Decision-making in the wild: Urgency and complexity drive feeding decision speed and the likelihood of revising a choice in a sex-dependent manner in great tit (*Parus major*) parents

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Abstract

Deciding which offspring to feed is one of the most critical decisions parents make for both parental and offspring fitness. Despite knowing much about what choices parents make, we know little about how parents choose. What we do know about how the brain integrates sensory evidence when choosing between options comes from laboratory studies and models. However, such studies may not adequately reflect decisions made in nature—with real-world complexity and consequences. Our naturalistic experiment on decision-making in 62 wild *Parus major* parents addresses this issue. Decision speed was impacted by whether parents chose to feed a typically-preferred chick or not, offspring starvation risk, decision complexity, and parental sex. Parents regularly moved food between chicks before committing, suggesting that parents perhaps were not confident in their initial decision, had made a mistake, were continuing to collect evidence, or could not execute their initial decision. Such decision changes were predicted by similar factors as speed. After moving food, parents were more likely to continue gathering evidence post-decision, and their next decision was slower. These results demonstrate several factors impacting cognition, and perhaps metacognition, in wild birds. More broadly, our study demonstrates how crucial evolutionarily relevant experiments in natural settings are.

Introduction

Although some organisms are born, hatch, bud or sprout fully self-sufficient and independent, the young of many species require extended periods of post-natal care to survive (Royle et al. 2012). During this dependent juvenile period, parents must decide how to allocate limited food amongst their offspring. If parents choose which offspring to feed optimally, they maximize the number and quality of surviving progeny (Clutton-Brock 1991; Stearns 1992; Royle et al. 2012). If they choose poorly, they risk losing young to starvation who could have survived, overfeeding chicks that will not benefit from additional food, or underfeeding high quality chicks who would have thrived if given more food (McCleery et al. 2004; Bize et al. 2006; Caro et al. 2016; Li et al. 2019; Brode et al. 2021). Obviously, these decisions also determine offspring fitness: being chosen to be fed is literally a matter of life and death. Despite knowing much about what choices parents make and the selection pressures causing parents to prefer to feed certain offspring (Kilner and Johnstone 1997; Davis et al. 1999; Lessells 2002; Koykka and Wild 2018; Brode et al. 2021), we know little about *how* parents arrive at those decisions.

Most insights into how parents likely make these crucial feeding decisions comes from laboratory studies on cognition (thinking) and metacognition (thinking about thinking) in neuroscience, psychology and neuroeconomics (Gold and Shadlen 2007; Serra 2021). According to this literature, individuals make decisions by accumulating sensory evidence such as which offspring is begging most, until enough evidence in favor of one option has accumulated, causing individuals to reach a decision threshold and execute an action (i.e. feed offspring A, termed drift diffusion, fig. 1) (Ratcliff 1978; Liu and Pleskac 2011; Bitzer et al. 2014; Ratcliff et al. 2016). Work in humans has also investigated the role of metacognition: top-down control or evaluation of the cognitive process. For instance, individuals can shift their decision thresholds to prioritize either accurate or fast decisions, or to favor one option *a priori* (fig. 1) (Bogacz et al. 2006; Chittka et al. 2009; Heitz 2014; Katsimpokis et al. 2020). Decision thresholds may also be shifted by how urgently individuals need to make a choice or how severe the consequences of making a mistake are (Cisek et al. 2009; Standage et al. 2011; Thura et al. 2012; Malhotra et al. 2017; Katsimpokis et al. 2020). Regarding metacognitive evaluation, individuals vary in confidence, which depends on the quality of sensory evidence and post-decision error monitoring (Kepecs et al. 2008, 2008; Pleskac and Busemeyer 2010; Fleming et al. 2012; Yeung and Summerfield 2012; Fetsch et al. 2014; Balsdon et al. 2021; Lee et al. 2023). In humans, confidence also controls the process of future evidence accumulation: lower confidence can cause individuals to spend more time accumulating evidence in subsequent decisions (Desender et al. 2019*a*, 2019*b*). Finally, humans sometimes remake decisions. These change-of-minds are associated with several aspects of metacognition, including verbal assessments of confidence, error detection, uncertainty about evidence, slow initial decisions, and continued evidence accumulation after making a decision (Fleming 2016, 2024; Stone et al. 2022).

