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nonclustered genes ($P = 0.014$, hypergeometric test) (Fig. 3C). Rice exhibited no enrichment patterns in either gene set. The differing results among the four species suggest that specialized metabolic gene clusters are a product of independent, lineage-specific metabolic evolution, rather than a broad mechanism underlying specialized metabolism evolution.

We used a large-scale microarray data set to test whether the *Arabidopsis* clusters exhibit co-expression (6, 16). Of the 128 clusters with at least three genes, 62 contained at least one specialized metabolism-related gene. The mean co-expression value for the specialized metabolic gene-containing clusters (0.390) was significantly higher than the mean for the remaining clusters (0.289) ($P = 0.020$, Wilcoxon rank sum test) (Fig. 3D). Coexpression of genes within the 62 specialized metabolism-related clusters differed significantly from randomized clusters of genes ($P = 2.71 \times 10^{-7}$, Wilcoxon rank sum test) and neighboring genes in the *Arabidopsis* genome ($P = 3.56 \times 10^{-5}$, Wilcoxon rank sum test) (Fig. 3D) (6). In contrast, coexpression values within the 66 nonspecialized metabolism-related clusters were similar to the examined controls (random clusters, $P = 0.191$; neighboring genes, $P = 0.817$). These results indicate that gene clusters containing specialized metabolic genes are more likely to be coexpressed than their nonspecialized counterparts. Given that genes in the same metabolic pathway

tend to coexpress with each other, newly identified clusters exhibiting high degrees of gene coexpression may represent novel metabolic pathways (fig. S9).

Our findings indicate that the major innovations across plant networks pertain to the emergence of specialized metabolic processes, which, relative to primary metabolic processes, exhibit larger numbers of associated enzymes, increased enzyme proliferation rates, and preferential retention after local gene duplication versus whole-genome duplication. Furthermore, specialized metabolic genes exhibit lineage-specific patterns of genome colocation and specialized metabolism-related gene clusters display heightened levels of gene coexpression in *Arabidopsis*. Collectively, these properties constitute a set of genomic signatures of specialized metabolic genes that may serve as a tool for the accelerated and rational discovery of genes involved in the synthesis of novel specialized compounds (4, 5, 17).

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Supplementary Materials

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Deception by Flexible Alarm Mimicry in an African Bird

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Deception is common in nature, but victims of deception discriminate against and ultimately ignore deceptive signals when they are produced too frequently. Flexible variation of signals could allow evasion of such constraints. Fork-tailed drongos (*Dicrurus adsimilis*) use false alarm calls to scare other species away from food that they then steal. We show that drongos mimic the alarms of targeted species. Further, target species reduce their response to false alarm calls when they are repeated. However, the fear response is maintained when the call is varied. Drongos exploit this propensity by changing their alarm-call type when making repeated theft attempts on a particular species. Our results show that drongos can evade the frequency-dependent constraints that typically limit deception payoffs through flexible variation of their alarm calls.

Animal signals tend to be honest (1–3), but deception can persist where it is beneficial for individuals to respond to a signal type on average (4). Such deception stops working when deceptive signals occur too often relative to their honest counterparts (5, 6). This balance

imposes a constraint on payoffs for individuals possessing a single inflexible deceptive signal whose success depends on the abundance of honest models (5). Novel deceptive signals can confer benefits because individuals that produce rare signals are at a selective advantage (7, 8). Nevertheless, individual success still declines as signal frequency increases (7, 8). Some deceivers can tune their signal to better deceive their host (9, 10). However, the benefits available from flexibly alternating between different deceptive signal types remain unknown. We tested whether such flexible variation enables individuals to produce the specific signal most likely to deceive

hosts, and to evade frequency-dependent constraints on deception, by changing their signal when hosts habituate to a previously used signal.

