

Repeatable randomness, invariant properties, and the design of biological signatures of identity

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Abstract

What makes a perfect signature? Optimal signatures should be consistent within individuals and distinctive between individuals. In defense against avian brood parasitism, some host species have evolved “signatures” of identity on their eggs, comprising interindividual variation in color and pattern. Tawny-flanked prinia (*Prinia subflava*) egg signatures facilitate recognition and rejection of parasitic cuckoo finch (*Anomalospiza imberbis*) eggs. Here, we show that consistency and distinctiveness of patterns are negatively correlated in prinia eggs, perhaps because non-random, repeatable pattern generation mechanisms increase consistency but limit distinctiveness. We hypothesize that pattern properties which are repeatable within individuals but random between individuals (“invariant properties”) allow hosts to circumvent this trade-off. To find invariant properties, we develop a method to quantify entire egg phenotypes from images taken from different perspectives. We find that marking scale (a fine-grained measure of size), but not marking orientation or position, is an invariant property in prinias. Hosts should therefore use differences in marking scale in egg recognition, but instead field experiments show that these differences do not predict rejection of conspecific eggs by prinias. Overall, we show that invariant properties allow consistency and distinctiveness to coexist, yet receiver behavior is not optimally tuned to make use of this information.

Keywords: coevolution, invariant properties, avian brood parasitism, optimality, mimicry, egg signatures

Introduction

What would make a perfect signature, or password? Signatures of identity have evolved in a range of systems, such as the vertebrate immune system (Hughes, 2002), facial recognition in insects (Tibbetts, 2002), and in hosts of insect and avian brood parasites (Kilner & Langmore, 2011; Swynnerton, 1918). All such signatures share the purpose of making forgery difficult, and being recognizable to the intended receivers of this signal (Spottiswoode & Busch, 2019). Therefore, optimal signatures share certain common attributes. Many signatures are complex, since this makes them more difficult to forge, though high complexity may carry costs (Dixit et al., 2021; Stoddard et al., 2014). Furthermore, high signature consistency (i.e., high replicability and low intraindividual variation (Caves et al., 2021; Davies & Brooke, 1989; Lahti, 2005, 2021; Langmore et al., 2010; Marchetti, 1992)), and high signature distinctiveness (i.e., high interindividual variation [Caves et al., 2021; Davies & Brooke, 1989; Langmore et al., 2010; Swynnerton, 1918]) would both increase the ability of an intended receiver to correctly recognize the signature

and identify forgeries (Figure 1A,B). Overall, therefore, an optimal identity signature should be (a) complex, (b) consistent within an individual, and (c) distinctive between individuals (Stoddard et al., 2014).

Optimality in these three traits is also a key problem in the context of digital communication protocols and cryptography, where there is a premium on the creation and error-free transmission of unforgeable signatures and on authentication mechanisms, which guarantee identity and prevent fraud. For example, the family of PGP protocols (e.g., Diffie-Hellman or the Rivest-Shamir-Adleman algorithms) function to transmit information securely using encryption and decryption via low-dimensional digital signatures (Bruen & Forcinito, 2011). These signatures consist of long strings using a finite alphabet, and the costs of producing such reproducible and complex digital signatures are negligible relative to their benefits in guaranteeing identity. In sharp contrast, the analogue world of morphological patterns is high dimensional and highly variable, and this means that the costs of producing reproducible and complex analogue signatures are not negligible. Therefore, for analogue signatures of identity, there

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are potential trade-offs between complexity, reproducibility (consistency), and identity (distinctiveness).

To understand such trade-offs in the design of biological signatures of identity, we must consider the mechanisms underpinning complexity, consistency, and distinctiveness in biological signatures. Complex signatures may be produced through increased informational content, such as more signature components or higher variation in these components (Caves et al., 2015; Dixit et al., 2022). By contrast, mechanisms underpinning consistency and distinctiveness have not previously been studied. In this study, we therefore focus on the causes and consequences of consistency and distinctiveness in signatures of identity.

In some systems, consistency can be easily achieved. For example, individually recognizable face patterns of wasps (Tibbetts, 2002) are constitutively expressed; the genotype produces only one phenotype, which will remain consistent unless directly affected by the environment. Similarly, self-referential signatures in vertebrate immune systems (such as major histocompatibility complex glycoproteins) are likely to be consistent throughout an individual's lifetime unless a somatic mutation results in a cell expressing a different molecule (Neeffjes et al., 2011). By contrast, some signatures must be produced multiple times during a lifetime by complex mechanisms which are affected by a range of environmental factors, resulting in variation between signatures produced by the same individual (Kilner, 2006). For example, individuals may lay multiple eggs, each expressing a signature of the same identity (Figure 1A). In this situation, the mechanisms which produce a signature must be repeatable within an individual. Individual distinctiveness (Figure 1B), on the other hand, could be produced by randomness in the mechanisms of signature generation, such that different individuals produce different signatures. Thus, mechanisms underpinning optimal signature generation should be both repeatable and random, producing signatures, which are consistent and distinctive (Caves et al., 2021).

Although an optimal signature generation mechanism should be repeatable and random, repeatability and randomness are opposites (Caves et al., 2021). This is because repeatability entails predictability, whereas randomness entails unpredictability (Eagle, 2005). In other words, in analogue signatures, repeatable mechanisms (which generate consistent signatures) must be non-random, and random mechanisms (which generate distinctive signatures) cannot be repeatable (Caves et al., 2021). For example, a random string of numbers cannot be repeatably produced because repeatability would make the string of numbers predictable and non-random. Similarly, a repeatable string of numbers cannot be produced by random mechanisms because these would entail unpredictability and, thus a lack of repeatability in number production. Such a mechanistic trade-off in analogue, biological signatures may explain the negative correlation found between consistency and distinctiveness in egg appearance across southern African warbler and weaver species (Caves et al., 2021), some of which are hosts of avian brood parasites.