Translating insights from humans and from the lab to how wild animals make decisions in nature is not straightforward. The extent of metacognition in nonhuman animals is contentious, especially outside of primates, dolphins, corvids and parrots (Smith et al. 2014; Arbilly and Lotem 2017; Baciadonna et al. 2021; Białek 2023). Research on animal minds runs the dual risk of anthropomorphism—attributing too much complexity to animals—and anthropodenialism—attributing too little (de Waal 1999). For example, in humans, confidence is easy to define and measure based on verbal reports; in nonhuman animals confidence has largely been ignored due to difficulties measuring it (Shadlen and Kiani 2013; Desender et al. 2019*b*, 2021). You cannot simply ask a macaque how it feels. Furthermore, while laboratory studies have been invaluable in uncovering much of how the brain and neurons function, few studies have examined how well insights from the laboratory hold up when they are faced with the greater complexity of the real world (table 1). Laboratory experiments are frequently divorced from evolutionary contexts and lack evolutionarily relevant consequences. Although decisions are often made in a social context, laboratory experiments have largely ignored the effects of other individuals on the process. Perhaps most importantly, decisions in laboratory studies are often necessarily controlled. Individuals typically choose quickly between just two options that vary in just one parameter. This is not how most decisions happen. Taking parental decision-making as an example: in the real world, parents regularly have to choose between many rather than two options; options vary simultaneously across numerous parameters and sensory modalities; decisions can take seconds or even minutes; offspring may seize control of or manipulate parents' decisions through scramble competition; and making the correct decision consistently determines whether your offspring live or die. Finally, although there have been advances on wild animal cognition, especially regarding foraging (e.g. Bateson 2002; Liker and Bókony 2009; Hollis et al. 2011; Beardsworth et al. 2021; Harrington et al. 2024), there has been a relative paucity of studies on the cognitive process of, rather than just the outcome of, animal decisions in nature (Rosati et al. 2022; Szabo et al. 2022). Such studies are needed to identify the various factors shaping wild decision making. Accounting for the greater complexity and consequences of decisions made in their appropriate evolutionary contexts may shift our understanding of how parents decide which offspring to feed, and of the mechanisms of decision-making more generally.

In the present study, we examined what factors influence parental feeding decision processes in a natural population of wild great tits (*Parus major*) by analyzing the time until a decision was reached (i.e., decision speed or latency, the time it takes for a parent to execute an action after exposure to the chick stimuli), the likelihood of changing one's choice, and the likelihood of gathering additional post-decision evidence. Great tit parents bring invertebrates back to the nest to feed their chicks for the first three weeks after hatching, typically one invertebrate at a time, making approximately 30 feeding visits per hour. Parents choose a chick to feed based on offspring behavior, begging signals and size. Parental feeding in birds provides a behavioral experimental system that is particularly tractable for research on decision-making in naturalistic settings. In many avian species, feedings are repeated, discrete, quantifiable, always occur at the same place in the nest, allow for interactions amongst all family members, and can be experimentally manipulated. We filmed these wild birds in their own nests to maintain the ecologically relevant context as much as possible (fig. 2).

Birds may "change their minds" by moving food items after giving them to an initial chick for several reasons: 1) they may be revising a decision due to uncertainty or a lack of confidence in pre-or post-decision evidence (Fleming 2016; Atiya et al. 2020; Stone et al. 2022); 2) they may be removing food from chicks who did not swallow fast enough, which could be considered an error in judging how ready for food the initial chick was (Zeng et al. 2023); 3) they may be removing too-large prey, which could be considered an error in judging whether the prey will fit in the mouth of the initial chick; or 4) they may be reacting to a constraint imposed by the chick that disrupts the execution of their decision. Our moving-food measure therefore parallels human cognitive neuroscience studies on confidence and error detection, with the added possibility of constrained decisions (Fleming 2016, 2024; Stone et al. 2022). While there is no single "correct" choice or "error" on any given feeding visit, prior research has shown that great tits prefer feeding larger offspring, closer offspring and offspring that are begging more, a preference that increases as ecological conditions become harsher (Cotton et al. 1999; Caro et al. 2016; Caro et al. 2025*a*).

In our population of great tits, larger, higher quality offspring are more likely to be recruited to the breeding population (Tinbergen and Boerlijst 1990; Visser and Verboven 1999).

Here, we manipulated the urgency of decisions by supplementing half of the parents in our population with additional food, greatly lowering the risk of offspring starvation. While changes to decision speed on the order of a few seconds may not seem to have obvious fitness consequences, these changes in decision efficiency could also lead to differences in how much food is brought back to the nest overall, potentially leading to the starvation of marginal offspring (Magrath 1990; Theofanellis et al. 2008; Wild et al. 2017). These changes could also impact how accurately parents choose which chick to feed, potentially leading to the starvation of chicks that could have survived or to investment in already doomed chicks if parents make too many errors. We also investigated how changing one's mind and decision speed are intertwined via decision path analyses. Taken together, our study addresses what effects, if any, decision context (complexity and urgency) and decision outcome (whether parents ultimately fed a chick with their preferred begging, size and/or proximity rank) have on cognition and metacognition in wild birds. Our study provides insights into whether the more serious consequences of decision-making in the real world reveal the role of urgency in decision-making, whether all individuals make decisions in the same way, how confidence, error detection and speed intersect in cognition; and what information is salient during parental decision-making.