We investigated the deceptive tactics of an African bird, the fork-tailed drongo (*Dicrurus*

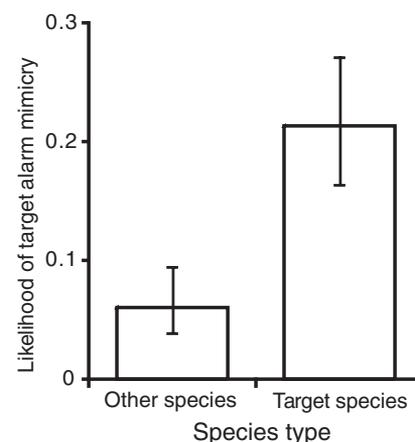


Fig. 1. Mimicry of target species alarm calls in food-theft attempts. Drongos mimicked a target species' alarm calls more often in food-theft attempts on them (target species) than in attempts on other target species (other species) [generalized linear mixed model (GLMM) (binomial), $\chi^2_1 = 2.55$, $P = 0.011$, $n = 147$ food-theft attempts by 10 drongos (table S1)]. Error bars indicate SEM.

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adsimilis), which uses false alarm calls, including mimicked alarm calls, to scare and steal food from a variety of targeted species (11–13). We hypothesized that wild drongos use vocal mimicry to flexibly vary their false alarm calls and thereby (i) increase the likelihood of target deception and (ii) maintain target deception during repeated interactions. Our research was conducted in the Kalahari Desert on 64 wild drongos habit-

uated to observers and individually recognizable by color rings (14). Drongos in this population spend over a quarter of their time following target species, including habituated groups of individually recognizable southern pied babblers (*Turdoides bicolor*) and meerkats (*Suricata suricatta*) (11, 12). When doing so, drongos honestly produce true alarm calls when they observe approaching predators (11, 12). Target species eavesdrop on these

alarm calls, as well as those of other species in the environment, and flee to cover in response just as they do to conspecific alarms (11, 12, 15). Additionally, target species benefit from drongo sentries by reducing their vigilance and increasing their foraging returns (12, 16). When a target individual finds a large food item, however, attending drongos may produce false alarm calls, causing the target to flee to cover and enabling the drongo

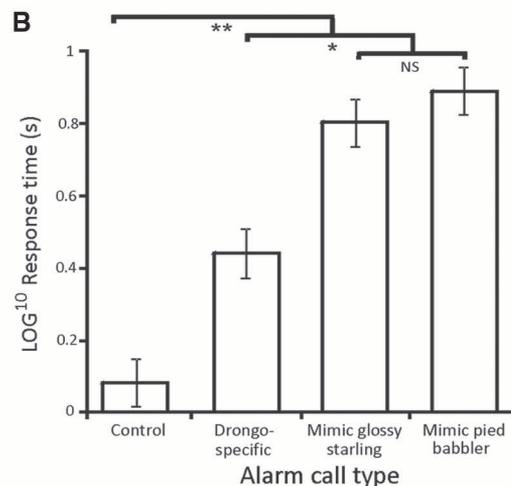
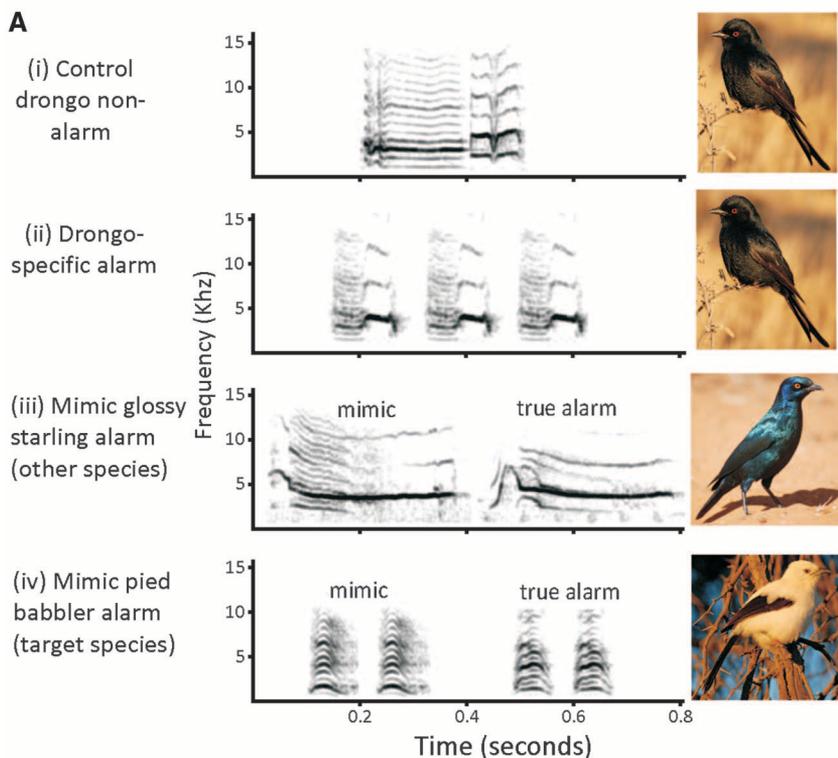