Brood parasites lay their eggs in host nests, foisting the costs of parental care onto the host, and in some cases leading to no host reproductive success in parasitized nests (Davies, 2000; Kilner & Langmore, 2011). In defense against parasites, both avian and insect hosts have evolved signatures of identity on their eggs (respectively visual and chemical), which allow the host to identify their own eggs and reject

foreign eggs (Kilner & Langmore, 2011; Lund et al., 2023; Spottiswoode & Busch, 2019). In birds, these signatures take the form of complex patterns on eggshells (Spottiswoode & Stevens, 2010; Stoddard et al., 2014). Mechanisms to increase the consistency of these egg signatures should benefit hosts, since consistent egg phenotypes should aid identification of foreign eggs, and reduce the likelihood that a female would reject her own egg (Davies & Brooke, 1989; Marchetti, 1992; Figure 1A). Similarly, mechanisms to increase the distinctiveness of egg signatures would likely benefit hosts, by reducing the probability that a given parasitic phenotype is a good match to a given host phenotype (Davies & Brooke, 1989; Lund et al., 2023; Swynnerton, 1918; Figure 1B).

How could consistent yet distinctive signatures be produced despite the trade-off between the two? One possible mechanism relies on consistency being a within-individual measure, while distinctiveness is a between-individual measure. Depending on how egg patterns are generated, some egg signature properties could remain consistent within individuals but with distinctiveness between individuals maintained. Specifically, properties of phenotypes that are invariant within individuals but variant between individuals should be the best signature traits, and so provide the most reliable information to use in rejection decisions. Mathematically, invariants are properties of shapes which remain constant under a specific class of transformations (Busemeyer et al., 2015; Lowe, 1999; Mundy et al., 1994; Tuytelaars & Mikolajczyk, 2008). Transformations are methods of changing the size, position, and/or orientation of a shape, including translations (moving a shape from one position to another), enlargements (increasing or decreasing the size of a shape), and rotations (changing the orientation of a shape). For example, the size of an object is invariant under translations in the x-y plane: no matter how the position of a shape is changed, its size remains constant. Which properties of egg signatures fulfil the criteria of being invariants within individuals, but varying between individuals, should depend on the mechanisms of pattern generation in the shell gland, which are poorly understood (Gosler et al., 2000; Sparks, 2011).

To illustrate the argument, consider the size and position of a specific marking on an egg. Let us assume that within an individual's shell gland, the position at which the marking is deposited is not repeatable (i.e., is random). In other words, translations are one of the transformations that occur as a result of pattern-generation processes occurring in the shell gland. Size is invariant under translations, but position is not, since translations change the position of a marking but not other characteristics such as its size (Figure 1C). Under these circumstances, hosts would not benefit from using the position of markings in rejection decisions. If they did use position in rejection decisions, the lack of within-individual consistency in marking position would make it more difficult to identify both their own eggs and parasitic eggs. However, the size of markings would be a useful feature to use, especially if individual hosts (and hence the parasites that mimic them) differ in pattern size. In this scenario, the size of markings is an invariant property under the class of transformations (specifically, translations) occurring in the shell gland: it is consistent within individuals, but distinctive between individuals. Therefore, it should benefit hosts to use the size of markings in rejection decisions, since this optimizes both repeatability and randomness despite the apparent trade-off between the two.

Here, we study invariant properties in an Afrotropical brood parasite-host system. The cuckoo finch *Anomalospiza*

