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.

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)

$$r = \frac{G - \overline{G}}{1 - \overline{G}}, \quad (1)$$

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
population structure dictates partner assortment, as when a partner is chosen at random from the evaluator’s interaction neighborhood (e.g., Frank 1986; Taylor 1992a, 1992b; 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 attempting to assess the similarity of a partner 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 1A, 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 1B: 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 L0, in a population with mean phenotype 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:

\[ P(G|L) = \frac{P(L|G)P(G)}{P(L)}. \]  

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 \( L \). 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 \( (1 − G)L \) and variance \( (1 − G)L(1 − L)/N \). 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.
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 $L$ 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 $L$, (found in eq. [2]), what is it to take as its estimate of $G$? 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 $L_y$:

$$E(G|L_y) = \int_0^1 GP(G|L_y)dG.$$  

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 $\bar{L} = 0.5$, $E(G|0.5) = 0.21$, 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,

$$E(G) = \int_0^1 GP(G)dG,$$  

and to substitute the results of equations (3) and (4) for $G$ and $\bar{G}$ in equation (1). Figure 2A 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 $\bar{L}$. 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 $\bar{L}$, whereas it is roughly parabolic in form when $L_0$ and $\bar{L}$ are closer (see the graph corresponding to $\bar{L} = 0.2$). 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

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

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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 co-
operative partners (Crozier 1986; Rousset and Roze 2007).

Figure 2B 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 popu-
lation 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 con-
sequence 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, simulta-
neously 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. Sec-
ond, the graphs depicted in figure 2A show that relatedness
changes sign approximately at the point at which a part-
ner’s phenotype becomes more or less similar to the eva-
luator’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 numer-
ous 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 tem-
plate. Third, the graphs depicted in figure 2B show that
evaluators need to have information about the variability
of phenotypes in the population. This information, per-
haps 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 computa-
tions 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 phe-
notype more closely resembles the kin template than does
the average template, the evaluator would perceive its part-
tner 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.

Information regarding the evaluator’s phenotype, the
distribution of phenotypes, and the distribution of coef-
ficients of consanguinity may be genetically determined,
learned, or acquired by some combination of the two.
There is compelling evidence of genetic influence on tem-
plate 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 deter-
mined (and therefore variable over time and space; Sher-
man et al. 1997). Linkage may pose fewer complications
for the average template and similarity scale, but environ-
mental determination remains problematic, as the average
phenotype and scale may shift with a changing environ-
ment. Nevertheless, given that genetically determined spe-
cies recognition templates exist, it is reasonable to hy-
pothesize that average templates and similarity scales are
likewise so determined. Indeed, species recognition and
average templates may overlap considerably, and the for-
mer may even serve as a substitute for the latter.

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**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.
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 include 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


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