Fig. 2. Effect of alarm mimicry on target response. (A) Spectrograms of call types played to pied babblers (i to iv) to determine whether mimicry of alarm calls increases target alarm response. Drongo mimics of glossy starling and babbler alarm calls (mimic) are shown alongside these species' alarm calls (true alarm). (B) Response duration was longer to mimicked (target species) or startling (other species) alarm calls than to drongo-specific alarm calls [LMM, $\chi^2_1 = 38.38$, $P < 0.001$, Tukey tests, $*P < 0.001$; $n = 80$ alarm responses by 20 babblers (table S2)] and longer to all alarms than to control nonalarm calls [Tukey tests, $**P < 0.001$ (table S2)]. NS, not significant.

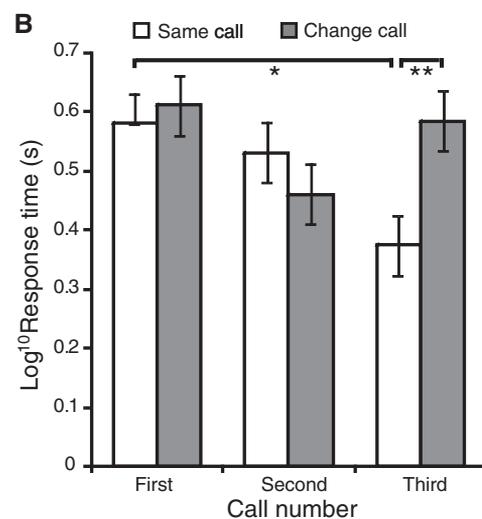
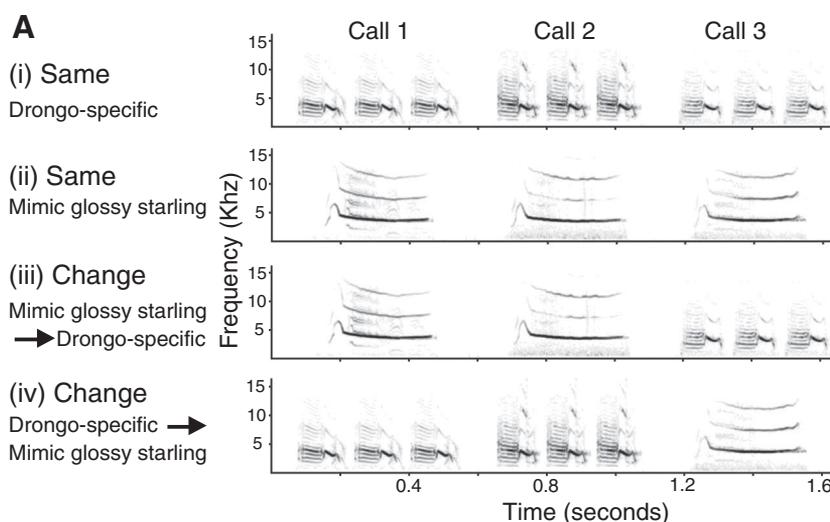