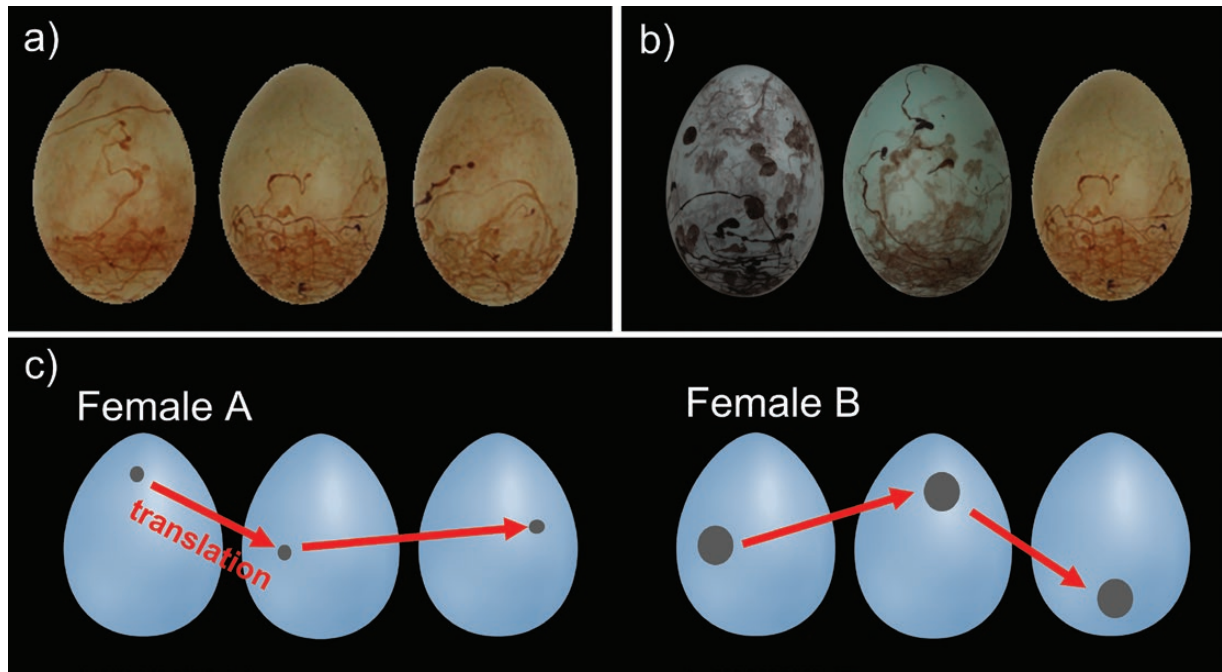


Figure 1. (A) Three tawny-flanked prinia eggs laid by the same female, illustrating consistency in signatures. (B) Three prinia eggs laid by different females, illustrating distinctiveness in signatures. (C) Hypothetical clutches from two different females (females A and B) of the same host species. Arrows represent translations (i.e., changes in position) of pattern markings between eggs within an individual (i.e., a translation would map a given pattern marking on one egg to the corresponding marking on another egg). If, as in this hypothetical example, translations occur as a result of shell gland pattern processing, then the position of markings varies within a clutch. However, because translations do not affect marking size, size remains consistent within individuals (but distinctive between individuals, as illustrated by female B exhibiting larger markings than female A). If parasites mimic this range of host variation in size and position of markings, it would benefit hosts to use size information rather than positional information in rejection decisions, since size provides more information about egg identity than position.

imberbis parasitizes and mimics the eggs of several cisticolid warblers, including tawny-flanked prinias *Prinia subflava* (hereafter, prinias). Prinia eggs show complex egg signatures, and cuckoo finch eggs show accurate yet imperfect “forgeries” of these signatures (Dixit et al., 2023; Spottiswoode & Stevens, 2010). First, we test whether there is a fundamental trade-off between consistency and distinctiveness of egg signatures in prinias. This within-species analysis is an essential extension of the between-species analysis in Caves et al. (2021), since a between-species negative correlation might result from selection for elevated consistency in some species and elevated distinctiveness in others. By contrast, a within-species negative correlation between consistency and distinctiveness would suggest that a mechanistic by-product causes the correlation. Second, we test the potential for this trade-off to be circumvented by invariant properties of egg traits, by investigating which properties of prinia eggs are invariant within individuals but variant between individuals. Third, we test whether prinias behave as the logic of invariant properties would suggest; that is, whether they use such properties in rejection decisions. In fulfilling these aims, we also develop and validate a novel method for recreating the full pattern of a three-dimensional object, such as an egg from multiple two-dimensional images, such that the entire pattern of one egg can be compared with the entire pattern of another.

Methods

Egg images and field experiments

We conducted field experiments and photographed eggs on Semahwa Farm (ca. 16.74°S, 26.90°E) and surrounding areas

in the Choma District of Southern Zambia in January–April 2018–2020. In field experiments ($n = 119$; published in Dixit et al. [2022]), we replaced an egg from a completed host nest with a conspecific egg (the “experimental egg”), and photographed the host clutch and the experimental egg. Such “experimental parasitism” allows us to quantify the traits, which predict egg rejection in hosts, by observing whether the experimentally added egg is rejected. We checked experiments daily for four days or until rejection of the experimental egg or one of the host eggs occurred; rejection typically occurs within 3 days (Spottiswoode & Stevens, 2010). Hosts were largely given close matches (to human vision) in order to focus on pattern features rather than color differences; therefore, egg color and the “lower-level” pattern features found to predict egg rejection in previous studies (Spottiswoode & Stevens, 2010; Stoddard et al., 2019) did not predict rejection in this dataset (Dixit et al., 2022). As well as clutches photographed as part of experiments, we photographed completed host clutches to identify invariant and variant properties between and within clutches. In total, we photographed eggs from 273 clutches, of which 219 clutches contained two or more photographed eggs, and of which 125 were photographed as part of egg rejection experiments.

Photography

We took linear RAW images of eggs in shade in natural daylight using a Nikon D90 camera with a 60 mm Micro-Nikkor lens. Images were normalized as in Dixit et al. (2022, 2023), using an X-Rite Color Checker Passport (X-Rite, MI, USA). To capture the full pattern, we photographed each egg from four different angles by rotating it thrice through 90° around

the long axis, resulting in four images (“sides” a, b, c, and d, where a is opposite c and b is opposite d). The overlap between adjacent images (e.g., a and b) allows the entire three-dimensional pattern to be recreated (see [Supplementary Material](#)).

