Flexibility training does not increase behavioral diversity of Florida scrub-jays

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ABSTRACT

Human modifications of environments are expanding, causing global changes that other species must adjust to or suffer from. Behavioral flexibility (hereafter 'flexibility') could be key to coping with rapid change. Behavioral research can contribute to conservation by determining which behaviors can predict the ability to adjust to human modified environments and whether these can be manipulated. When research that manipulates behavior in a conservation context occurs, it primarily trains a specific behavior to address one potential threat improve individual success in the wild. However, training a domain general cognitive ability, such as flexibility, has the potential to change a whole suite of behaviors, which could have a larger impact on influencing success in adjusting to human modified environments. This project asks whether flexibility can be increased by experimentally increasing environmental heterogeneity and whether such an increase can help species succeed in human modified environments. We explore whether it is possible to take insights from highly divergent species and apply them to address critical conservation challenges. This pushes the limits in terms of understanding how conserved these abilities may be and to what extent they can be shaped by the environment. We aim to 1) conduct flexibility interventions in flexible species that are successful in human modified environments (California scrub-jays or blue jays) to understand how flexibility relates to success; and 2) implement these interventions in a vulnerable species (Florida scrub-jays) to determine whether flexibility as a generalizable cognitive ability can be trained and whether such training improves success in human-modified environments. This research will significantly advance our understanding of the causes and consequences of flexibility, linking behavior to environmental change, cognition, and success in human modified environments through a comparative framework.

REGISTERED REPORT DETAILS

- **Level of bias = 6:** This registered report was written (Jul 2021-May 2022), and revised after round one of peer review at Peer Community in Registered Reports (Jul 2022) prior to collecting any data.
- **Programmatic registered report:** This is one of three Stage 2 articles that will result from the original, comprehensive Stage 1 registered report: one for toutouwai, one for grackles, and one for jays (this current manuscript).
- **Deviations from the Stage 1 registered report:** We were unable to sample disturbance-resilient blue jays or California scrub-jays and so we cannot address J.Q2 (one of four specific research questions) at this time. However, to begin to test the question of whether behavior relates to success in human-modified environments, we conducted an unregistered analysis comparing behavior of Florida scrub-jays (FLSJ; a species that is overall disturbance-sensitive) that were persisting in suburban areas to FLSJ in natural habitat managed without human disturbance.

INTRODUCTION

Human modified environments are expanding (Goldewijk, 2001; X. Liu et al., 2020; Wu et al., 2011), causing global changes that other species must adjust to or suffer from (Alberti, 2015; Chejanovski et al., 2017; Ciani, 1986; Federspiel et al., 2017). Behavioral flexibility (hereafter 'flexibility') could be key for adjusting to such change: individuals interact with their environment through behavior, making it crucial to an ecologically valid understanding of how species adjust to environmental changes (Lee & Thornton, 2021). One of the top priorities for behavioral research to maximize conservation progress is to determine which cognitive abilities and behaviors can predict the ability to adjust to human modified environments and whether these can be manipulated (Moseby et al., 2016). The rare research that manipulates behavior in a conservation context usually focuses on training specific behaviors (for example, predator recognition through predator exposure) to improve individual success in the wild (Jolly et al., 2018; Moseby et al., 2012; Ross et al., 2019; West et al., 2018; see review in Tetzlaff et al., 2019). However, training a general cognitive ability, such as flexibility – the ability to rapidly adapt behavior to changes through learning throughout the lifetime (see the theory behind this definition in Mikhalevich et al., 2017) – has the potential to change a whole suite of behaviors and more broadly influence success in adjusting to human modified environments. Recent evidence supports this hypothesis: as far as we are aware, our previous research in the great-tailed grackle was the first to show that flexibility can be manipulated using serial reversal learning of color preferences, and that the manipulated individuals were more flexible during foraging (Logan et al., 2025), in a different experimental context (locus switching on a puzzlebox) as well as being more innovative (solved more loci on a puzzlebox) (Logan et al., 2023).

Environments where informational cues about resources vary in a heterogeneous (but non-random) way across space and time are hypothesized to open a pathway for species to functionally detect and react to such cues via flexibility (Mikhalevich et al., 2017). Human modified environments likely provide a different set of informational cues that vary heterogeneously across space and time, and the species that are successful in such environments are likely those who are able to detect and track such cues. Because heterogeneous environments are hypothesized to select for flexibility (Wright et al., 2010), we expect that exposing individuals to experimentally increased environmental heterogeneity will train individuals to be more flexible, which will then increase their success in such environments (Fig. 1). Success can relate to any number of variables regarding the usage of and investment in resources and response to threats, from improved foraging efficiency to increased dispersal and survival within human modified environments, to placing nests in more protective locations. Whether a measure of success is predicted to relate to flexibility depends on what is already known about the particular population and their particular environment.

Figure 1. The theory behind this research illustrated by a directed acyclic graph (DAG), which is a theoretical model of the causal relationships among the key variables in our investigation. Based on the theoretical background provided by Mikhalevich et al. (2017), we assume that more heterogeneity causes more flexibility, which then causes more success in human modified environments.

This investigation asks whether a method of experimentally increasing environmental heterogeneity through serial reversal learning leads to increased behavioral flexibility and greater fitness in human modified environments. Serial reversal learning tasks have been performed with a wide diversity of species (birds: Bond et al., 2007; bumblebees: Strang & Sherry, 2014; stingrays: Daniel & Schluessel, 2020). There is variation across individuals and species in their performance, however almost all previous studies show that individuals improve their flexibility if the reversal intervention is given multiple times in sequence (rats: Mackintosh et al., 1968; guppies: Lucon-Xiccato & Bisazza, 2014; poison frogs: Y. Liu et al., 2016; grackles: Logan et al., 2023). We aim to conduct a flexibility intervention in species that are successful in human modified environments (California scrub-jays or blue jays) to understand how flexibility relates to success, and implement these interventions in a vulnerable species (Florida scrub-jays).

While we do not examine the potential spread of the post-manipulation success behaviors from manipulated individuals to individuals that are not involved in our studies, we acknowledge that this is a possibility worthy of future investigation. Manipulating the flexibility of a few individuals could have population-level effects because significant research on social information use in birds (e.g., Valente et al., 2021) demonstrates the potential for the manipulated behavior to disseminate to conspecifics (for example, if manipulated individuals are faster at locating new resources, which could attract the attention of conspecifics, or if unmanipulated individuals copy the manipulated individuals' nesting or foraging locations). Indeed, there is evidence for social learning in the focal species for this investigation (K. B. McCune et al., 2022; Midford et al., 2000). In the event that social learning is not used by a given population to spread the behaviors of manipulated individuals, investing in the training of specific individuals to increase their success in the wild could still have conservation impacts. In some cases, it is possible to train many individuals in a population or a species because there are not many individuals left (Greggor et al., 2021). It is also possible to train all individuals involved in a conservation management event such as a translocation (Greggor et al., 2021). Therefore, there can still be significant population consequences even if each individual needs to be trained to achieve the goal.

This comparative approach will ultimately reveal the role of behavioral flexibility in adaptation to environmental change and whether there is a causal relationship between this general cognitive trait and behavioral interactions with human-modified environments, such as foraging and habitat use. Our previous research on great-tailed grackles provided support that this causal relationship does exist in a generalist, invasive species. However, the research presented here will evaluate the generalizability of this technique across distinct species differentially affected by anthropogenic change. Consequently, the results from this research will substantially advance our understanding of the causes and consequences of flexibility, linking behavior to environmental change, cognition, and success in human modified environments to facilitate conservation of declining species.

RESEARCH QUESTIONS

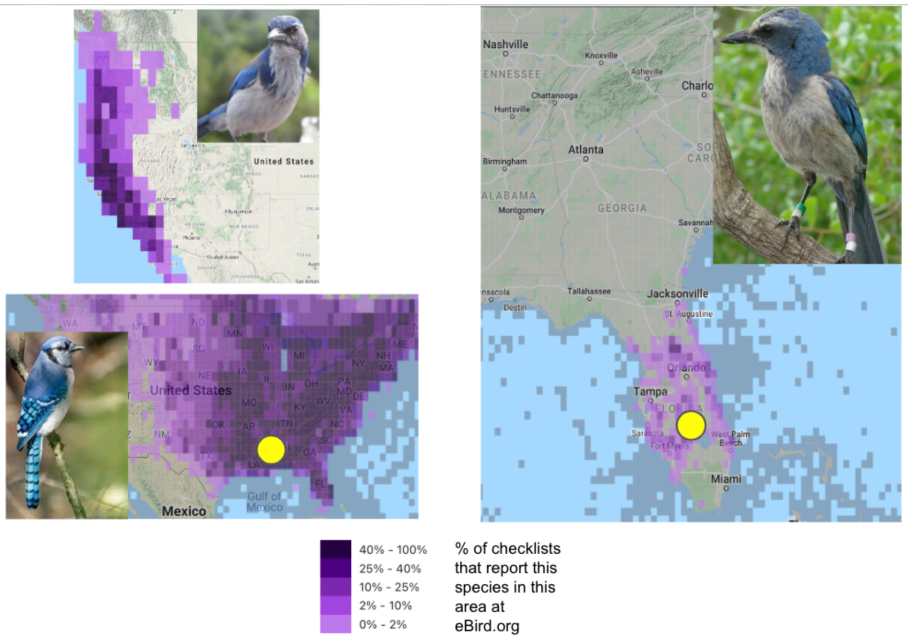
Can behavioral flexibility in individuals be increased by increasing environmental heterogeneity? If so, does increased flexibility help individuals succeed in human modified environments?