Fig. 3. Effect of alarm variation on target response. (A) Spectrograms of call treatments (i to iv) played to pied babblers to determine whether targets reduce their alarm response when the same alarm call is repeated (i and ii) but not when it is changed (iii and iv). (B) Response duration declined when the same alarm call was made three times in succession [LMM interaction: $\chi^2_1 =$

5.73, $P = 0.004$, $n = 264$ alarm responses by 22 babblers; Tukey test, $*P < 0.004$ (table S3)] but not when the third call was changed [Tukey test, $P < 0.996$ (table S3)], regardless of whether drongo-specific or mimicked starling alarm calls were made. The response to the third call was longer when changed than when it was kept the same [Tukey test, $**P < 0.002$ (table S3)].

to steal the abandoned food (11, 12). Drongos associate with a target species for several hours each day, during which time they give multiple true and false alarms and food theft accounts for 23% of drongo biomass intake (17).

Drongos produce a diversity of alarm call types (11). Individual repertoires range from 9 to 32 different calls (mean \pm SE = 17 ± 1), and a total of 51 different alarm call types have been recorded in false alarms (11). Six calls are drongo-specific, but 45 mimic other species' alarm calls, including those of target species (11). Highlighting the importance of alarm mimicry, drongos exclusively produce mimicked alarm calls in 42% of false alarms and combine mimicked and drongo-specific alarm calls in a further 27% of false alarms (11). However, the specific benefit drongos gain from producing such a large array of mimetic alarm calls is unclear.

One possibility is that target species are more likely to be deceived by mimicked versions of their own calls than by drongo-specific alarm calls. Observations of 688 food theft attempts made during 847.5 hours of focal observations on 64 drongos (10.75 ± 1.62 attempts per drongo) (7) revealed that drongos able to mimic a specific target's alarm call more frequently mimicked the target in food-theft attempts on them, as compared with their attempts on other species (Fig. 1 and table S1). We experimentally tested our hypothesis that mimicry of target species alarms increases the intensity of target responses by playing four different call types at 20-min intervals [equivalent to natural alarm rates (7)] to individual pied babblers ($n = 20$ babblers in 10 groups) experimentally provisioned with a food item. The drongo-generated calls were (i) a nonalarm territory call (control), (ii) a drongo-specific alarm call, (iii) a mimicked Cape glossy starling (*Lamprotornis nitens*) alarm call (other species), and (iv) a mimicked pied babbler alarm call (target species) (Fig. 2A). Mimicked starling alarms were selected because starlings are common throughout the study site and are frequently mimicked by drongos (11). We measured the babbler's response time (seconds) from when a call was played and the individual

stopped handling the food item (looked up, moved toward cover, or combined these behaviors) to when it resumed foraging (0 s when calls ignored) (7).

Babblers were slower to resume foraging in response to mimicked alarm calls than to drongo-specific alarm calls (Fig. 2B and table S2). Alarm mimicry therefore increased target deception, but there was no difference between the babbler's response to their own mimicked alarms relative to those of starlings (table S2). Starlings may be reliable alarm callers, accurately signaling threatening predators. Nevertheless, in a dynamic environment where drongos target numerous species and the value of different alarm calls is likely to vary with recent usage (15), target-specific mimicry could represent a reliable heuristic rule of thumb (18).

Although these results indicate that alarm mimicry by drongos increases target deception, targets are still predicted to habituate to repeated use of the same false alarm call regardless of its type (5). We used a second experiment to test our hypothesis that, by flexibly varying their false alarm calls during repeated food-theft attempts, drongos maintain the intensity of target responses. We played four treatments of three alarm calls to individual babblers ($n = 22$ babblers in 11 groups) provisioned with a food item and measured their response time (3 days between treatments and 20 min between calls). Of the four treatments, two contained three alarm calls of the same type, either drongo-specific or mimicked starling, whereas in the other two treatments the third call was changed to the opposite type, either drongo-specific to mimicked starling or vice versa (Fig. 3A) (7). Babblers decreased their response when the same alarm call type was played three times in succession but maintained their response when the third alarm was changed (Fig. 3B and table S3). Furthermore, the duration of their response to the third alarm was greater when it was changed relative to when it was kept the same (Fig. 3B and table S3).