Measuring consistency and distinctiveness of pattern within a species

The finding that consistency and distinctiveness are negatively correlated across both host and non-host species ([Caves et al., 2021](#)) is consistent with a mechanistic trade-off between these two defenses, but does not rule out different selection pressures acting on different species. Therefore, we calculated values of consistency and distinctiveness for clutches within a single species, the tawny-flanked prinia ($n = 410$ eggs from the 125 clutches photographed for experiments). We extracted the same measures of pattern as in [Caves et al. \(2021\)](#): (1) the principal marking size, (2) the variation in marking size, (3) the total pattern contrast, (4) the extent of pattern coverage of the egg, and (5) the extent to which pattern was dispersed between narrow and wide poles. Measures 1, 2, and 3 were produced using a granularity analysis, identical to that of ([Spottiswoode & Stevens, 2010](#)), except that two, rather than three, square regions corresponding to 5×5 mm on the egg were analyzed; these two regions were located at the narrow and wide poles respectively. In brief, granularity analysis converts an image into multiple (here, six) images at different spatial scales, and measures the contribution of markings at different spatial scales to the overall image ([Barbosa et al., 2008](#); [Chiao et al., 2010](#); [Stoddard & Stevens, 2010](#)). Measures 4 and 5 were extracted using the adaptive thresholding tool in the MICA toolbox ([Troscianko & Stevens, 2015](#)), which separates pattern markings from background coloration allowing measurement of the total area and distribution of pattern on the egg’s surface. We could then calculate a distance between any two eggs in multidimensional space by mapping each egg in a five-dimensional space (with the five dimensions corresponding to the five pattern traits we measured), and quantifying the Euclidean distance between the two points corresponding to the two eggs ([Caves et al., 2021](#)).

We calculated consistency by randomly selecting two eggs from each clutch, and quantifying consistency as one minus the distance in multidimensional phenotypic space (MDPS distance) between them ([Caves et al., 2021](#)). We calculated distinctiveness as the MDPS distance of a randomly selected egg from a clutch from the centroid of all prinia eggs in the

dataset. We then tested whether, across prinia clutches, distinctiveness was negatively correlated with consistency, as predicted by the hypothesis that repeatability and randomness trade off against each other.

The definition of distinctiveness used here differs slightly from that in [Caves et al. \(2021\)](#); in the latter, distinctiveness is necessarily a species-level measure as it is defined as the total variation between clutches. The definition used here is a within-species measure of the distinctiveness of a pattern; the more distinctive an egg pattern, the further away it would lie from the centroid of all egg patterns.

Egg stitching

We used NaturePatternMatch (NPM; [Stoddard et al., 2014](#)) to stitch together egg images taken from different angles ([Figure 2](#)). Stitching different images of the same egg together ensures that all possible matching features can be matched together, which would not be the case if the entire pattern of the egg was not analyzed. Details of the stitching method can be found in the [Supplementary Material](#) and are illustrated in [Supplementary Figure S1](#).

Pattern “distances” between eggs (c.f. [Stoddard et al. 2014, 2019](#)) can also be calculated using NPM. These pattern distances (calculated using one “side” of each egg) have previously been shown to predict egg rejection in this system ([Stoddard et al., 2019](#)). Therefore, we could validate whether stitched images are biologically relevant by testing whether NPM pattern distances calculated using stitched images also predict egg rejection. Furthermore, given that stitched images provide more information (i.e., information on the full egg pattern) than single images of “one side” of the egg, we might expect pattern distances calculated using stitched images to perform better at predicting rejection than distances calculated using single images (e.g., comparing side “a” of egg 1 with side “a” of egg 2). Therefore, we used likelihood ratio tests to determine whether pattern distances calculated with stitched images predicted rejection better than pattern distances calculated using only one side of each egg.

Identifying invariant properties

We used NPM ([Stoddard et al., 2014](#)) to identify SIFT features on stitched images of each egg. SIFT features are 132-dimensional vectors which correspond loosely to individual pattern markings. Of these dimensions, the first gives a measure of orientation of a feature, the second a measure of scale (i.e., size) of a feature, and the third and fourth

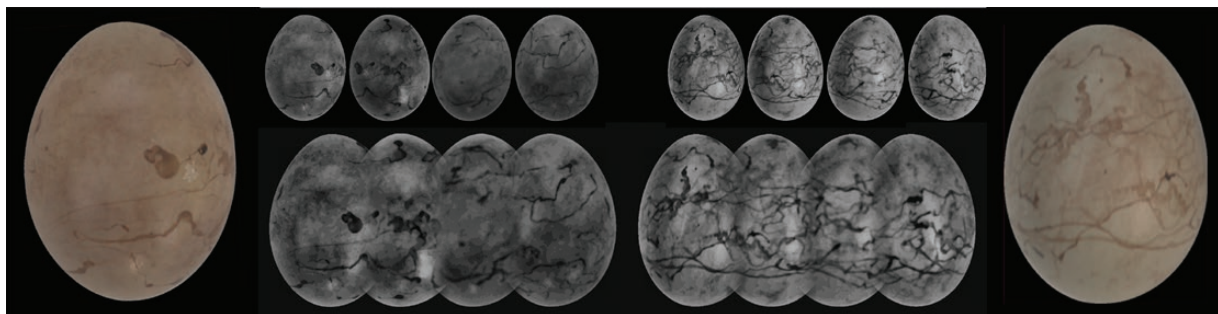


Figure 2. Two examples of stitched grayscale images of prinia eggs. Left and Right: color images of one “side” of two eggs. Centre above: normalized and enhanced grayscale images of the four sides of the two eggs. Centre below: stitched images produced from each set of four grayscale images. While the stitching algorithm is imperfect, and some features may be duplicated or lost, in general the full pattern is well-represented.

positional information of a feature (x, y coordinates); the other 128 dimensions provide other feature information related to shape.