Methods

Study area and species

Great tits (*Parus major*) are a passerine bird species common across Eurasia. We studied a wild long-term nest box population living in a mixed pine-deciduous forest covering approximately 75 ha in The Netherlands (5°85'E, 52°01'N, in the Great Warnsborn Estate, (Serrano-Davies et al. 2023). From March through June 2017, we monitored 130 nest boxes, and were able to include 34 broods in our study. We checked nest boxes every other day to determine the onset of egg laying and clutch size. We began visiting nests daily the day before hatching was expected to determine hatch date (day 0), brood size and post-hatching mortality rates. Study broods hatched within a 9-day period.

Great tits lay clutches of multiple eggs, and provision their nestlings with invertebrates for approximately three weeks after hatching. Both parents feed many times per hour, usually bringing back one prey item. On each of these nest visits, parents must choose which of their offspring to feed while being confronted with a complex set of information, including offspring begging signals, size differences, and spatial proximity. Nestling starvation is common in this species—across all broods, 11% of chicks (33 of 302 chicks) died in the first week after hatching, most likely of starvation.

Environmental urgency treatment

To create varying levels of urgency, we simulated variation in ecological conditions by experimentally manipulating food availability. We installed a small feeding tray inside each nest box, and gave extra food to parents in an alternating pattern: half of the broods received supplemental food, while the other half experienced natural conditions for the week after hatching (supplemental food represented approximately 20% of the daily needs of the brood, see Supplemental Methods for details; van Balen 1973; Eeva et al. 2009). Nests in both treatments were visited daily, to standardize the disruption from opening up the nest box. Our supplementation treatment was effective in improving environmental conditions: 82% of urgency treatment (unsupplemented) broods experienced chick starvation in the first week after hatching, compared to only 41% of non-urgency treatment (food supplemented) broods ($z = 2.94$, $p = 0.0033$**; $n = 34$ broods). There was no supplemental food given on filming day, and parents from both treatments experienced standardized stimulus broods on filming day.

Decision-making assay procedures: Cross-fostering, hand-feeding, and filming

We created cross-fostered broods for parents in order to standardize the stimuli parents received when choosing which chick to feed. These broods ensured parents interacted with a constant number of nestlings of comparable begging intensity, similar size asymmetry between the largest and smallest nestlings, and similar behavioral backgrounds. On day 8 after hatching, we cross-fostered chicks and used an infrared camera on the ceiling of the nest box to film parents interacting with these foster broods for either 4 hours or until each parent had fed at least 20 times, whichever came sooner (see Supplemental Methods for details, fig. S1). Chicks remained in their foster broods until fledging.

To ensure that all parents were choosing from the same number of options, we standardized brood size to 7 chicks (27 broods) or 6 chicks (4 broods, where a same-aged 7^{th} chick was not available for cross-fostering). To ensure that differences in the behavior of unsupplemented and supplemented chicks did not constrain parental decisions, we created mixed filming broods: approximately half of the chicks in each filming brood were from supplemented broods, and the other half of the chicks were from unsupplemented broods. To ensure that differences in the behavior of chicks of different weight ranks did not constrain parent decisions, we ranked chicks by weight in their biological broods. The heaviest chick was assigned to filming brood A, and the second heaviest to filming brood B, the third heaviest to brood A, etc. This pattern alternated by nest. This ensured an even distribution of weights in filming broods. Finally, to ensure that there would be sufficient variation in begging intensity for parents to use this information when making decisions, and to ensure initial begging intensity would vary independently across weight ranks, we hand-fed half of the chicks in each filming brood to satiation, in an alternating pattern by weight rank in the filming brood. This ensured that not all chicks begged maximally during filming and that not all small chicks begged at highest intensity the whole time.

These experimental manipulations ensured that all parents experienced equivalent stimuli for feeding decisions, even under mostly natural conditions. Great tits were filmed in their own nest boxes, at the same time of day, feeding broods of an equivalent size, feeding chicks with equivalent begging behavior and size disparities, comprising unrelated supplemented and unsupplemented chicks, half of which were satiated when the filming began. Parents were not filmed interacting with their own offspring, to control for familiarity effects. See Videos S1, S2 and S3 for examples of what these feedings visits look like.