Prediction 1: Flexibility can be increased in individuals and such an increase **improves the likelihood of success in human modified environments**. This would indicate that the abilities involved in tracking changing resources in the environment are the same as or related to the abilities involved in succeeding in human modified environments. It would also indicate that flexibility is trainable and that such training could be a useful conservation tool for threatened and endangered species.

Prediction 1 alternative 1: Flexibility can be increased in individuals, but such an increase **does not improve the likelihood of success** in human modified environments. This would indicate that species associated with human modified environments form this association for reasons other than their flexibility, and that threatened species are likely not very successful in human modified environments for reasons unrelated to their ability to change their behavior with changing circumstances. An alternative could be that the changes induced by the increase in flexibility do not persist for sufficiently long times to make a difference on the subsequent likelihood of success (changes in great-tailed grackles were still present for four weeks after the manipulation and longer time periods were not attempted so the threshold is unknown Logan et al., 2022).

Prediction 1 alternative 2: Flexibility can be increased in some populations, but not others. This would indicate that **flexibility manipulations may not work for all populations**, and that the effectiveness of such experiments should first be tested in the population of interest before including such an intervention in a conservation plan. If flexibility is not manipulatable in threatened populations, this would indicate that they are likely not very successful in human modified environments because of their inability to change their behavior with changing circumstances, and that flexibility is not trainable. If flexibility is not manipulatable in populations that are successful in human modified environments, this could indicate that they might have used flexibility in the past when originally forming the association, but the need to maintain flexibility in their repertoire is no longer necessary (Wright et al., 2010). In populations where flexibility is not manipulatable, this would indicate that the abilities involved in tracking changing resources in the environment are independent of the abilities involved in succeeding in human modified environments.

Population-specific background and tailored research questions



Species	**Disturbance-resilient jays** Top: *Aphelocoma californica* (CASJ) Bottom: *Cyanocitta cristata* (BLJA)	**Disturbance-sensitive jays** *Aphelocoma coerulescens* (FLSJ)
Status	Successful	At risk - in decline
Habitat	Human modified environments + Pine oak scrub	Pine oak scrub
Sightings in cities	Yes	Rare
Field site	TBD & Auburn, AL	Florida, USA

Figure 2. Comparing the species involved in this investigation relative to their geographic range and association with human modified habitats. The yellow dots represent field site locations. Photo credit: CASJ, Corina Logan; BLJA, Rhododendrites; FLSJ, VvAndromedavV.

Background

Jay species exhibit a diversity of social systems and success in colonizing suburban and urban areas (Fig. 2). California scrub-jays (*Aphelocoma californica*, hereafter "CASJ") and blue jays (*Cyanocitta cristata*, hereafter "BLJA") are singular, monogamous breeders that are increasing in abundance, expanding their range sizes, and highly successful in natural, suburban, and urban areas (Blair, 1996; Curry et al., 2017). We therefore consider these "disturbance-resilient" (DR) jay species. In contrast, the Florida scrub-jay (*A. coerulescens*; hereafter "FLSJ") is a "disturbance-sensitive" (DS) jay species that is threatened, endemic, and range-restricted to xeric oak scrub habitat in Florida (Woolfenden & Fitzpatrick, 1996).

These species forage primarily on mast (acorns, hazelnuts, etc.) that they cache throughout their territory, which makes it available to eat year-round. They are also opportunistic omnivores and specifically need high-fat and high-protein arthropods to feed to nestlings and fledglings (Curry et al., 2017). Nesting and foraging substrates can be drastically different in human modified environments compared to natural areas [e.g., predominance of non-native vegetation; Tuomainen & Candolin (2011)], and it is unknown whether suburban and urban jays are able to persist in these environments through behavioral adjustments. The DS jay species, the FLSJ, can persist in suburban habitats after conversion from xeric oak scrub, however suburban populations of FLSJ steadily decline (Bowman pers. comm.). This is potentially due to the presence of suboptimal habitat resulting from fire suppression (Woolfenden & Fitzpatrick, 1996), higher rates of brood reduction through nestling starvation (Shawkey et al., 2004), and the lack of nutritionally complete prey items (Shawkey et al., 2004) in suburban habitats. It is possible that behavioral flexibility in habitat use and foraging breadth underlies the ability of some FLSJ to persist in human-dominated areas.

We aimed to compare behavioral flexibility within species, between suburban and natural populations to determine whether variation in flexibility relates to variation in presence in these habitats. Subsequently, we planned to compare flexibility between DS and DR jay species to determine whether this trait is related to the greater success of DR jay species, like the CASJ and BLJA, in human-dominated areas (but see Deviations section). Lastly, we tested whether manipulating flexibility increases the foraging and microhabitat breadth of jays in suburban and natural environments. Manipulating the flexibility of a subset of individuals has the potential to affect the population because previous research demonstrates that these species have the capacity to use foraging information discovered by others (social learning) to flexibly change their behavior (K. B. McCune et al., 2022; Midford et al., 2000).

Tailored Research Questions

For all research questions, Table 1 summarizes our predictions, analysis plans, interpretations for the various directions the results could go, and the hypotheses that could be contradicted given the various outcomes.

- **J.Q1: Do jay populations in human modified areas differ in baseline behavioral flexibility compared to populations in natural areas?** We will investigate this question by comparing performance on serial reversal learning in the wild between jays in natural areas and jays in human modified areas.
- **J.Q2: Are disturbance-resilient (DR) jays more behaviorally flexible than disturbance-sensitive (DS) jays?** We will investigate this question by comparing performance on serial reversal learning in the wild between DR and DS jay species.
- **J.Q3: Does manipulating behavioral flexibility alter the number of microhabitats used?** We will investigate this question by tracking their presence in a variety of microhabitats before and after manipulating their flexibility using serial reversal learning in the wild. We only count that a microhabitat was used if the individual had at least 5% of their data points there. This prevents a microhabitat from being counted even if an individual was simply moving through it, and therefore not necessarily using it.
- **J.Q4: Does manipulating flexibility alter the number of different food items taken by jays?** We will investigate this question by tracking the various food items they take before and after manipulating their flexibility using serial reversal learning in the wild.

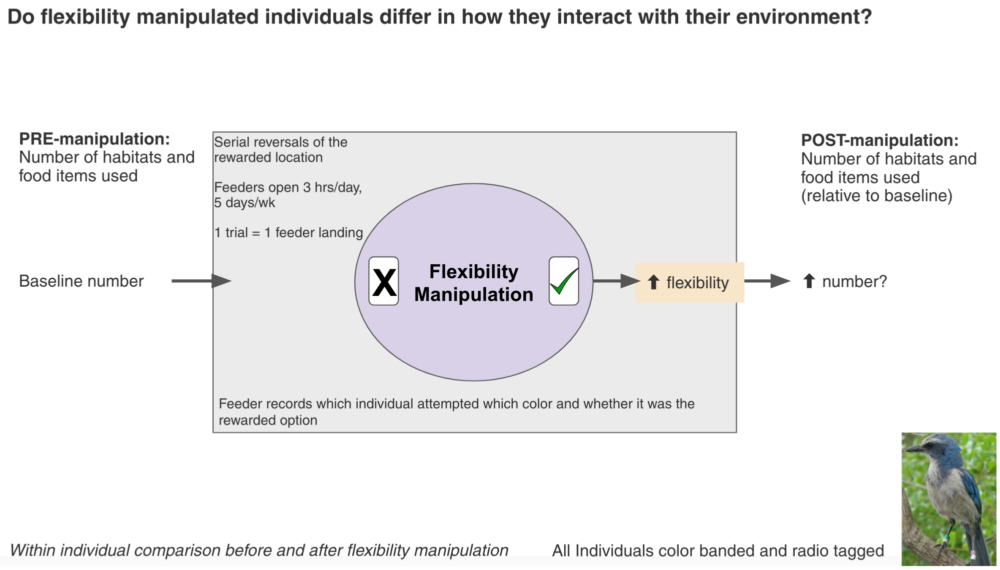


Figure 3. The reversal learning experiment in a group context (Design 2 from the ManyIndividuals registered report) tailored to the jay research questions. The white rectangles represent feeder locations, the feeder with the X is in the unrewarded location while the feeder with the green check is the rewarded location.

Table 1. Study design for the jay research. Note that we are unable to test Q2 because it was not possible to sample CASJ or BLJA within the timeframe of this study. References that were not already cited in the introduction: Galbraith et al. (2015), Lapiedra et al. (2017), Rice et al. (2003), Emery & Clayton (2004), Sol et al. (2002), Peterson et al. (2011), Grinnell (1917).