To identify invariant properties, we matched SIFT features between each pair of eggs according to 128 dimensions of the 132-dimensional SIFT vector (excluding the first four dimensions, and therefore ignoring orientation, position, and scale of features). By matching features based on the complex multidimensional trait of feature shape, we could test whether orientation, position, and scale of matched features varied between clutches. For each pair of matched SIFT features, we calculated the difference between the features in orientation, y-coordinate position, and scale. Taking the mean of these differences between matched features on each pair of eggs gave us the difference between each pair of eggs in orientation, position, and scale. We excluded from further analysis any pair of eggs in which no feature matches were found, since such differences cannot be calculated for these eggs. Such cases were rare (we excluded 2% of inter-clutch comparisons, and 0.9% of intra-clutch comparisons), and the exclusion of pairs of eggs without matching features should not bias any subsequent analysis of invariance.

We calculated inter-clutch (i.e., between-individual) distances in orientation, position, and scale by finding these distances for each pair of eggs from different clutches. We used only one egg from each clutch to avoid pseudoreplication. This gave 36,321 comparisons between pairs of eggs from different clutches.

We calculated intra-clutch (i.e., within-individual) distances in orientation, position, and scale by finding the distances for a randomly selected pair of eggs from each clutch. This gave 219 comparisons between pairs of eggs from the same clutch.

We compared inter-clutch and intra-clutch variation using one-way analysis of variance tests. To ensure that the unequal sample sizes were not affecting the results, we took a random sample of 219 inter-clutch comparisons to compare it to the 219 intra-clutch comparisons.

Testing whether invariant properties predict rejection

To test whether orientation, position, or scale of markings predict rejection, we calculated differences in orientation, position, or scale between experimental eggs and each egg in the host clutch in which they were placed. We modeled these differences as predictor variables in a logistic regression model to test whether they predicted rejection in the experimental dataset ($n = 119$). Differences were calculated both including and excluding the replaced host egg (these were strongly correlated, with Pearson's $r > .9$ for each of the three traits). We used differences excluding the replaced egg as predictor variables in models. Correlations between differences in orientation, position, and scale were all low ($r < .32$).

Statistical analyses (logistic regressions)

We used logistic regressions (function `glm`) in R version 4.0.2 (R Development Core Team, 2020) to model rejection behavior when testing hypotheses relating to rejection. In all analyses of experimental data, we excluded the replaced host egg from averages calculated for the host clutch. We compared models using Akaike Information Criteria (AIC) (Akaike,

1974). Because “scale” is a measure of marking size, we also tested for correlations between the average scale value and another measure of marking size, called “principal marking size.” Principal marking size (E_{\max}) is calculated using granularity analysis and has been shown to predict egg rejection in this system (Spottiswoode & Stevens, 2010). Because E_{\max} is a categorical measure on a nonlinear scale (Stoddard & Stevens, 2010), we calculated the nonparametric Spearman's Rank Correlation Coefficient. We also tested whether differences in scale of matched markings were correlated with differences in E_{\max} , again by calculating the Spearman's Rank Correlation Coefficient.

Results

Measuring consistency and distinctiveness of pattern within a species

We tested whether consistency and distinctiveness were negatively correlated (indicating a mechanistic trade-off between these properties) within a single species, as was the case between species of warblers and weavers (Caves et al., 2021). A significant negative correlation was found between consistency and distinctiveness across 125 clutches of prinia eggs ($r = -.39$, $df = 123$, $p < .001$, 95% confidence interval = $-0.53, -0.23$; Figure 3).

Egg stitching

Stitching images produces non-regular egg shapes unlike those that have been previously analyzed in NPM. Therefore, to confirm that stitching does not invalidate the use of NPM and its prediction of rejection, we compared NPM distances calculated with both stitched and unstitched images. Distances between eggs calculated using stitched images predicted egg rejection (estimate \pm SE = 46.01 ± 13.71 , $Z = 3.36$, $df = 117$, $p < .001$, Nagelkerke's $R^2 = .17$) at least as well as distances calculated using one image—side “a”—of each egg (estimate \pm SE = 28.42 ± 10.06 , $Z = 2.83$, $df = 117$, $p = .004$, Nagelkerke's $R^2 = .12$). The addition of the distances calculated from side “a” to a rejection model with distances calculated from stitched images as the only predictor did not significantly improve the model (likelihood ratio test $\chi^2_1 = 2.77$, $p = .1$), whereas the addition of distances calculated from stitched images to a rejection model with distances calculated from side “a” as the only predictor significantly improved the model ($\chi^2_1 = 6.9$, $p = .008$). Similarly, the addition of distances calculated from stitched images to rejection models with distances calculated from sides “b,” “c,” and “d,” respectively improved the models ($\chi^2_1 = 8.5$, $p = .004$; $\chi^2_1 = 6.7$, $p = .01$; $\chi^2_1 = 4.3$, $p = .04$, respectively). This indicates that the stitched images provide additional information to single images of eggs and improve the extent to which rejection is predicted by NPM distances.

Identifying invariant properties

To identify invariant properties, we tested whether within-clutch distances ($n = 219$) were lower than between-clutch distances ($n = 36,321$) for orientation, position, and scale; in other words, whether these signature traits were consistent within clutches. Due to such unequal sample sizes, we re-sampled the between-clutch comparisons to a subset of 219. We found no significant difference between within-clutch and between-clutch variation in orientation ($F = 0.907$, $df = 1$, $p = .342$, Figure 4). Similarly, for position, there was no significant difference between within-clutch and between-clutch