Drongos thus could benefit by flexibly varying their call type to maintain target deception. We tested whether drongos exploit this possibility under natural circumstances by changing their false alarm calls during repeated food-theft attempts on a target

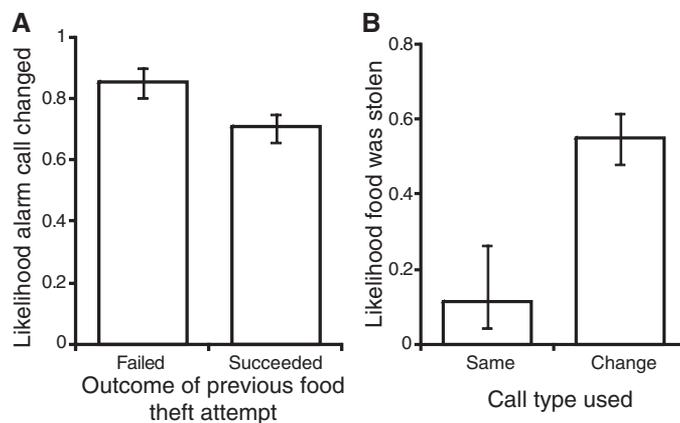
and, more specifically, whether they change their call type when their previous food-theft attempt failed. We observed repeated food-theft attempts by drongos on the same target on 151 occasions ($n = 42$ drongos) and found that they changed their alarm call type on $74 \pm 6\%$ of occasions (7). In particular, drongos were more likely to change the type of false alarm call when their previous food-theft attempt failed (Fig. 4A and table S4). Furthermore, when drongos changed their false alarm-call type after a failed food-theft attempt, they were more likely to successfully steal food than when they made the same alarm call (Fig. 4B and table S5).

Our results suggest that, by flexibly varying their deceptive signal, drongos benefit in two ways. First, they produce signals more likely to deceive their targets. Second, they avoid target habituation to repeated use of the same deceptive signal and thereby evade the frequency-dependent constraints that typically limit payoffs from deceptive communication. Such benefits are analogous to those provided by antigenic variation, whereby infectious organisms, including those responsible for influenza, sleeping sickness (*Trypanosomiasis brucei*), and malaria (*Plasmodium falciparum*), vary cell-surface proteins to evade host immune responses (19).

Flexible variation maintained deception because target habituation to one alarm signal did not result in habituation to other signals. This finding is similar to that of research on habituation mechanisms in bird song systems (20). However, flexible variation might not maintain deception indefinitely because deceived species may ultimately habituate to all the deceptive signals in an individual's repertoire. Furthermore, species able to recognize individuals could combat deception by assessing signaler reputation across different signals (21, 22). Selection may therefore favor mechanisms that enable deceivers to elaborate their signal repertoire and disguise their identity.

Our results suggest a deceptive function for vocal mimicry, a behavior for which few adaptive benefits have been demonstrated (23). Further, we found that drongos specifically change their alarm calls to both mimic targets and exploit feedback from target alarm responses, thereby increasing their success. This shows that attending to feedback in deceptive communication may be adaptive, complementing recent research on feedback in other communication systems where individuals repeatedly interact (21, 24, 25). Such deceptive flexibility and the drongos' production of both honest and dishonest alarms, termed tactical deception (26), are considered evidence that species possess cognitive abilities, including mental state attribution, akin to theory of mind (26–28). However, the evolved mechanisms responsible for similar behavior in different species are not necessarily the same and likely vary with species' ecology. Determining what different mechanisms enable the production of complex behavior and when these are selectively advantageous remain key questions in evolutionary biology.