Question	Hypothesis	Sampling plan	Analysis plan	Rationale for deciding test sensitivity to confirm/ disconfirm hypothesis	Interpretation given different outcomes	Theory that could be shown wrong by the outcomes
1. Do jay populations in human modified areas differ in baseline behavioral flexibility compared to populations in natural areas?	**Prediction 1.1:** Suburban jays are **more flexible** than jays in natural areas	Simulations using bespoke Bayesian models in Logan et al. (2021) showed a high likelihood of detecting differences with a sample size of 15 when mean differences in phi were at least 0.01 and lambda at least 3 *(see Analysis Plan)*	Bayesian model: Response: phi and lambda Explanatory: Habitat (suburban/ natural) *(see Analysis Plan)*	Contrasts will determine whether the before and after conditions differed from each other. We will conclude there is a difference if the confidence interval does not cross zero. False positives: the power analyses suggest that false positives are unlikely even with small sample sizes. Accordingly, we will interpret any contrast that does not cross zero as indicating an effect. False negatives: the power analyses suggest that, especially with small sample sizes, we will not have sufficient power to exclude the possibility that an effect exists even though our model does not indicate an effect (contrast crosses zero).	This implies that flexibility is related to the ability to occupy human modified environments where spatial and temporal heterogeneity of resources is high.	Selection for exploitation of supplementary food (Galbraith et al. 2015), where individuals learn to depend on anthropogenic food sources and are less likely to flexibly sample alternative resources.
	Prediction 1.2: Suburban jays are **less flexible** than jays in natural areas				This implies that human modification of the environment has led to less spatial and temporal heterogeneity of resources. For example, the prevalence of bird feeders in suburban areas leads to consistently available food.	(1) Flexibility facilitates adapting to environmental change (see Introduction)
	Prediction 1.3: There is **no difference** in flexibility between suburban jays and jays in natural areas				This implies that additional behavioral (e.g. boldness, Lapiedra et al., 2017) or genetic traits may facilitate success in human modified environments.	(1) The urban filter (Lapiedra et al. 2017) where novel anthropogenic pressures select for flexible individuals.
2. Are disturbance resilient (DR) jays) more behaviorally flexible than disturbance sensitive (DS) jays)?	**Prediction 2.1:** DR jays are **more flexible** than DS jays		Bayesian model: Response: phi and lambda Explanatory: Species *(see Analysis Plan)*		This difference may explain the range expansion and greater success of DR jays in human modified environments.	Range expansion instead relates to ecological niche differentiation (Rice et al. 2003), where DR jays evolved to occupy a niche that more closely resembles human modified environments than DS jays.
	Prediction 2.2: DR jays are **less flexible** than DS jays				This implies that flexibility is not related to success in human modified environments and that flexibility may instead be related to a different, unknown social or environmental characteristic. For example, the cooperative breeding system of the DS jay species, the Florida scrub-jay, may favor increased flexibility for responding to group mates' behavior.	(1)
	Prediction 2.3: DR jays and DS jays are **equally flexible**				This implies flexibility is not related to success in human modified environments and the level of flexibility is potentially an evolutionary conserved trait from a corvid common ancestor (Emery & Clayton 2004).	(1)
3. Habitat: Does manipulating behavioral flexibility alter the number of microhabitats used?	**Prediction 3.1:** Flexibility can be increased and such an increase alters daily habitat use to include **more variety of habitats**	Simulations using bespoke Bayesian models showed a high likelihood of detecting differences with a sample size of 20 when mean difference in the proportion of microhabitats used was at least 0.1 (standard deviation=0.1) or 0.15 (SD=0.2) *(see Analysis Plan)*	Bayesian model: Response: Number of microhabitats used per individual Explanatory: Condition (before/after) Random: Condition | ID *(see Analysis Plan)*		Increasing behavioral flexibility, with a serial reversal learning manipulation, increases the likelihood the individual will sample new areas while foraging.	(2) Habitat preferences and the foraging niche are fixed within species because each species evolves within a specific ecological niche (Grinnell 1917; Peterson et al. 2011).
	Prediction 3.2: Flexibility can be increased and such an increase alters daily habitat use to **decrease the variety of habitats** used				Increasing behavioral flexibility potentially leads to increased foraging breadth or use of resources within one habitat, rather than leading to sampling across habitat types.	Behavioral flexibility facilitates the use of novel habitats and invasion success through dietary generalism (Sol et al. 2002)
	Prediction 3.3: Flexibility can be increased but has **no effect** on the variety of habitats used				This suggests that the cognitive ability behavioral flexibility may not generalize to all domains (e.g. may relate to foraging but not habitat use). Alternatively, it could indicate that they might have used flexibility in the past when originally forming the association, but the need to maintain flexibility in their repertoire is no longer necessary, or that changes induced by the increase in flexibility do not persist for sufficiently long times to make a difference on the subsequent likelihood of success.	(1) (3) Behavioral flexibility is a general cognitive ability (see Introduction)
4. Foraging: Does manipulating flexibility alter the number of different food items taken by jays?	**Prediction 4.1:** Flexibility can be increased and such an increase alters daily foraging breadth to include **more variety of food** items	Simulations using bespoke Bayesian models showed a high likelihood of detecting differences with a sample size of 20 when mean differences in the number of foods taken were at least 1 (and a standard deviation of 2) *(see Analysis Plan)*	Bayesian model: Response: Number of foods taken per individual Explanatory: Condition (before/after) Random: Condition | ID *(see Analysis Plan)*		Increasing behavioral flexibility, with a serial reversal learning manipulation, increases the likelihood the individual will sample new food sources while foraging.	(2)
	Prediction 4.2: Flexibility can be increased and such an increase alters daily foraging breadth to **decrease the variety of food** items taken				Increasing behavioral flexibility potentially leads to increased use of the same type of food items across habitat types, rather than leading to sampling more food items within one habitat.	Behavioral flexibility facilitates the use of novel foods through sampling new foods and foraging strategies (Sol et al. 2002)
	Prediction 4.3: Flexibility can be increased but has **no effect** on foraging breadth				This suggests that the cognitive ability behavioral flexibility may not generalize to all domains (e.g. may relate to habitat use but not foraging breadth). Alternatively, it could indicate that they might have used flexibility in the past when originally forming the association, but the need to maintain flexibility in their repertoire is no longer necessary, or that changes induced by the increase in flexibility do not persist for sufficiently long times to make a difference on the subsequent likelihood of success.	(1) (3)

METHODS

Planned sample

We studied Florida scrub-jays in unfragmented, fire-maintained habitat at Archbold Biological Station (natural areas), as well as in the adjacent suburbs of Lake Placid, FL (human modified areas). Much of the study population at Archbold Biological Station was already individually identifiable with color leg bands. We caught an additional 24 jays using walk-in traps and mist nets; collected their biometric data, and a blood sample; applied colored leg bands; and released them at their point of capture. We collected data on pre- and post-manipulation success measures (foraging and habitat use, see below) and conducted the experiment within the non-breeding season to control for potential temporal differences in the environment and behavior. We planned to use radio tags to find jays for observing before and after manipulation success measures. However, Florida scrub-jays are highly territorial, and we were always able to find the jays to collect observational data without the radio tags.

To determine whether the flexibility manipulation has influenced the ability of jays to persist in human modified environments, we planned for half of the total sample of jays from areas with access to human-supplemented food (i.e. private property, university campus, parks adjacent to neighborhoods with feeders) and the other half from natural areas (wildlife management areas, reserves). To address Q1, testing for differences in baseline behavioral flexibility between jays in natural or human-modified environments, the power analysis (see Supplementary materials S1) showed a high likelihood of detecting differences with a minimum sample of 15. We were able to quantify baseline behavioral flexibility in 14 Florida scrub-jays (8 in natural areas, 6 in human-modified areas).

To address Q3 and Q4, we tracked baseline behavior and changes after the flexibility manipulation via all-occurrence sampling during focal observations (Altmann, 1974) that last for 60 min. During observations, we documented all occurrences of microhabitats used within the territory and foraging behavior (see Observational methods, below). Our planned minimum sample size was 20 individuals per species with a minimum of 4 observations per individual (at least 2 per month) pre-manipulation and a minimum of 4 per individual (at least 2 per month) post-manipulation (at least 320 observations in total). We were only able to conduct the serial reversal manipulation on 9 color-banded individuals, but we met or exceeded the minimum sample size for observations before and after the manipulation. There was one exception where an individual disappeared after the manipulation and was not found during extensive searching of the territory and surrounding areas and so was presumed dead. We only collected one-third of the necessary post-manipulation data on this individual.

Observational methods

During observations, we recorded each microhabitat the individual is present in and all food items consumed. Before data analysis, to ensure that we were only including the microhabitats individuals use (rather than just pass through), we filtered the data to include only microhabitats that account for at least 5% of their data points. Although we may not observe every possible microhabitat or food item the individual may use, by equally sampling before and after the manipulation we can detect changes in habitat use. We counterbalanced observations across the morning and afternoon for all individuals in the study. In this way, we collected a random sample of data from active and inactive time periods for all individuals.

Microhabitat types in the suburban habitat (<100m from human structure) included: vertical human structure (e.g. building, bench), native vegetation, non-native vegetation, grass, impervious surface, and dirt. In the natural habitat (>100m from human structure), microhabitat types included all previous categories, but not human structure or impervious surface. All categories were further defined by whether the subject was high (>3m) or low (<3m). For example, grass and impervious surfaces can occur above 3m if grass is on the roof of a building, and if an individual is walking on the impervious surface of an upper floor parking garage.

Food types were broken down into plant (seed, fruit, human-provided, or unknown plant) and animal (insect larva, adult insect, amphibian, crustacean, reptile, mammal, bird, egg, human-provided, or unknown animal). "Human-provided" indicates any food item that was acquired from a store at some point and is left out by humans. For example, sunflower seeds would be considered human-provided if they are in the form of bird seed or a human snack. Sunflower seeds would only be counted in the "seed" category if the bird is seen eating it from a plant.

Additionally, for all observations we used binoculars so that we could remain far enough from the focal individual that our presence was not affecting their behavior. Because that distance can be different for each individual and species, we hesitate to give a specific number. However, if at any point the focal individual showed that it was affected by our presence, by looking directly at the researcher, alarm calling or startling, then we ended the observation immediately, dropped all data from that observation session and attempted the observation again the next day.

Flexibility manipulation (Design 2 from the registered report)

Our approach involved individual jays participating in a serial reversal learning task in the wild. We set up remote-controlled feeders at multiple study sites, each containing several jay territories, spaced at least 2km apart: 2 sites in natural habitat, 2 in human-modified habitat.

Feeder habituation

One feeder at each location contained food and the experimenter used the remote to feed the focal individual every time it approached. Habituation consisted of 2-hour sessions between 8a-3p on a minimum of 4 consecutive days or until at least 1 banded jay per territory had visited the feeder at least 3 times without showing fear behaviors.