Video scoring

Videos were scored by one of two blinded observers. The order in which the observers scored the videos was random with respect to environmental urgency treatment. We painted all chicks with a dot of red, non-toxic acrylic paint on the head (Kate Lessells, pers. comm.) just prior to filming, so that we could individually identify chicks in the videos. Observers scored 76 feeding visits per nest on average. The mean number of visits scored per female bird was 36, and per male was 40. Parental sex was determined by the difference in crown feather glossiness of males and females, and confirmed by nest cleaning behavior, which only females perform (Christe et al. 1996). For each feeding visit, the observer recorded decision speed, whether the parent moved food between chicks before committing to a feed, prey size, the sex of parent, the identity of the fed chick, the begging intensity of all chicks, the identities of all begging chicks, and how close the fed chick was to parents.

A total of 1508 feeding visits had complete data and were included in analyses. Figure S2 contains a river plot showing the decision path during feeding visits, including whether the parent moved food or not, whether they ultimately fed the closest chick or not, and whether they ultimately fed a chick begging as much or more than its nestmates.

Decision-making speed, confidence and error detection

We measured parent's decision-making speed as the time in seconds between when a parent entered the nest box and when they deposited the prey item in the mouth of the chick who was ultimately fed. Since parents cannot see chicks when they are outside of the nest box, this measure captures the time from the onset of the stimulus (chick begging and size) to the executed action (feeding a chick). If the parents placed the prey item in one chick's mouth before moving it to another chick, the decision speed is the time it was placed in the final chosen chick's mouth. Most decisions were made quickly (median = 2 seconds, mean = 4 seconds, range = 0 - 62 seconds).

We measured parent's confidence and/or error detection in their decisions as whether or not the parent changed their mind before their final decision (Video S2). In other words, if they placed the prey item in one chick's mouth before moving it to another chick, compared to only ever placing the prey item in the ultimately fed (chosen) chick's mouth. We recorded this as a 2-level factor: mind changed or not. We also recorded how many times a parent "probed" chicks—after feeding a chick, parents sometimes dip their now empty beak into the mouth of one or more additional chicks (21% of feeding visits, n = 404 visits in 1907 visits). This probing may represent parents gathering additional evidence about chick need or condition, for example testing how much chicks pull on the parents' beak (Diego Gil, pers. comm.).

As speed, confidence and error detection may be intertwined, we analyzed speed and changes-of-mind in two ways. First, through standard GLMMs. Secondly, through path analyses (piecewise Structural Equation Modeling) that allow changes-of-mind to affect speed. We also examined a second set of models on decision speed to test the effect confidence and/or error detection may have on subsequent evidence gathering during future decisions.

Begging

We recorded whether the fed (chosen) chick was begging at least as much or more than its nestmates or not. Begging intensity was coded on a standard scale, following Hinde 2009, adapted from Kilner (1995): 0 = non-gaping, 1 = gaping with a bent neck, 2 = gaping with neck stretched out, 3 = gaping with raised body (Kilner 1995; Hinde et al. 2009). We quantified relative begging intensity by dividing the begging posture of each chick by the mean posture of all begging chicks on that feeding visit. This relative measure accounts for differences in overall begging intensity on different feeding visits, which could confound measures of food distribution based on absolute begging intensity (Hinde et al. 2009). Because parents almost always chose to feed a chick begging the most (95% of the time), we converted this variable to a 2-level factor: fed chick begging the most or not. We also recorded the number of chicks begging per feeding visit, to account for how many options parents were deciding amongst and for the overall demands of the brood. The total number of begging chicks varied from 1 (only 1 chick begging when parent arrives) to 7 (all chicks begging when parent arrives).

Chick size rank

We recorded the weight rank of the fed (chosen) chick. We ranked chicks by weight (mass in grams) in their filming brood, with chick 1 being the heaviest and chick 7 being the lightest. Using weight rank as opposed to absolute weight makes broods more directly comparable—parents may always prefer feeding the largest chick, whether the largest chick weighs 12g or 10g.

Proximity rank

We recorded how close the fed (chosen) chick was to parents, to account for chick influences on parental decisions. The chick closest to the parent was ranked 1, the chick second closest was ranked 2, etc. Offspring can attempt to seize control of feeding through scramble competition where they compete for the spot closest to their parent (Van Heezik and Seddon 1996; Cotton et al. 1999; Royle et al. 2002). Parents can accede to the outcome of scramble competition, or they can use it as another cue of competitive ability, like size (Royle et al. 2002; Wild et al. 2017). This variable may capture i) chicks' hijacking parental decisions; ii) the cue of the outcome of chick scramble competition; iii) a physical constraint on decision speed (if by necessity it takes longer to reach over chicks to feed far away chicks); iv) or some combination of these.