Fig. 4. Repeated food-theft attempts by individual drongos. (A) Drongos were more likely to change their false alarm call type in food-theft attempts when they had failed in their previous attempt on that target species [GLMM (binomial): $\chi^2_1 = 2.15$, $P = 0.039$, $n = 151$ (table S4)] and (B) were more successful when they did so compared with when they made the same call type [GLMM (binomial), $\chi^2_1 = 2.01$, $P = 0.045$, $n = 60$ (table S5)].



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Greater Sensitivity to Drought Accompanies Maize Yield Increase in the U.S. Midwest

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A key question for climate change adaptation is whether existing cropping systems can become less sensitive to climate variations. We use a field-level data set on maize and soybean yields in the central United States for 1995 through 2012 to examine changes in drought sensitivity. Although yields have increased in absolute value under all levels of stress for both crops, the sensitivity of maize yields to drought stress associated with high vapor pressure deficits has increased. The greater sensitivity has occurred despite cultivar improvements and increased carbon dioxide and reflects the agronomic trend toward higher sowing densities. The results suggest that agronomic changes tend to translate improved drought tolerance of plants to higher average yields but not to decreasing drought sensitivity of yields at the field scale.

Drought is currently one of the main constraints to crop production in rainfed systems throughout the world, including in the United States. As a result, much breeding and agronomic research has been designed, at least in part, to improve performance under drought conditions (1). However, success in experimental fields does not always easily or completely translate to yield progress in farmers' fields because drought characteristics in farmers' commercial fields can differ substantially from trial condi-

tions (2) and because different drought scenarios can favor different genotypes or management practices (3, 4).

In the United States, which typically supplies 40% of global annual maize production and 35%

of global soybean production (5), several factors could be affecting drought sensitivity in farmers' fields. On the positive side, increased use of low or no-till systems has likely increased soil moisture in dry years, and increasing CO₂ concentrations typically lead to higher plant water-use efficiencies, thereby reducing drought sensitivity (6, 7). At the same time, in maize, modern genetics has facilitated increased sowing density because individual plants are better able to develop ears under stress (8, 9), roots are able to penetrate deeper and access more water (10), and genetically engineered pest resistance has reduced root damage from soil insects (11). All of these have contributed to historical gains in biomass and yields, but increased density can be detrimental under drought conditions because of excessive stress exposure for individual plants (12). Thus, the net effect of recent genetic, agronomic, and environmental changes on drought sensitivity remains an open empirical question.

An obstacle to measuring progress in farmers' fields has been lack of accurate field-level data on both environmental conditions and yield performance that span a range of drought conditions and time. Here, we use a data set of field-level records

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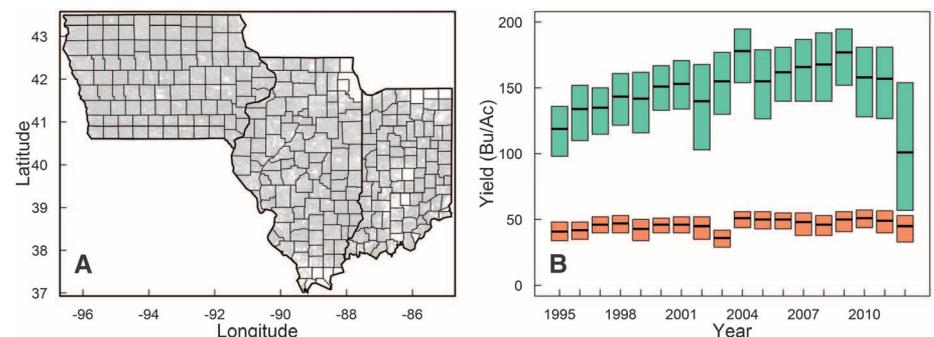


Fig. 1. Study area and yield distributions. (A) Map of main study region, with individual points showing locations of fields for maize in the USDA data. (B) Summary statistics of field-level maize (green) and soybean (orange) yields over the study period. Horizontal bands indicate sample median, and bars show interquartile range (25th to 75th percentile). Bu/Ac, bushels per acre.