The experiment

Prior to the flexibility manipulation, we collected the 4 minimum observation sessions to determine the baseline values for microhabitat use and foraging breadth. Afterwards, we set up the remote-controlled feeders to initiate the serial reversal learning flexibility manipulation phase. All feeders contained one type of high value food (i.e., peanuts). In addition, feeders were opaque and always had food in them to eliminate a confound with performance due to olfactory differences between the feeders that could be introduced if only the rewarded feeders had food in them. If a feeder needed to be refilled, we refilled all feeders consecutively in the same time period and for the same amount of time even if that feeder did not need much or any food (in these cases, we pretended to fill the feeder). This eliminated potential confounds in jay performance from cues provided by a differential amount of experimenter attention given to the feeders during refilling.

At the beginning of serial reversal learning, one of the two feeders, at a consistent location (north or south, east or west) within the territory, was randomly selected to dispense food when the focal jay approached. If the subject visited the non-rewarded feeder, this incorrect choice was recorded, but the feeder did not open. Reversal sessions for the manipulation treatment consisted of 30-120 min sessions per day per territory, up to 4 days per week. Each visit by the focal jay to the correct or incorrect feeder was considered a trial. Jays passed a given reversal when they correctly chose the rewarded feeder in at least 10 trials out of the most recent 12 trials (see S1 of the supplementary materials for details on the simulations that determined that threshold). After passing one reversal, we switched to rewarding jays at the other feeder location. Serial reversals continued until jays passed two consecutive reversals in 12 trials or less (see S2 of the supplementary materials for details on the simulations that determined that threshold). At this criterion, the jays were considered to have increased their behavioral flexibility.

After the manipulation was complete for the focal individual, we again conducted the all-occurrences focal observation sessions to measure microhabitat use and foraging breadth. We began collecting post-manipulation data on an individual as soon as it passed the manipulation because it is unknown for how long any potential effects of the manipulation will last.

For more social species, like the Florida scrub-jay, who may experience the experiment in groups, there is the potential that individuals who were not in the manipulation condition or who have not yet passed the manipulation condition will learn about post-manipulation success behaviors from the manipulated individuals who passed the experiment. We are ultimately interested in determining whether we can change success behaviors of threatened populations or species as a result of the flexibility manipulation. If part of this change is the result of social learning from some of the manipulated individuals, it will still result in a change even if we do not quantify what percentage of the mechanism comes from individual learning as a result of the manipulation or social learning after the manipulation. If there is a change in success measures between before and after the manipulation, the manipulation will have been the cause in either case.

Open data

The data will be published in the Knowledge Network for Biocomplexity's data repository.

Protocols

- Jay protocol and data sheet templates
- Protocol for applying radio tags and conducting GPS tracks from McCune KB et al. (2020)
- Jay processing protocol

Analysis plan

We run analyses in R [current version 4.5.0; R Core Team (2017)] using the following R packages: rethinking (McElreath, 2020a), rstan (Stan Development Team, 2020), cmdstanr (Gabry & Češnovar, 2022), knitr (Xie, 2018), and irr (Gamer et al., 2012). We describe below the Bayesian models we developed to address each of the specific research questions. All Bayesian models were developed using McElreath (2020b) as a guide. Code for running these models is available in supplementary materials S4.

J.Q1 Do jay populations in human modified areas differ in baseline behavioral flexibility compared to populations in natural areas?

The model

We used the reversal learning Bayesian model in Logan CJ et al. (2020) to simulate and analyze population differences in reversal learning, and calculate our ability to detect differences between populations. The model "accounts for every choice made in the reversal learning experiment and updates the probability of choosing either option after the choice was made depending on whether that choice contained a food reward or not. It does this by updating three main components for each choice: an attraction score, a learning rate (ϕ), and a rate of deviating from learned attractions (λ)" (Logan CJ et al., 2020).

Equation 1 (attraction and ϕ): $A_{i,j,t+1} = (1-\phi_j)A_{i,j,t} + \phi_j \pi_{i,j,t}$

Equation 1 "tells us how attractions to different behavioral options $A_{i,j,t+1}$ (i.e., how preferable option i is to the bird j at time $t+1$) change over time as a function of previous attractions $A_{i,j,t}$ and recently experienced payoffs $\pi_{i,j,t}$ (i.e., whether they received a reward in a given trial or not). Attraction scores thus reflect the accumulated learning history up to this point. The (bird-specific) parameter ϕ_j describes the weight of recent experience. The higher the value of ϕ_j, the faster the bird updates their attraction. It thus can be interpreted as the *learning or updating rate of an individual*. A value of $\phi_j = 0.04$, for example, means that receiving a single reward for one of the two options will shift preferences by 0.02 from initial 0.5-0.5 attractions, a value of $\phi_j = 0.06$ will shift preferences by 0.03 and so on" (Blaisdell et al., 2021).

Equation 2 (λ): $P(i)_{t+1} = \frac{\exp(\lambda_j A_{i,j,t})}{\sum_{m=1}^{2} \exp(\lambda_j A_{m,j,t})}$.

Equation 2 "expresses the probability an individual j chooses option i in the next round, $t+1$, based on the latent attractions. The parameter λ_j represents the *rate of deviating from learned attractions* of an individual (also called inverse temperature). It controls how sensitive choices are to differences in attraction scores. As λ_j gets larger, choices become more deterministic, as it gets smaller, choices become more exploratory (random choice if $\lambda_j = 0$). For instance, if an individual has a 0.6-0.4 preference for option A, a value of

$\lambda_j = 3$ means they choose A 65% of the time, a value of $\lambda_j = 10$ means they choose A 88% of the time and a value of $\lambda_j = 0.5$ means they choose A only 53% of the time" (Blaisdell et al., 2021).

We used the c values as the response variable in the Bayesian model to examine whether there were differences in flexibility between the habitats:

y ~ α[habitat]

y is the response variable (ϕ_j and λ_j, which are extracted from the correct and incorrect choices in the serial reversals). There is one intercept, α, per habitat (suburban or natural) and we will estimate the habitat's average and standard deviation of the response variable.

J.Q2 Are disturbance-resiliant jays more flexible than disturbance-resistant jays?

We were not able to collect data on disturbance-resilient species within the timeframe of this study and the funding of our grant. However, we were able to conduct an *unregistered analysis* testing for differences in behavior between disturbance-resilient Florida scrub-jay individuals persisting in human-modified areas and conspecifics in natural habitat lacking human disturbance.

The model

We used poisson regression to assess whether jays in human-modified areas foraged on more kinds of foods and used more substrate types relative to jays in natural areas. Models were not overdispersed or heteroscedastic.

J.Q3 More flexible = use more microhabitats?

The model

Bayesian model with a normal distribution:

habitatuse ~ α[ind] + β[ind]*before

habitatuse is the response variable: the total number of different microhabitats used per individual. There was one intercept, α, and one slope β per individual, which was estimated for the two conditions, before (and after) the manipulation. ID is nested within condition as a random effect because there was more than one data point per individual: each individual has a data point in the before condition and in the after condition. A normal distribution was used because the response variable is a sum without an expected skew to the curve (see Figure 10.6 in McElreath, 2020b).

J.Q4 More flexible = more food types?

The model

Bayesian model with a normal distribution:

y ~ α[ind] + β[ind]*before

y is the response variable: the total number of different food types taken per individual. There will be one intercept, α, and one slope β per individual, which will be estimated for the two conditions, before (and after) the manipulation. ID is nested within condition as a random effect because there is more than one data point per individual: each individual has a data point in the before condition and in the after condition. A normal distribution was used because the response variable is a sum without an expected skew to the curve (see Figure 10.6 in McElreath, 2020b).

RESULTS

Very few Florida scrub-jay were found in human-modified areas at our study site in Lake Placid, FL. Across two years we collected focal observations and baseline behavioral flexibility on 6 individuals in these human-modified areas and 8 jays in natural areas at Archbold Biological Station. A smaller subset of 9 jays (all 8 jays in the areas and 1 from the human-modified areas) received the serial research learning flexibility manipulation because it was not feasible to conduct this longer experiment on more jays within the constraints of our field season.

J.Q1 Do jay populations in human modified areas differ in baseline behavioral flexibility compared to populations in natural areas?

There was no difference in baseline behavioral flexibility performance between jays in suburban or natural areas. This was true when we considered either of the two behavioral flexibility components, ϕ_j, the rate of learning the newly rewarded option (β = -0.23, sd = 1.27, CI = -2.22 - 1.4, $p > 0.05$), or λ_j, the rate of deviation from previously rewarded options (β = -0.01, sd = 0.18, CI = -0.28 - 0.28, $p > 0.05$).