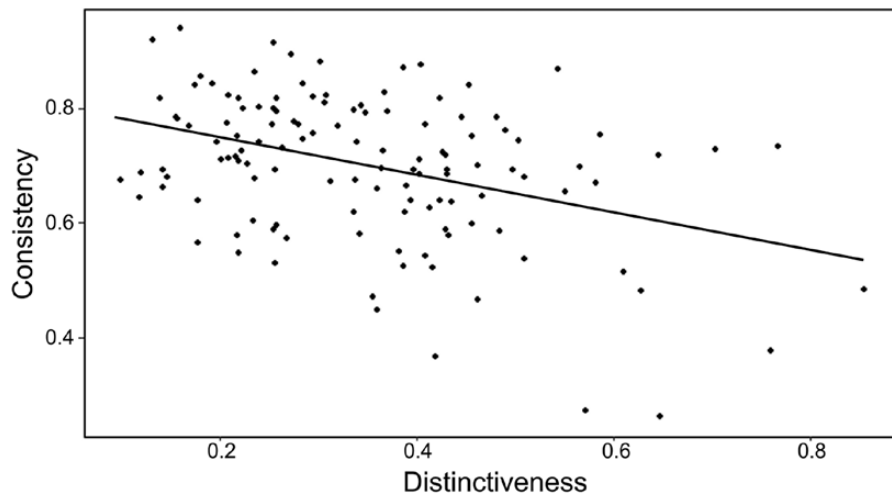


Figure 3. Consistency within clutches is negatively correlated with distinctiveness between clutches in prinias. Each point corresponds to a single clutch and the line of best fit is given in black.

variation ($F = 0.239$, $df = 1$, $p = .625$, Figure 4). For scale, within-clutch variation was significantly lower than between-clutch variation ($F = 29.9$, $df = 1$, $p < .001$, Figure 4). Thus, only scale showed the pattern expected for an invariant property.

Testing whether invariant properties predict rejection

Using a logistic regression model with a binary response variable (accepted or rejected) and predictor variables of orientational difference, positional difference, and scale difference, we found that no predictor in this full model significantly predicted rejection (orientational difference: estimate \pm SE = 0.25 ± 1.01 , $Z = 0.14$, $p = .89$; positional difference: estimate \pm SE = -0.01 ± 0.03 , $Z = -0.24$, $p = .81$, scale difference: estimate \pm SE = 0.75 ± 0.80 , $Z = 0.94$, $p = .35$; $df = 115$). We then constructed all possible subsets of these models (i.e., using zero, one, or two of the predictor variables). The model with the lowest AIC was the null model (Rejection ~ 1 ; AIC = 107); the only other model within 2 AIC of this model included only scale difference as a predictor (AIC = 108; estimate \pm SE = 0.73 ± 0.79 , $df = 116$, $Z = 0.92$, $p = .36$). Taken together, these results suggest that differences in orientation, position, and scale did not predict rejection.

To determine whether the metrics of scale that we calculated are analogous to principal marking size (calculated using granularity analysis), we tested for correlations between these variables. Average scale (across all features on an egg) was significantly but weakly correlated with principal marking size (Spearman's $\rho = -0.34$, $p < .001$); note that the negative correlation here is because large values for principal marking size in granularity analysis correspond to small marking sizes and vice versa. We also tested whether the difference in scale between matched features on pairs of eggs was correlated with the difference in principal marking size of pairs of eggs, and found no significant correlation (Spearman's $\rho = 0.15$, $p = .10$).

Discussion

In this study, we focused on two hallmarks of an optimal signature: consistency and distinctiveness. We studied visual

signatures on eggs, which have evolved to foil mimicry by brood-parasitic birds, to investigate a mechanistic trade-off between consistency and distinctiveness. We investigated whether this trade-off could be circumvented using invariant properties of egg pattern; in other words, traits that vary less within clutches than between clutches. We showed that there is a negative correlation between consistency and distinctiveness within species, and that scale (i.e., size) of markings was the only property we tested which was invariant within but not between clutches. However, contrary to predictions, egg rejection decisions by host parents in field experiments were not predicted by differences in scale between eggs.

We first showed that consistency was negatively correlated with distinctiveness, which indicates a trade-off between consistency and distinctiveness. It echoes the between-species result that both parasitized and unparasitized bird species show a negative correlation between consistency and distinctiveness of egg traits (Caves et al., 2021), and suggests that the latter is at least in part due to a mechanistic constraint rather than different species experiencing different selection pressures on consistency and distinctiveness. In contrast to digital signature generation, this trade-off may be unavoidable in the production of biological signatures, since biological signature-generating mechanisms cannot be both repeatable and random.

How could hosts get around such a trade-off between consistency and distinctiveness? Invariant properties, if used in rejection decisions, would allow hosts to circumvent the trade-off, since such properties are by definition consistent within clutches yet distinctive between clutches. We first developed an algorithm to stitch eggs together, based on SIFT features extracted using NPM. Because these features themselves are invariant to orientation, position, and scale (Lowe, 1999), they allow matching of images taken at different resolutions, and angles, of the same object. We found that NPM distances calculated using stitched images predicted egg rejection better than images that were not stitched. This is likely because comparing only individual perspectives of each egg (or another 3D object) might result in some matching features being excluded, simply because they might be absent in a particular 2D perspective of the pattern. This would reduce the precision of an analysis such as ours, which relies