Prey size

Provisioning larger prey items may take more time as handling them is more difficult and mouth size limitations make it more challenging to feed them to offspring. We therefore controlled for the effect of prey size (small, medium or large) on decision speed and changes-of-mind. Parents were more likely to bring back larger prey items earlier in the day ($t = -13.6$, $p < 0.0001$***), and males brought back larger prey ($t = 2.3$, $p = 0.031$*), controlling for nest and parental ID. There was no interaction between prey size and the size of the fed chick.

Offspring mortality risk

We recorded offspring mortality every other day for the first week after hatching, again on day 14, and finally on day 21 when chicks should have fledged. We only included instances of mortality where a subset of the brood died, as these deaths are more likely due to offspring starvation rather than predation or brood abandonment. Mortality risk at the nest level was measured by whether the nest had experienced any brood reduction, i.e. the starvation of one or more chick.

Statistical analyses

We analyzed decision-making speed using a generalized linear mixed model with a Poisson distribution and a bobyqa optimizer, using the glmer function from the lme4 package in R (Bates et al. 2015; R Core Team 2023). We analyzed changes-of-mind using a mixed logistic regression (glmer function with a binomial distribution and a bobyqa optimizer). We scaled and centered all fixed effects before analysis (Cohen et al. 2003; Dalal and Zickar 2011). We created figures using ggplot2 (Wickham 2016). We calculated repeatability through intraclass correlation coefficients using the icc function in the performance package (Lüdecke et al. 2021).We included fed chick begging intensity, fed chick size rank, fed chick proximity rank, urgency treatment, parent sex, and prey size in all our models. We controlled for the random effects of Parent ID and Nest ID. Because our decision-making speed data was over-dispersed, and because glmer does not support a Quasi-Poisson distribution with random effects, we adjusted the coefficients, Z scores and p values to account for the dispersion factor, following Bolker 2023, so as not to inflate our false positive rate. We estimated p-values using the lmerTest package, which uses Satterthwaite's degrees of freedom method (Kuznetsova et al. 2017). We used backwards elimination to select final models: a maximum model with all possible two-way interactions was run, and interactions were sequentially removed if a likelihood ratio test was not significant. We did not remove any main effects from the final models because they were planned *a priori*. As a robustness check, we compared AIC values for the final speed model with interaction terms (AIC = 7084) and without interactions (AIC = 7093), which supported the inclusion of the interactions. For changes-of-mind, AIC values also supported the inclusion of interactions in the final model (AIC = 1558 vs AIC = 1574). We investigated the impact of collinearity on our model using variance inflation factors (VIF), and found that all factors for all models had a VIF score of <3, indicating low correlation between each factor with other factors (Adam Petrie 2016; James et al. 2021). Table S1 shows a model with main effects only. We also investigate the main effects only of our factors with no interactions through structural equation modeling.

We analyzed the intersection of changes-of-mind and speed using structural equation modeling (SEM), also known as path analysis, using both the lavaan and piecewiseSEM packages in R (Rosseel 2012; Lefcheck 2016). We did this because the act of moving food from one chick's mouth to that of another mouth necessarily takes time, and thus decisions where food is moved cannot be as fast as decisions where the food is not moved. Structural equation modelling allows variables to function as both predictors and responses. Our path models included the same variables as the GLMMs, with some slight changes. Specifically, because PiecewiseSEM was originally derived to consider only continuous variables, it does not deal well with categorical variables, although it can incorporate them as dummy numerical values (Lefcheck 2024). We therefore used the numerical variable fed chick begging rank, as opposed to the categorical variable of fed chick begging the most or not. For changes-of-mind, we used the numerical variable number of chicks tested before final decision, as opposed to the categorical variable of food moved or not. As there was no continuous alternative for supplementation treatment and parent sex, these were coded as dummy numerical variables. Additionally, SEM is not fully appropriate for analyzing interactions and so these were not modeled (Lefcheck 2024). The PiecewiseSEM models had a Poisson distribution and controlled for the random effect of parent ID. However, they were unable to converge when including the over-dispersion random effect, and so this was removed. Models were compared using AIC values. These path analyses are informative but should be interpreted with care, as our data structure was not fully appropriate for this kind of analysis (Lefcheck 2024). We found some support for composite latent variables of urgency and which decision was made arising from our measured variables, and since we assume other factors may contribute to these variables, we treat them as latent variables with error in our models (Lefcheck 2024).

We analyzed the effect of confidence and/or error detection on future decisions and evidence gathering in two ways. We measured whether parents spent more time making their next decision if the prior decision had been changed or not. In other words, if a parent moved food between chicks before actually feeding one, did they spend more time making a choice during the next nest visit? We also assessed if changes-of-mind affected whether parents continued gathering evidence during that same visit after executing their decision, measured by the number of probes parents made into different chicks' mouths after the food had already been consumed by the fed chick. These analyses were conducted on a subset of the data (n = 1433 feeding visits) because we did not have previous change-of-mind measures for all visits.