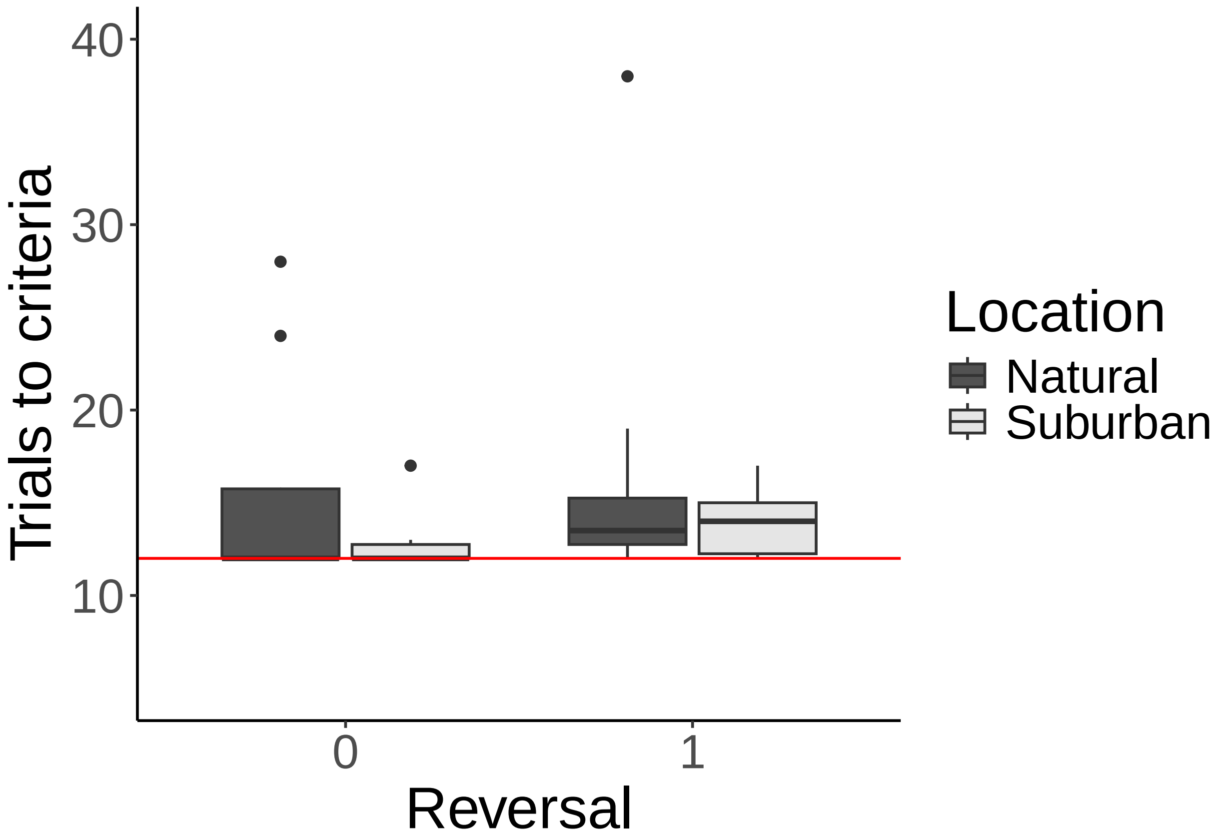


Figure 3: Before the flexibility training, jays in the suburban and natural habitats performed exceptionally well on the baseline behavioral flexibility task and did not differ in ability. These boxplots show the performance as the number of trials to reach the passing criterion on baseline associative learning (Reversal 0) and behavioral flexibility (Reversal 1) for jays in the natural (dark grey) and human modified (light grey) areas. We use trials to pass, rather than or in this plot for more interpretable illustration of the speed of performance on this task. The horizontal red line illustrates the minimum number of trials to pass criteria (10 out of the most recent 12 trials correct).

J.Q2 Are disturbance-resilient jays more flexible than disturbance-resistant jays?

We were not able to test this question within the timeframe and funding of the grant. However, we conducted an unregistered analysis using Poisson models to compare foraging and habitat use behavior of Florida scrub-jays in human modified areas to those in natural areas. In other words, within this disturbance sensitive species, a subset of individuals were resilient to disturbance, at least during the timeline of this study. The disturbance-resilient individuals in the suburbs were not more diverse foragers ($\beta = 0.26 \pm 0.19$, $p = 0.15$), but did use a greater variety of microhabitats ($\beta = 0.52 \pm 0.16$, $p = 0.001$) compared to the jays in undisturbed, natural habitat at Archbold Biological Station.

J.Q3 More flexible = use more microhabitats?

Even though all jays increased the speed with which they switched their preference in the serial reversal learning training, there was no effect on subsequent habitat use diversity (before relative to after log-odds difference = -0.06, CI = -0.41 - 0.30, $p > 0.05$; Fig. 4).

J.Q4 More flexible = more food types?

Similarly, after the serial reversal flexibility training, jays were not more likely to eat a greater diversity of food types ($\beta = 0.26$, CI = -0.45 - 0.96, $p > 0.05$; Fig. 4).

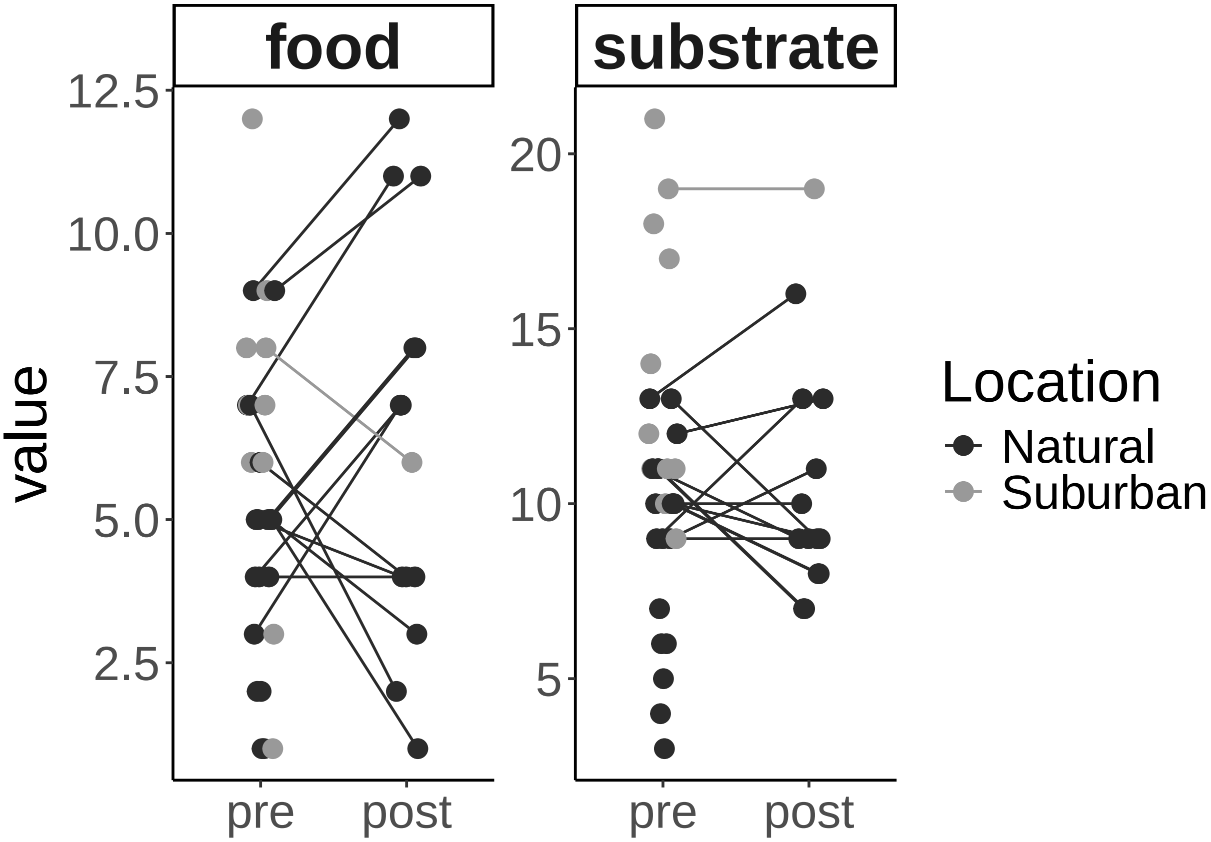


Figure 4: Jays did not predictably change their foraging or microhabitat use behaviors after they underwent the flexibility training manipulation. Values indicate the number of different foods or substrates jays were observed to use during the all-occurrences focal observation session before (pre) and after (post) we conducted serial reversal learning to increase behavioral flexibility. Each dot represents a jay and lines

connect the dots of jays with data both pre and post. We collected pre observations on some jays for which we were not able to conduct the flexibility training and so we did not need to collect post observations.

DISCUSSION

Anthropogenic change is creating unpredictable heterogeneity in the environment that requires some level of fast, adaptable learning in wildlife populations. In some species, the general cognitive trait, behavioral flexibility, is thought to underlie the ability to cope with rapid changes in human-modified environments (Sol et al., 2002; Vardi & Berger-Tal, 2022). Our previous work in the great-tailed grackle supported this hypothesis because grackles that were trained to be more flexible foraged on more diverse food and used more distinct behaviors to forage in the wild (Logan et al., 2025). The grackle is an urban-adapted generalist species that has demonstrated adaptability to environmental change through a rapid range expansion (Wehtje, 2003). We tested whether the same training to increase behavioral flexibility in a threatened species, the Florida scrub-jay (FLSJ), would lead to more adaptable foraging and habitat use behaviors in the wild. However, we found no effect of the behavioral flexibility training in this species.

Unlike great-tailed grackles, FLSJ populations have rapidly declined coincident with anthropogenic change and there is little evidence for adaptation to human-modified environments. Yet, for many species, suburban environments can also provide significantly more foraging opportunities through the provision of novel foods, ornamental plants or agricultural activities that increase survival and reproductive success. For example, use of food at bird feeders has been linked to population growth and range expansions (Greig et al., 2017; Veech et al., 2011). One such species is the California scrub-jay, a congener to the FLSJ, that similarly prefers xeric scrub-oak habitat along the west coast of the United States. In contrast to the FLSJ, this species has been able to adapt to persist in highly developed areas (e.g., Los Angeles, CA) and expand its range north, while taking advantage of bird feeders (Curry et al., 2017).

In our population of FLSJ, a small population does persist in suburban areas. Anecdotally, homeowners report frequently seeing these individuals at their backyard bird feeders or other human-provided food sources. We compared foraging and habitat use of these individuals to FLSJ in pristine, unfragmented and fire-maintained scrub habitat at Archbold Biological Station. Jays in both habitat types foraged on equally diverse food items, but suburban jays used more distinct kinds of microhabitats (substrate type and height) relative to the jays at Archbold. In other words, suburban jays did not completely restrict their habitat use to the small remnant fragments of undeveloped scrub in the suburbs. This demonstrates that FLSJ are capable of adapting their habitat use behavior to include novel, human-modified environments. However, when we compared baseline behavioral flexibility between the two jay populations, suburban jays were not more behaviorally flexible than Archbold jays. Consequently, it is likely that behavioral flexibility, as we measured it through spatial reversal learning, does not underlie adaptation to human-disturbance in this species.