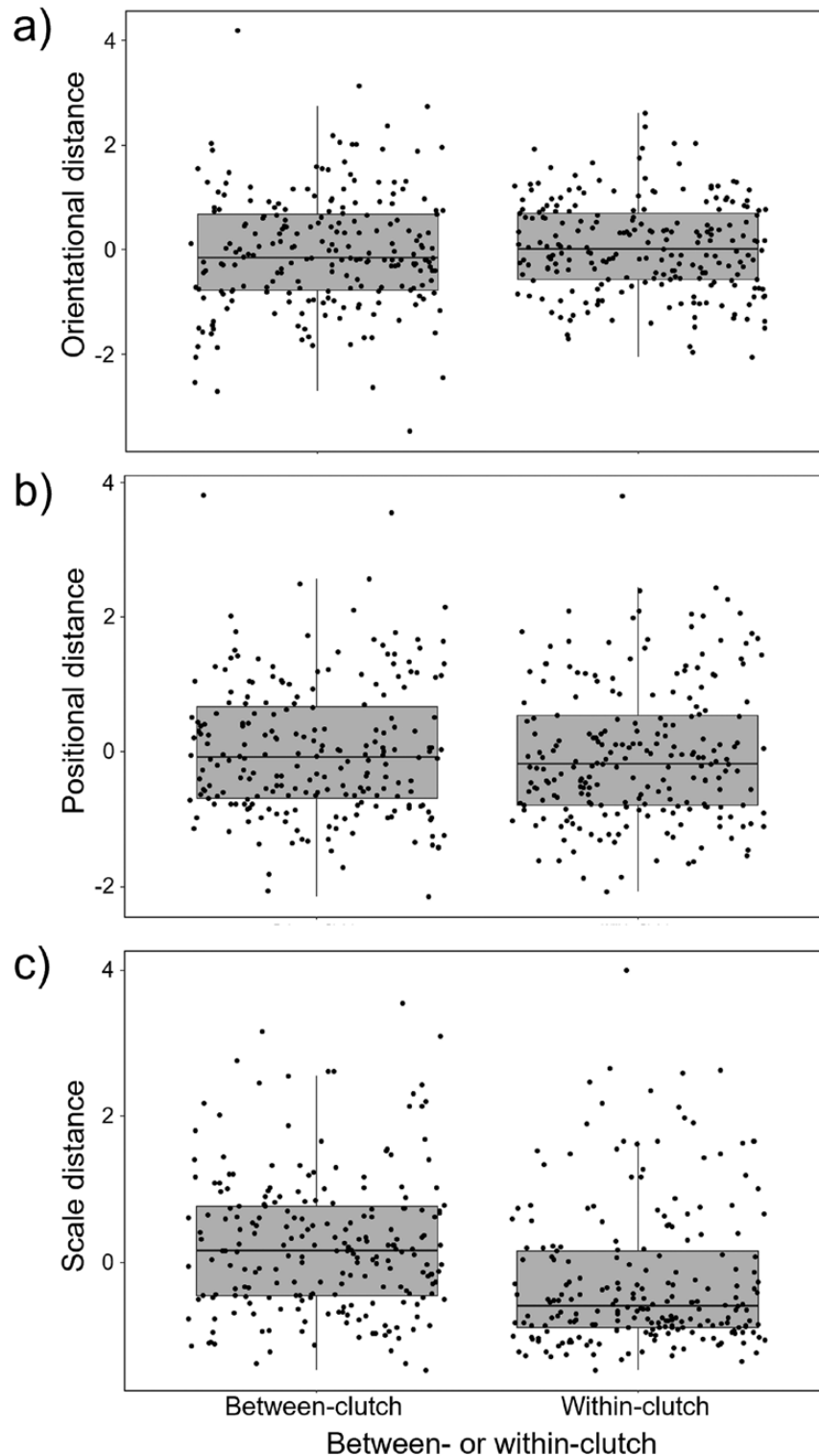


Figure 4. Boxplots showing the distributions of between- and within-clutch distances for orientation, position, and scale, with $n = 219$ for within-clutch comparisons, and a random subset of $n = 219$ between-clutch comparisons from the $n = 36,321$ possible such comparisons. Within-clutch variation is lower than between-clutch variation only in scale differences.

on matching features between eggs to infer which properties of pattern features varied within and between clutches. Such stitching methods, therefore, can and should be employed to recreate other 3D patterns in nature.

What could invariant properties imply about the pattern generation processes occurring in the shell gland? We found that size was invariant within clutches, but orientation and

position were not. Rotations, reflections, and translations are transformations which do not alter size. Thus, rotations and/or reflections (which would alter orientation) and translations (which would alter position) are likely to be transformations that can occur in the shell gland of a single individual. This may indicate that deposition of pattern occurs as the egg is moving and rotating within the shell

gland, and that either the egg does not move at a constant rate between eggs in a clutch, or that pattern deposition is imprecisely timed between eggs in a clutch. Such variation in the timing of pattern deposition could result in the observed variation in orientation and position within clutches. The invariance of marking size within clutches implies that enlargements do not occur; in other words, that however scribbles and spots are deposited, the mechanism results in fixed sizes of corresponding markings. Very little is known about the mechanisms or genetic control of pattern generation in the shell gland (Gosler et al., 2000; Sparks, 2011), but studies on hens have shown that eggs may rotate in the shell gland (Bradfield, 1951). The characteristic squiggles of prinia eggs (Dixit et al., 2023; Spottiswoode & Stevens, 2010) could be produced by such rotation of the egg during pattern deposition. Furthermore, variation in the timing of pigment deposition has been hypothesized (Sparks, 2011), which could affect the position of markings. The mechanisms of pattern generation, and consequently, the constraints on patterns that can be produced, clearly warrant further study.

