: evidence that humans can perceive both positive and negative relatedness. Journal of Evolutionary Biology 25:1472–1478.

Lacy, R. C., and P. W. Sherman. 1983. Kin recognition by phenotype matching. American Naturalist 121:489–512.

Moskát, C., J. M. Avilés, M. Bán, R. Hargitai, and A. Zölei. 2008. Experimental support for the use of egg uniformity in parasite egg discrimination by cuckoo hosts. Behavioral Ecology and Sociobiology 62:1885–1890.

Newey, P. 2011. Not one odour but two: a new model for nestmate recognition. Journal of Theoretical Biology 270:7–12.

Newey, P. S., S. K. A. Robson, and R. H. Crozier. 2010. Know thine enemy: why some weaver ants do but others do not. Behavioral Ecology 21:381–386.

Queller, D. C. 1994. Genetic relatedness in viscous populations. Evolutionary Ecology 8:70–73.

Reeve, H. K. 1989. The evolution of conspecific acceptance thresholds. American Naturalist 133:407–435.

Rousset, F., and S. Billiard. 2000. A theoretical basis for measures of kin selection in subdivided populations: finite populations and localized dispersal. Journal of Evolutionary Biology 13:814–825.

Rousset, F., and D. Roze. 2007. Constraints on the origin and maintenance of genetic kin recognition. Evolution 61:2320–2330.

Seger, J. 1983. Conditional relatedness, recombination, and the chromosome number of insects. Pages 596–612 *in* A. G. J. Rhodin and K. Miyata, eds. Advances in herpetology and evolutionary biology: essays in honor of Ernest E. Williams. Harvard University Press, Cambridge, MA.

Shaw, K. L. 2000. Interspecific genetics of mate recognition: inheritance of female acoustic preference in Hawaiian crickets. Evolution 54:1303–1312.

Sherman, P. W., H. K. Reeve, and D. W. Pfennig. 1997. Recognition systems. Pages 69–96 *in* J. R. Krebs and N. B. Davies, eds. Behavioural ecology. Blackwell, Oxford.

Stokke, B. G., A. Moksnes, E. Røskaft, G. Rudolfsen, and M. Honza. 1999. Rejection of artificial cuckoo (*Cuculus canorus*) eggs in relation to variation in egg appearance among reed warblers (*Acrocephalus scirpaceus*). Proceedings of the Royal Society B: Biological Sciences 266:1483–1488.

Taylor, P. D. 1992*a*. Altruism in viscous populations—an inclusive fitness model. Evolutionary Ecology 6:352–356.

———. 1992*b*. Inclusive fitness in a homogeneous environment. Proceedings of the Royal Society B: Biological Sciences 249:299–302.

Taylor, P. D., T. Day, and G. Wild. 2007. Evolution of cooperation in a finite homogeneous graph. Nature 447:469–472.

Taylor, P. D., A. J. Irwin, and T. Day. 2000. Inclusive fitness in finite deme-structured and stepping-stone populations. Selection 1:153–163.

Thomas, M. L., N. D. Tsutsui, and D. A. Holway. 2005. Intraspecific competition influences the symmetry and intensity of aggression in the Argentine ant. Behavioral Ecology 16:472–481.

Tsutsui, N. D., A. V. Suarez, and R. K. Grosberg. 2003. Genetic diversity, asymmetrical aggression, and recognition in a widespread invasive species. Proceedings of the National Academy of Sciences of the USA 100:1078–1083.

Van Wilgenburg, E., J. Clemencet, and N. D. Tsutsui. 2010. Experience influences aggressive behaviour in the Argentine ant. Biology Letters 6:152–155.

Waldman, B. 1987. Mechanisms of kin recognition. Journal of Theoretical Biology 128:159–185.

Webster, M. A., D. Kaping, Y. Mizokami, and P. Duhamel. 2004. Adaptation to natural facial categories. Nature 428:557–561.

West, S. A., and A. Buckling. 2003. Cooperation, virulence and siderophore production in bacterial parasites. Proceedings of the Royal Society B: Biological Sciences 270:37–44.

West, S. A., and A. Gardner. 2010. Altruism, spite, and greenbeards. Science 327:1341–1344.

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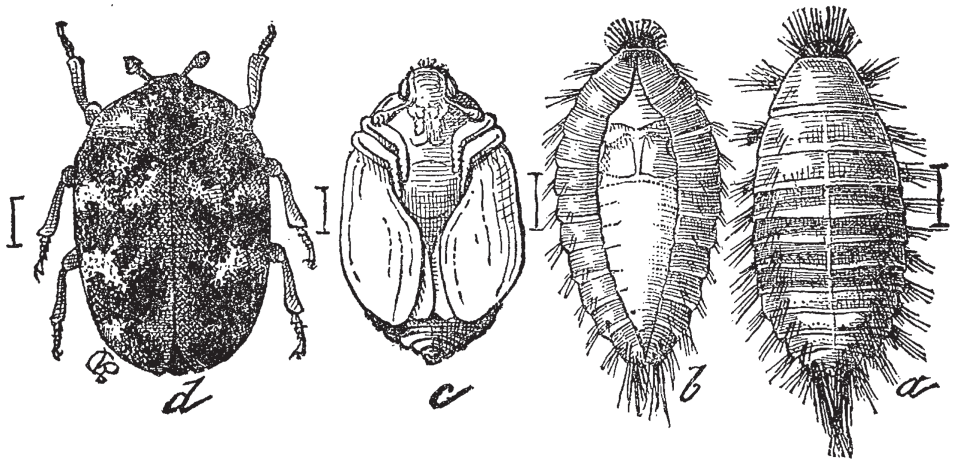

"It is a beautifully marked little insect in its contrasting colors of white, black and scarlet." From "The New Carpet Beetle—*Anthrenus scrophulariae*" by J. A. Lintner (*American Naturalist*, 1878, 12:536–544).