This was supported by our finding of no change in foraging and habitat use behavior after undergoing behavioral flexibility training. Our results support our Prediction 1 alternative 1; all jays improved their reversal learning speed to meet the criterion, indicating they had increased their behavioral flexibility. But there was no consistent trend in the change in food item or microhabitat diversity measured before and after the training. There are a few potential explanations for why the training worked in great-tailed grackles but led to no behavior change in FLSJ. First, it is possible that the serial reversal learning task and passing criterion were too easy for FLSJ and so the training did not lead to a large enough change in flexibility to be seen in resulting behavior. We determined the criteria for when an individual was considered to have passed a given reversal from simulations using the performance of captive great-tailed grackles in color cue reversal in the previous experiment (supplementary material S1). While the criterion to pass in the previous study was 17 correct out of the 20 most recent trials, simulations indicated we could detect a significant change in preference for the newly rewarded option after 10 correct choices out of the most recent 12 trials. Half of the jays reached this criterion in 12 or 13 trials (average = 15.6, range = 12 - 38) which is almost as fast as possible (Fig. 3). FLSJ have excellent spatial memory because they are dependent on cached food for survival and reproductive success (Beauchamp et al., 2025). Consequently, the spatial cue was likely easier to learn than a color cue. Testing individuals in the wild can also impact performance (K. B. McCune et al., 2019) to yield the faster reversal speeds relative to the captive grackles. In support of this, a new study on grackles in the wild is more comparable to the FLSJ results because they used the same passing criterion. Preliminary evidence shows wild grackles are slower than FLSJ to pass the first reversal (n = 8, average = 33 trials, range = 13 - 50; Logan 2026, pers comm), though the range overlaps significantly with FLSJ. Moreover, in a previous study of color reversal learning, captive FLSJ required amount of time (3 days) to pass the reversal (Bebus et al., 2016). Together, this suggests that the spatial cue, rather than testing context, led to the fast performance of jays on reversal learning.

Another potential reason we failed to see a change in natural behavior after the flexibility training is that jays were already using the majority of foods and substrates available. Due to time constraints, size and accessibility of the suburban population, the majority of jays (8 out of 9 total) that underwent the flexibility training were from Archbold Biological Station where the scrub-oak habitat is maintained at high quality and mid-successional state through prescribed fire and other management techniques. Thus, this habitat is far more homogenous than jays experience in the suburban areas. Consequently, it is possible that there was no opportunity for flexibility training to alter the foods or microhabitats used by these jays. However, this is unlikely to be a large confound because the suburban and Archbold jays did not differ in the number of different food items they ate before training and the one jay from the suburban area that we were able to train, also did not show a change in the variety of substrates used and showed a slight decrease in the diversity of food items used after the training (Fig. 4, single grey line).

To better understand the role of behavior in adaptation or resilience to human disturbance, ongoing and future work in FLSJ will evaluate variation in other relevant behavioral traits like boldness, foraging role (producer-scrounger dynamics), exploration and movement behavior (Snell-Rood & Steck, 2019). The ManyIndividuals registered report also creates a versatile structure for testing behavioral flexibility in other species or systems. Although we were unable to test disturbance resilient jay species within the timeline of our current funding, we hope the research we present here will provide guidance and motivation for other investigators to address this question. As humans accelerate the frequency and degree of environmental change, experimental interventions such as this, that train species in behaviors that facilitate resilience, may become increasingly important.

ETHICS

This research is carried out in accordance with permits from the: **1.** US Fish and Wildlife Service (scientific collecting permit number ES824723). **2.** US Geological Survey Bird Banding Laboratory (federal bird banding permit number 07732). **3.** Institutional Animal Care and Use Committee (University of California Santa Barbara protocol number 958 and Auburn University protocol number 2022-5132).

AUTHOR CONTRIBUTIONS

McCune: Hypothesis development, data collection, data analysis and interpretation, write up, revising/editing.

Barve: Interpretation, revising/editing, materials/funding

FUNDING

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CONFLICT OF INTEREST DISCLOSURE

We, the authors, declare that we have no financial conflicts of interest with the content of this article.

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We are grateful to our funders: Richard McElreath at the Max Planck Institute for Evolutionary Anthropology (whole project), as well as Corina Logan and Dieter Lukas for assistance with analyses and coding. In addition, we are grateful for the ManyIndividuals co-founders, Drs. Corina Logan and Rachel Shaw. We are thankful for the input and assistance of Dr. Reed Bowman when designing the Florida scrub-jay data collection.

SUPPLEMENTARY MATERIALS

S1 - Determining when to switch each individual to the next reversal: reversal passing criterion

Different criteria exist to decide whether an individual has learned an association between the presence of a reward and some other feature (e.g., color or shape). The two main two criteria used are to switch an individual after it either has chosen 10 out of 12 choices correct (e.g., Shaw et al., 2015) or 17 out of 20 choices correct (e.g., C. J. Logan, 2016). The criteria are further modified depending on whether choices are assessed continuously or grouped in predetermined blocks.

Here, we assess whether achieving 10 correct choices out of the last 12 continuously counted choices can be used as a reliable reversal passing criterion. To determine reliability and suitability, we investigated five questions (see below) by generalizing previously simulated reversal learning data from Logan CJ et al. (2020), based on data from great-tailed grackles. We simulated the choices individuals with different learning rates (phi) and rates of deviating from learned associations (lambda) would make in the initial discrimination and in the first reversal. Grackles are fast to reverse preferences compared with many other species (C. J. Logan, 2016), therefore we generalized the simulations to other species by setting the parameters that guide performance (phi and lambda) to lead to slower performances.

The findings from these simulated data indicate that deciding that an individual has passed the reversal when they choose 10 out of the last 12 consecutive trials correctly is functional and reliable because of the following:

1) individuals will be finished after fewer trials than with other criteria

With the 10 out of 12 criterion, individuals pass the reversal 8 trials faster (median) than with the 17 out of 20 criterion. This means that, for most individuals, the two rules are equally effective because they will pass both in the same amount of trials (i.e., the individual who met the 17/20 criterion in 50 trials would have met the 10/12 criterion in 42 trials), but because the 10 out of 12 criterion is restricted to 12 trials instead of 20, individuals need 8 fewer trials to meet the passing criterion. No individual needs more trials with the 10 out of 12 criterion. When trials are grouped into blocks of 10 such that they could only pass on trial 20, 30, etc., individuals need a median of 5 more trials compared to when choices are assessed continuously.

2) classification of individuals using the 10/12 criterion is less noisy because there is less of a chance for individuals to approach the criterion and not pass or never pass

The average improvement in the number of trials individuals need to reach the respective criterion is larger than the median of 8 trials. This occurs because there are no individuals who are faster with the 17 out of 20 criterion, and because there is a subset of individuals who need considerably fewer trials with the 10/12 criterion (Figure 7). Individuals who require a larger number of trials (>100) to pass almost never occur with the 10/12 criterion, whereas they are more common with the 17/20. With more trials, there is a higher chance that an individual will deviate from their preference by chance. This is also reflected in that 65 of the 626 simulated individuals never reached the 17/20 criterion within the maximum 300 trials, whereas there were only 4 individuals with the 10/12 criterion. Accordingly, an additional benefit of choosing the 10/12 criterion is that it is more likely that data for all individuals, even those who are slow to learn an association, can be collected.

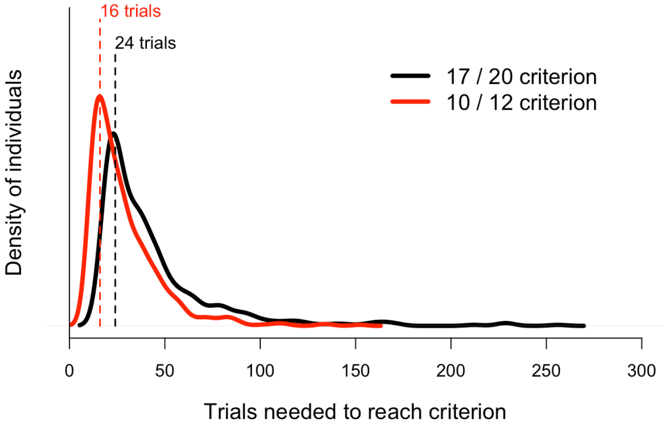

Figure S1. There is less variation with the 10/12 reversal learning passing criterion and it requires fewer trials to reach than the 17/20 passing criterion. The lines represent the densities of individuals (estimated with smoothing which means values can go down to zero) across the 626 simulated individuals that needed a certain number of trials to either reach the 10/12 (red) or the 17/20 (black) criterion. With the 10/12 criterion, most individuals need 8 fewer trials (indicated by the lines showing the mode of the two density distributions). In addition, there are only very few individuals who need 100 or more trials with the 10/12 criterion, while there are several individuals that needed such large numbers with the 17/20 criterion.

3) variation among individuals with the 10/12 criterion is still present and similar to the variation detected with other criteria

As described in point 1, when changing the criterion from 17/20 to 10/12, most individuals need 8 fewer trials. This also means that the differences among individuals, which might contain relevant information about variation among them, is preserved. When transforming performance with the two criteria to ranks, individuals are sorted essentially in the same order independent of which criterion is used. This is shown in Figure 7: most points are shifted up by exactly 8 trials.