We excluded feeding visits where the parent obscured the camera's view of the feeding to the extent where no data could be observed for three or more chicks, or where the feeding itself was too obscured to pinpoint which chick was fed, when a chick was chosen, or missing data on our fixed effects. We excluded visits where parents brought multiple prey items. Finally, we excluded one visit where the male brings a prey item to an already brooding female who transfers it to a chick, as this visit differs fundamentally from the other feeding visits. This resulted in a dataset of 1508 unique feeding visits from 32 broods, with data from 32 individual females and 30 individual males.

We analyzed offspring mortality at the nest level using generalized linear models in R (lme4) with a binomial distribution (n = 32 broods). We recorded whether a nest had experienced the starvation at least one offspring and whether the nest had received supplemental food or not. We calculated the mean decision speed of the parents for each nest. We analyzed effects on mortality before and after cross-fostering separately, because parents were interacting with different nestlings before and after cross-fostering, and because parents only received supplemental food before cross-fostering. We compared mortality before day 8 to decision speed of the natal parents, and mortality after day 8 to the decision speed of the foster parents. We analyzed mortality at the nest level rather than parent level to avoid pseudoreplication. For models after day 8, we controlled for any change in brood size that occurred with cross-fostering.

Ethics Statement

Permission to do fieldwork in the Boslust forest was granted by ‘Stichting Geldersch Landschap en Kasteelen’. Permission for animal experiments was granted by Central Authority for Scientific Procedures on Animals (CCD) of The Netherlands under project number AVD-801002017831 to KVO.

Results

Decision speed depends on the number of begging chicks, which chick is chosen, parental sex and urgency

We first asked how quickly great tit parents made feeding decisions in general. Overall, parents decided which chick to feed on each nest visit very quickly (median = 2 seconds, mean = 4 seconds, n = 1508 feeding visits, table 1, Video S1). There was, however, considerable variation in decision-making speed, with some feeding visits taking more than a minute before parents finally chose a chick to feed. The mean number of total nest visits per hour was 31.3 ± 1.7 SE, with males visiting 17.6 ± 1.2 SE per hour and females visiting 15.7 ± 0.8 SE per hour. Parents preferred feeding begging chicks, large chicks, and close chicks. Parents fed a chick begging the most 95% of the time. Parents fed the largest chick 15% of the time, compared to the smallest chick just 9% of the time. Parents feed the nearest chick 57% of the time.

How long it takes great tit parents to decide which chick to feed depends on several factors, including whether they ultimately fed a usually preferred (near, large, begging) chick or not, urgency (food supplementation treatment), the number of begging chicks and potential constraints (table 2, fig. 3). This variation occurred even though on filming day, all parents experienced equivalent stimuli for feeding decisions due to our cross-fostering manipulation. Decisions were faster when parents chose preferred chicks: when they fed larger chicks ($Z = 3.47$, $P = 0.0005$***), when the fed chick was nearer to the parent ($Z = 5.99$, $P < 0.0001$***), and when the fed chick was begging more than its nestmates ($Z = 2.99$, $P = 0.0028$**, fig. 3A). Decisions were slower when parents were feeding larger prey items ($Z= 5.19$, $P < 0.0001$***).

The number of chicks begging on a given visit affected decision speed. This variable may encapsulate both the demandingness of the brood (urgency) and the number of options parents had (complexity) on a given feeding visit. The more chicks were begging, the less decision speed changed based on the weight rank of the chosen chick (interaction Z = -3.49, P = 0.00048***, table 2, fig. 3B). When few chicks were begging, the longer it took parents to decide to feed smaller chicks compared to larger chicks.

We examined whether previously receiving supplemental food—which we considered a measure of urgency because it changed how likely chick starvation was—impacted parental decision speed, even after cross-fostering broods so that all parents were interacting with standardized broods of equivalent begging intensity and size on filming day. Supplemented parents, considered the low urgency treatment, made faster decisions than unsupplemented parents. Furthermore, high-urgency parents took an especially long time when deciding to feed chicks that were farther away, but low-urgency parents did not show this bias against feeding farther chicks (interaction Z = -2.48, P = 0.013*, table 2, fig. 3C).