We would expect features that are invariant within but not between clutches to provide the most reliable information about egg identity, and so to be used in egg rejection decisions. Therefore, we should expect that scale (but not orientation or position) should be used in rejection. Instead, we found that none of these traits significantly predicted rejection. This was surprising because the scale provides reliable information about identity. Given that scale differences are not used in rejection decisions, it seems likely that the mechanisms of pattern generation in the shell gland, which lead to scale being invariant within clutches, have not evolved due to selection in the context of egg rejection. Instead, these pattern-generation mechanisms have likely evolved in other contexts, and just happen to lead to scale-invariance within clutches. Nevertheless, the question of why prinias do not use this salient trait in rejection decision-making remains. One possibility is that scale is too fine-grained a feature to be used. The difference in feature scale between matched features is a very fine-grained measure, since this measure focuses solely on matched features, rather than considering the pattern as a whole. The genetic, physiological, or energetic constraints on visual processing (e.g., Dixit et al., 2022; Medina & Langmore, 2016; Stoddard & Stevens, 2010) may prevent hosts from being able to use such fine-grained traits. Moreover, perhaps there is insufficiently strong selection on hosts for them to evolve the cognitive or sensory abilities required to recognize such key fine-grained differences because other coarser-grained traits (such as those measured in Spottiswoode & Stevens, 2010; Stoddard et al., 2019) are used instead, or because the presence of signatures already constitutes a strong defense against parasites (Lund et al., 2023). Insufficiently strong selection on hosts can also arise because, although parasitism may carry a high cost for hosts (as is the case in this system), not all hosts experience parasitism (Davies, 2000)—this is an example of the “rare enemy” effect (Dawkins & Krebs, 1979).

Another measure of marking size, principal marking size (E_{\max} ; calculated using granularity analysis), predicted rejection in previous studies on this system (Spottiswoode & Stevens, 2010; Stoddard et al., 2019), though not in this dataset, likely because experimental eggs were chosen to be good

matches in “lower-level” pattern traits such as E_{\max} (Dixit et al., 2022). Furthermore, in the present dataset, E_{\max} was only weakly correlated with the average scale of features on an egg, and differences in E_{\max} were not correlated with differences in scale between matched features. These different results using different measures of marking size are likely explained by key differences in the type of information they capture: E_{\max} is the filter size at which a pattern has the highest “energy” in a granularity spectrum (Stoddard & Stevens, 2010), and thus it is a coarse measure of the modal size of pattern components. Feature scale, by contrast, is a very fine-grained measure of size, since it incorporates the sizes of each marking that is located by SIFT. As mentioned above, the difference in feature scale between matched features is an even finer-grained measure, since this specifically considers whether size varies between matched features. Thus, it may not be surprising that differences in principal marking size and differences in scale of matched features were uncorrelated, and that different measures of size have differing ability to predict egg rejection in this system.

Our findings also have implications for the validity of using SIFT features in studies of egg rejection and more broadly. Specifically, SIFT features are invariant to scale, position, and orientation (Lowe, 1999, 2004), and thus matching in NPM generally excludes information about orientation, position, or scale (Stoddard et al., 2014). If hosts used these forms of information in egg rejection decisions, this would indicate that SIFT features ignore important information. However, because hosts did not appear to use differences in these traits, SIFT’s exclusion of orientational, positional, and scale information does not diminish the value of NPM metrics in quantifying egg signature features, at least in this system. By contrast, differences in shape (which are quantified by NPM distances) do predict rejection in this system (Stoddard et al., 2019; also see Results). Therefore, quantifying pattern using SIFT as well as other orientation-, position-, and scale-invariant approaches (Harris & Dux, 2005; Lindeberg, 2013; Lowe, 1999, 2004; Muralidharan & Vasoncelos, 2010) may be a sufficiently good approximation to actual vision, particularly because many animal (including human) visual systems show at least some orientational-, position-, and size-invariant pattern processing (Cooper et al., 1992; Han et al., 2020; Isik et al., 2013; Newport et al., 2018; Reitboeck & Altmann, 1984; Wallis & Rolls, 1997; Zoccolan, 2015).

Conclusion

In this study, we found evidence for a mechanistic trade-off between consistency and distinctiveness in the production of egg signatures; these are two attributes that should be optimized in signatures across biology and society, to reliably convey individual identity. We identified a potential mechanism to circumvent this trade-off, specifically, that hosts should use invariant properties of pattern markings in egg rejection. We found one such property, the scale of features, but found that differences in this trait did not predict egg rejection. We may speculate that hosts display suboptimal rejection behavior due to genetic, physiological, or evolutionary constraints. Our results validate the use of SIFT and other orientation-, position-, and scale-invariant keypoint-based approaches to pattern quantification, and introduce and validate a method of stitching images. Our results also provide

clues as to the mechanisms of pattern generation in the shell gland. The ability to quantify and test hypotheses relating to invariant properties may improve our understanding of other signature-based systems, such as kin recognition systems and immune systems. Ultimately, the testing of hypotheses such as these allows us to evaluate the extent to which behavioral and physiological mechanisms are optimally tuned to produce logical behaviors.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

Code for egg stitching is available at <https://github.com/sakuraky1412/egg-stitching/tree/master>. All other code and data are available on Dryad at <https://doi.org/10.5061/dryad.9ghx3ffmc>.

Author contributions

T.D.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, and writing—original draft; K.-C.C.: formal analysis, investigation, methodology, and writing—review and editing; M.C.S.: conceptualization and writing—review and editing; L.M.: conceptualization and writing—review and editing; C.P.T.: resources, supervision, and writing—review and editing; C.N.S.: conceptualization, funding acquisition, investigation, methodology, supervision, and writing—review and editing.

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