4) individuals can be assumed to have reliably learned the association using the 10/12 criterion

Based on the two reversal passing criteria (10/12 and 17/20), we can extract the attractions that simulated individuals have formed toward both the rewarded and the unrewarded option at the point at which they meet each of these criteria. Comparing the two attractions (to the rewarded and unrewarded options), we can determine whether individuals are likely to have learned an association or not. Independent of the criterion, individuals generally formed a preference for the rewarded option: 89% of individuals favor the rewarded option between 2.5 and 14 times more than the unrewarded option. With both criteria, individuals always have a stronger attraction to the rewarded than the unrewarded option. The smallest difference between the attraction scores to the rewarded and unrewarded options we observe at the point of passing is the same with both criteria. With the 10/12 criterion, individuals would in the next trial, on average, choose the rewarded option with a probability of 76% (3 times more likely to choose rewarded over unrewarded option), whereas this is 84% with the 17/20 criterion (5 times more likely).

5) the learned association means that individuals who move to the next reversal are unlikely to solve the reversed association by chance

As expected, based on the relative attraction scores at the end of the previous reversal, most individuals are unlikely to choose the now rewarded option. We expect that, on average, individuals will choose the newly rewarded option in 4 or fewer trials out of the first 12 trials (red line in Figure 8). This is a lower number of trials compared to individuals who have no association with either option (gray line in Figure 8), and a slightly higher number compared to individuals who use the 17/20 criterion (black line in Figure 8). The probability that an individual would, after a reversal, immediately choose the rewarded option 10 times during the first 12 trials (and pass) by chance is 0.001. However, even such rare individuals will have actually reversed their preference during their first 12 trials because they update their attractions on every trial.

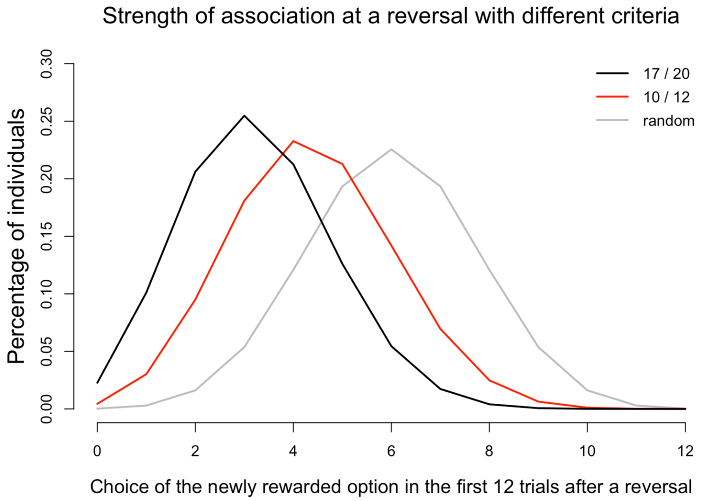

Figure S2. Individuals form strong enough preferences using the 10/12 passing criterion as indicated by the fact that they are unlikely to pass in the first 12 trials of their next reversal (red line). These individuals would take longer to switch their preference than individuals who have no preference (gray line), and they would be slightly faster at switching their preference than individuals who formed their previous association using the 17/20 criterion (black line).

S2 - Determining after which reversal an individual has completed the experiment: serial reversal passing criterion

Data from previous serial reversal experiments suggests that individuals who go through multiple reversals will end up with a performance that is similar to the individuals who needed the fewest trials on the first reversal (Logan et al., 2022; Lucon-Xiccato & Bisazza, 2014). This suggests that the manipulation changes individuals within their natural range of variation rather than pushing them to new limits. This means that we can use the performance of the fastest individuals in the first reversal to set the criterion for passing the serial reversal experiment. Accordingly, we can only set the serial reversal passing criterion after the data from the first reversal begins to become available. Some species might already have data from previous studies on reversal learning, however it is important to set the passing criterion for this experiment using this particular setup. Therefore, the criterion must be established from scratch for each species using this setup.

The serial reversal passing criterion: reach the reversal passing criterion (10 out of 12 trials correct) in X trials or fewer in two consecutive reversals.

X = the number of trials required that marks the fastest 20% of individuals in the first reversal. For example, if you test 20 individuals, the number of trials for the 4th fastest individual will be the criterion. For 10 individuals, use the number of trials for the 2nd fastest individual. The fastest 20% was validated using the grackle data (Logan et al., 2022): it aligns with the one sigma rule from a normal distribution, indicating the percentage of individuals who are faster than the mean number of trials minus one standard deviation. If more than 20% of individuals reach this number of trials in their first reversal (because there might be a tie), choose the next fastest number of trials to pass. Particularly near the beginning of the experiment, it will be important to set the passing criterion to a lower number to ensure that individuals will be overtrained rather than undertrained.

As the data for additional individuals becomes available, this number can change accordingly. If the number changes across the experiment, we will check whether any currently participating individuals would have already passed according to this criterion and end their experiment.

Individuals need to meet this criterion in two consecutive reversals to pass the serial reversal experiment to ensure that their behavior is consistent and that their speedy performance did not occur by chance. Previous serial reversal experiments show that reversal performance plateaus after a certain number of reversals (e.g., 6-8 reversals in great-tailed grackles Logan et al., 2022). If individuals show no consistent improvement after 12 reversals and have not yet met the serial reversal passing criterion, they will be excluded from the experiment. We will plan to start with many more individuals than the minimum sample size to allow for potential drop outs.

We do not expect that the serial reversal manipulation will introduce new negative effects because the passing criterion is set such that the manipulated individuals are only as fast as the fastest 20% of tested individuals. This means that we are not introducing an unnatural amount of flexibility because we are not making any individuals more flexible than what already exists in their population.

There will be individual variation in terms of baseline flexibility before the manipulation such that the flexibility training might influence individuals differently. For example, individuals who are already flexible before the manipulation will not benefit much from the manipulation, while the less flexible individuals will benefit more. Individuals who are already flexible and pass the serial reversals in fewer reversals will still meet the experiment's passing criterion and be considered to have completed the manipulation, even if they did not improve. Baseline flexibility differences could also be reflected in their pre-manipulation success measures (i.e., individuals with high baseline flexibility might already be successful before the manipulation) if these success measures relate to flexibility. Our statistical models account for these baseline individual differences in success as they might relate to performance on the flexibility manipulation because they include an interaction between the intercept (the value at which individuals start) and slope (by how much they change).

S3 - Planned Sample

For each population, depending on the response variable, we ran separate power analyses to determine the planned sample size (see Analysis Plan). For each population, we will aim to reach the minimum sample size required to detect the expected effects of the intervention on the response variables. However, given the difficulties of working with wild individuals, there might be instances where we might not reach a particular target. In such a case, we will interpret the result in light of the power that the particular sample size provides, as indicated by the power analyses. The minimum sample size depends on whether the intervention is performed as a within-subject design (higher power), measuring the response for the same individuals before and after the intervention, or whether it is performed as a between-subjects design, where half the individuals are randomly assigned to the intervention group. In addition, it will depend on whether the response variable has a binary or a continuous outcome (higher power), and in the latter case whether the measure is open-ended (lower power) and therefore individuals will show a large range of values (e.g., dispersal distance).

We will stop collecting data for the flexibility manipulation experiment when a buffer above the minimum sample size is reached or when the season in which the minimum sample size is reached comes to an end, or when the minimum sample sizes for the success measures have been reached. When conducting the manipulation experiment, it is important to aim to test more than the minimum number of individuals because some might not have data in the post-intervention stage.

S4 - Power analyses simulations and model code

We run analyses in R [current version 4.5.0; R Core Team (2017)] using the following R packages: rethinking (McElreath, 2020a), rstan (Stan Development Team, 2020), cmdstanr (Gabry & Češnovar, 2022), knitr (Xie, 2018), and irr (Gamer et al., 2012). We describe below the Bayesian models we developed to address each of the specific research questions. All Bayesian models were developed using McElreath (2020b) as a guide. Code for running these models is available in supplementary materials S4.

J.Q1 Do jay populations in human modified areas differ in baseline behavioral flexibility compared to populations in natural areas?

The model

We used the reversal learning Bayesian model in Logan CJ et al. (2020) to simulate and analyze population differences in reversal learning, and calculate our ability to detect differences between populations. The model "accounts for every choice made in the reversal learning experiment and updates the probability of choosing either option after the choice was made depending on whether that choice contained a food reward or not. It does this by updating three main components for each choice: an attraction score, a learning rate (ϕ), and a rate of deviating from learned attractions (λ)" (Logan CJ et al., 2020).

Equation 1 (attraction and ϕ): $A_{i,j,t+1} = (1-\phi_j)A_{i,j,t} + \phi_j \pi_{i,j,t}$

Equation 1 "tells us how attractions to different behavioral options $A_{i,j,t+1}$ (i.e., how preferable option i is to the bird j at time $t+1$) change over time as a function of previous attractions $A_{i,j,t}$ and recently experienced payoffs $\pi_{i,j,t}$ (i.e., whether they received a reward in a given trial or not). Attraction scores thus reflect the accumulated learning history up to this point. The (bird-specific) parameter ϕ_j describes the weight of recent experience. The higher the value of ϕ_j, the faster the bird updates their attraction. It thus can be interpreted as the *learning or updating rate of an individual.* A value of $\phi_j = 0.04$, for example, means that receiving a single reward for one of the two options will shift preferences by 0.02 from initial 0.5-0.5 attractions, a value of $\phi_j = 0.06$ will shift preferences by 0.03 and so on" (Blaisdell et al., 2021).

Equation 2 (λ): $P(i)_{t+1} = \frac{\exp(\lambda_j A_{i,j,t})}{\sum\limits_{m=1}^{2} \exp(\lambda_j A_{m,j,t})}$.