Finally, the sexes differed in their decision speed. Females took longer to make decisions than males, especially when deciding to feed chicks who were farther away, while male decision speed was less affected by chick proximity (interaction Z = -2.64, P = 0.0084**, table 2, fig. 3D). Females took a mean of 4.6 +/- 0.5 SE seconds to make a decision, while males took 4.0 +/- 0.5 SE seconds. Individuals varied greatly in their mean decision speed, from less than 2 seconds to more than 10 seconds on average (the intraclass correlation coefficient for individual ID was = 0.27). Speeds within pairs were not significantly correlated (r = 0.31, P = 0.10, fig. 4). Some pairs showed extremely similar decision speeds (e.g. broods 207, 240, 300), while others did not (e.g. broods 216, 363, 373).

The likelihood of moving food between chicks varies with the proximity of the fed chick and parental sex

In 71% of feeding visits, great tit parents placed the food only in the mouth of the chosen chick. In the remaining 29% of feeding visits, parents placed a prey item in the mouth of one or more additional chicks before moving the food to final (chosen) chick's mouth (431 out of 1508 visits, Video S2). The likelihood of this refeeding behavior was affected by some but not all of the same factors as decision speed. Females were more likely to move food from one chick to another before making a final choice compared to males, especially when feeding a chick farther away ($Z = -2.14$, $P = 0.033$*, table 3, fig. 5B). When parents ultimately fed a chick that was farther away, the likelihood of having moved food around first was higher ($Z = 10.06$, $P < 0.0001$***, table 3). However, the more chicks were begging on a feeding visit, i.e. the more options parents had and the more demanding the brood was, the less refeeding was impacted by chick proximity (interaction $Z = -4.04$, $P < 0.0001$***, table 3, fig. 5A). This interaction may be due to structure in the data rather than a biological phenomenon: if only one or two chicks were begging, those chicks were almost never farther away than the 2nd closest chick. The intraclass correlation coefficient for individuals was 0.05. Although not significant, parents showed a trend towards being more likely to move food at least once when choosing to feed a chick that was begging less than its nestmates ($Z = 1.74$, $P = 0.08$, table 3, fig. S3). Finally, parents were more likely to move food when feeding larger prey items ($Z = 2.85$, $P = 0.0044$**). This is likely not due to trouble fitting larger prey items into smaller chicks' mouth, as there was no interaction between prey size and the size of the fed chick ($P = 0.65$) on the likelihood of moving food.

Finally, we investigated parental decision speed in the subset of our data representing the most common scenario: the parent fed the chick begging the most without having moved food between chicks ($n = 1030$ feeding visits, table 4). Here we found a sex-dependent impact of decision urgency (interaction $z = -2.18$, $P = 0.029$*). In the high urgency treatment, females make faster decisions than males. In the low urgency treatment, males make faster decisions. Parents made slower decisions when they chose to feed smaller chicks ($z = 8.98$, $P < 0.0001$***) and when fewer chicks begged ($z = 10.57$, $p < 0.0001$***). Notably, chick proximity rank did not impact decision speed in these feeding visits ($z = -0.081$, $P = 0.40$), while it did have an impact during visits where food was moved or where the parent fed a chick not begging the most (table 2).

Pathways of parental decision-making

Decision speed and changes-of-mind are intertwined (fig. 6). Decision speed comprises several stages: sensory evidence accumulation, the decision itself, and the execution of the decision. Decisions necessarily take longer if parents execute one decision, but then change their minds and restart this process. Decisions thus took longer when great tit parents moved prey items from one chick to another ($r = 0.42$, $P < 0.0001$***, mean decision speed with no mind changes = 2.65 seconds +/- 0.19 SE; with mind changes = 8.1 seconds +/- 0.30 SE, fig. S4). Thus, the act of moving food between chicks is one mechanism leading to longer decision speeds, although there is still considerable variation in decision speed after this is accounted for. To investigate this further, particularly to see if our measured variables have independent links to speed or only via moving food, we ran piecewise structural equation models, i.e. path analyses. We created composite latent variables for whether parents chose a preferred chick or not ("which decision made," comprising the begging, weight and proximity rank of the fed chick) and how urgent the decision was ("urgency of decision", comprising the supplementation treatment and the number of chicks begging during that feeding visit).