Equation 2 "expresses the probability an individual j chooses option i in the next round, $t+1$, based on the latent attractions. The parameter λ_j represents the *rate of deviating from learned attractions* of an individual (also called inverse temperature). It controls how sensitive choices are to differences in attraction scores. As λ_j gets larger, choices become more deterministic, as it gets smaller, choices become more exploratory (random choice if $\lambda_j = 0$). For instance, if an individual has a 0.6-0.4 preference for option A, a value of $\lambda_j = 3$ means they choose A 65% of the time, a value of $\lambda_j = 10$ means they choose A 88% of the time and a value of $\lambda_j = 0.5$ means they choose A only 53% of the time" (Blaisdell et al., 2021).

We used the ϕ_j and λ_j values as the response variable in the Bayesian model to examine whether there were differences in flexibility between the habitats:

y ~ α[habitat]

y is the response variable (ϕ_j and λ_j, which are extracted from the correct and incorrect choices in the serial reversals). There is one intercept, α, per habitat (suburban or natural) and we will estimate the habitat's average and standard deviation of the response variable.

Power analysis

Simulations using bespoke Bayesian models in Logan CJ et al. (2020) (the same model structure we use here) showed a high likelihood of detecting differences with a minimum sample size of 15 when mean differences in phi were at least 0.01 and mean differences in lambda at least 3.

Run this model on the actual data

Run the code below to determine whether there were differences between the two habitats in their phi and lambda flexibility measures.

J.Q2 Are disturbance-resiliant jays more flexible than disturbance-resistant jays? The model

Same as in J.Q1 above.

Power analysis

Same as in J.Q1 above.

J.Q3 More flexible = use more microhabitats? The model

Bayesian model with a normal distribution:

habitatuse ~ α[ind] + β[ind]*before

habitatuse is the response variable: the total number of different microhabitats used per individual. There will be one intercept, α, and one slope β per individual, which will be estimated for the two conditions, before (and after) the manipulation. ID is nested within condition as a random effect because there is more than one data point per individual: each individual has a data point in the before condition and in the after condition. A normal distribution was used because the response variable is a sum without an expected skew to the curve (see Figure 10.6 in McElreath, 2020b). The Bayesian model was developed using McElreath (2020b) as a guide.

Power analysis

We estimated our power to detect differences between conditions at different sample sizes and with different mean changes in the proportion of different microhabitats used per individual in the before vs. after conditions (Figure 11). We simulated the proportion of habitats used for different sample sizes of individuals before and after the flexibility manipulation. We analyzed these simulated data with the model we will use to analyze the actual data, estimating the change in the proportion of habitats used between the before and after conditions. From the posterior estimates of the model, we extracted both the mean change as well as the ratio of the posterior estimates that were below zero.

If the mean ratio of estimates below zero is close to 0.5, the model assumes that the change in the proportion of habitats used before the flexibility manipulation is similar to after. If the ratio is close to zero, the model assumes individuals have changed their behavior. For changes in the proportion of habitats used smaller than 0.15 (standard deviation=0.2) or 0.1 (SD=0.1), models are likely to assume that no changes occurred even with large sample sizes. If the change in the proportion of habitats used before the flexibility manipulation vs. after is 0.15 with a standard deviation of 0.2, on average 94% of the posterior of the model based on a sample size of 20 individuals will be larger than zero (93% with a standard deviation of 0.1). This means that the model is quite certain there is a difference that is larger than zero. In addition, only four of the 30 models for a sample size of 20 at the mean change of 0.15 have a ratio larger than 0.3, meaning that the risk of having a false negative is not very likely.

In general, with sample sizes at or above 20 and mean changes in the proportion of habitats used at 0.1 or larger, it is highly likely that the model will indicate that individuals have changed their behavior. Mean changes below 0.1 can still be detected, however there is a higher risk that there will be a false negative and this risk is independent of sample size.

With small mean changes in the response variable, some individuals might not increase or even decrease their response after the manipulation because there is variation around the mean change in individual responses. With small sample sizes, there is a risk that only individuals who did not clearly increase their response will be studied, whereas larger sample sizes are more likely to include a wider spectrum of individuals.

To estimate the risk of detecting false positives, we set the mean change in the proportion of habitats used to zero so there was no change between the before and after conditions. As expected, the average ratio of estimates below zero is close to but below 0.5 and independent of sample size. The estimates went generally below 0.5 because the maximum number of habitats used was set to 10 and we had a condition where individuals before the manipulation used a mean of 7 habitats. Accordingly, if individuals randomly either increase or decrease their number of habitats used, decreases will be more severe because individuals can only increase by 3 habitats, but potentially decrease by 6 habitats. With a sample size of 20, 27% have a ratio smaller than 0.3, meaning that the risk of having a false positive is high. The risk would be lower if the variation among individuals was lower than what we assumed (the standard deviation of the mean change in number of habitats was 0.2, which is a conservative estimate).

Figure 11. Risk of false positives and false negatives depending on sample and effect sizes. Curves of the mean ratio of estimates below zero (vertical lines show the minimum and maximum ratios), which illustrates the power we have to detect differences between conditions at different sample sizes. Across all models, the standard deviation of the mean change in proportion of habitats used was 0.2 (A) or 0.1 (B). A mean change in proportion of habitats of 0.3 is associated with a difference of 3 habitats (when the maximum number of habitats is 10). The curves show the model estimates as the effect increases (larger changes in the mean proportion time spent after versus before on the x-axis) for different potential sample sizes (10-60, illustrated by different colors). When there is no change (x value of zero), estimates suggest that, as expected, half of the estimates are below zero because the before and after conditions are not different from each other. As the change increases, the estimates decrease because models are able to reliably tell that the before and after conditions differ from each other.

Run this model on the actual data

Run the code below to determine whether there were differences between the before and after conditions in the proportion of microhabitats used. Only count that a microhabitat was used if the individual had at least 5% of their data points there. This prevents a microhabitat from being counted even if an individual was simply moving through it, and therefore not necessarily using it.

J.Q4 More flexible = more food types? The model

Bayesian model with a normal distribution:

y ~ α[ind] + β[ind]*before

y is the response variable: the total number of different food types taken per individual. There will be one intercept, α, and one slope β per individual, which will be estimated for the two conditions, before (and after) the manipulation. ID is nested within condition as a random effect because there is more than one data point per individual: each individual has a data point in the before condition and in the after condition. A normal distribution was used because the response variable is a sum without an expected skew to the curve (see Figure 10.6 in McElreath, 2020b). The Bayesian model was developed using McElreath (2020b) as a guide.

Power analysis

We estimated our power to detect differences between conditions at different sample sizes and with different mean changes in the total number of different food types taken per individual in the before vs. after conditions (Figure 12). We simulated the number of food types taken for different sample sizes of individuals before and after the flexibility manipulation. We analyzed these simulated data with the model we will use to analyze the actual data, estimating the change in the number of food types taken between the before and after conditions. From the posterior estimates of the model, we extracted both the mean change as well as the ratio of the posterior estimates that were below zero.

If the mean ratio of estimates below zero is close to 0.5, the model assumes that the change in the number of food types taken before the flexibility manipulation is similar to after. If the ratio is close to zero, the model assumes individuals have changed their behavior. For changes in the number of food types taken smaller than 1, models are likely to assume that no changes occurred even with large sample sizes. If the change in the number of food types taken before the flexibility manipulation vs. after is 1 with a standard deviation of 2, on average 99.96% of the posterior of the model based on a sample size of 20 individuals will be larger than zero. This means that the model is quite certain there is a difference that is larger than zero. In addition, none of the 30 models for a sample size of 20 at the mean change of 1 have a ratio larger than 0.3, meaning that the risk of having a false negative is not very likely.

In general, with sample sizes at or above 20 and mean changes in the number of food types taken at 1 or larger, it is likely that the model will indicate that individuals have changed their behavior. Mean changes below 1 can still be detected, however there is a higher risk that there will be a false negative and this risk is independent of sample size. For example, 17% of the models for a sample size of 20 at the mean change of 0.5 have a ratio larger than 0.3, meaning there is a risk of having a false negative.

With small mean changes in the response variable, some individuals might not increase or even decrease their response after the manipulation because there is variation around the mean change in individual responses. With small sample sizes, there is a risk that only individuals who did not clearly increase their response will be studied, whereas larger sample sizes are more likely to include a wider spectrum of individuals.

To estimate the risk of detecting false positives, we set the mean change in the number of food types taken to zero so there was no change between the before and after conditions. As expected, the average ratio of estimates below zero is close to 0.5 and independent of sample size. With a sample size of 20, 30% have a ratio smaller than 0.3, meaning that the risk of having a false positive is high. The risk would be lower if the variation among individuals was lower than what we assumed (the standard deviation of the mean change in number of foods was 2, which is a conservative estimate).

Figure 12. Risk of false positives and false negatives depending on sample and effect sizes. Curves of the mean ratio of estimates below zero (vertical lines show the minimum and maximum ratios), which illustrates the power we have to detect differences between conditions at different sample sizes. Across all models, the standard deviation of the mean change in number of food types taken was 2 (A) or 1 (B), and the number of food types taken before the flexibility manipulation was 6.5. A mean change in proportion of habitats of 0.3 is associated with a difference of 3 habitats (when the maximum number of habitats is 10). The curves show the model estimates as the effect increases (larger changes in the mean proportion time spent after versus before on the x-axis) for different potential sample sizes (10-60, illustrated by different colors). When there is no change (x value of zero), estimates suggest that, as expected, half of the estimates are below zero because the before and after conditions are not different from each other. As the change increases, the estimates decrease because models are able to reliably tell that the before and after conditions differ from each other.

Run this model on the actual data

Run the code to determine whether there were differences between the before and after conditions in the number of food types taken.

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