Our latent variable path analysis suggests a strong path from the urgency of the decision to which decision was made, followed by which decision was made strongly connecting to moving food, which then strongly connects to speed, with additional direct connections to speed (fig. 6). Essentially, the urgency of the decision (starvation likelihood, number of chicks begging); which decision was made (the beg rank, weight rank and proximity rank of the fed chick); prey size; and parent sex have direct and indirect impacts on both speed and changes-of-mind. The number of begging chicks and the proximity rank of the fed chick appear to be the most important of our measured variables (fig. 6). There is a strong indirect effect where moving food impacts speed. Since piecewiseSEM cannot accommodate paths between latent composite variables (Shipley and Douma 2021; Lefcheck 2024), we also analyzed pathway models without latent variables, but including the random effect of parent ID and using a Poisson distribution. The piecewiseSEM pathway most supported by our data was for both direct and indirect (via changes-of-mind) effects on decision speed (table S2, fig. S4). A model with only indirect effects on speed via changes-of-mind was worse than the model that also included direct effects (Δ AIC +287), indicating that speed is not solely determined by the extra time it takes parents to move prey from one chick to another. The worst model was one without any path between changes-of-mind and speed (Δ AIC +1,723), indicating that changes-of-mind do affect speed. Models with work-arounds for latent composite variables had higher AICs values, but these may not be directly comparable to the other models tested. Since piecewiseSEM models cannot easily accommodate categorical variables, interactions, or paths between latent composite variables, this analysis should be interpreted as a conceptual framework for how the parental brain achieves a feeding decision, rather than as a conclusive explanation.

Effects of moving food between chicks on future cognition

Moving food from one chick to another before making a final feeding decision had long-lasting effects on decision speed: when parents moved food, they took longer to make a decision during their next visit to the nest ($Z = 2.17$, $P = 0.030$*, table S3, fig. 7, $n = 1433$ feeding visits), controlling for the effects of all other variables, including offspring behavior and individual identity. The time between visits was, on average, 205 seconds for males and 229 seconds for females—this effect of confidence or error detection therefore persists over several minutes. We also analyzed this delayed confidence or error detection effect using piecewiseSEM to investigate how exactly changes-of-mind in decision 1 influenced speed decision 2. We compared AIC values for three pathway models: 1) without any direct effect of previous changes-of-mind on either current changes-of-mind or speed; 2) with a direct effect of previous changes-of-mind only on current changes-of-mind; and 3) with paths between previous changes-of-mind to both current changes-of-mind and current speed (fig. S6). The final model with direct paths between previous and current changes-of-mind and current speed was the best (Δ AIC -13 compared to a SEM with no previous changes-of-mind at all; Δ AIC -7.1 compared to a SEM with a path only between previous and current changes-of-mind).

Parents can also continue gathering evidence even after making a decision before they leave the nest to forage for more food (Video S3). They can do this by probing their beak into a chick's mouth without putting food into it; this behavior may allow parents to sense how much food is stored in a chick's crop, an indicator of how much additional food it needs, or assess some other aspect of chick condition. This differs from our measure of confidence and/or error detection because it occurs after food has been eaten and no food is transferred during these dips. After feeding a chick, parents probed other chicks 20% of the time by dipping their beaks into other chicks' mouths during the same nest visit (301 out of 1501 feeding visits). The likelihood that a parent probed chicks after it had already executed its feeding decision was predicted by whether parents had moved food between chicks before making a decision; if parents had moved food, they were more likely to keep probing chicks ($Z = 4.80$, $P < 0.0001$***, table S4). The more chicks were begging on the feeding visit, the more likely parents were to keep probing chicks after making a choice ($Z = 2.95$, $P = 0.0032$**). Parents that had made a faster decision, controlling for whether they had moved food, were also more likely to keep probing chicks after already having fed a chick ($Z = -3.73$, $P = 0.0002$***).

Potential fitness consequences of decision speed

Offspring mortality was common in our population of great tits. In the first week after hatching, 60% of broods experienced the death of at least one chick. In the two weeks between filming and fledging (i.e. day 8 to day 21), 44% of broods experienced the death of at least one chick. Prior to filming and cross-fostering (i.e. before day 8), our urgency treatment of food supplementation alone determined the risk of mortality (urgency treatment $Z = 2.09$, $P = 0.037$*, decision speed of natal parents $z = 0.04$, $P = 0.97$). After filming there was an interactive effect of prior supplementation and decision speed on subsequent mortality ($Z = 2.16$, $P = 0.031$*, fig. 8). Broods with parents that made slower decisions on average were more likely to experience offspring mortality in the two weeks following filming, if those parents had been in the high-urgency, unsupplemented treatment. The opposite pattern held in low-urgency, supplemented broods: slower decisions were associated with lower risks of future offspring mortality. Changes in brood size with cross-fostering did not affect the likelihood of mortality ($z = 0.03$, $P = 0.98$).

Discussion

In our naturalistic study of cognition and metacognition, we investigated how wild great tit parents choose which chick to feed at their own nest, while the urgency of the decision varied by whether the birds had experienced high or low risks of offspring starvation and while the seven chicks varied in size, begging signals and sibling competition. While laboratory studies rarely find an unambiguous effect of urgency, we found that urgency modulated decision thresholds, perhaps because parental feeding decisions have more direct impact on fitness than the mostly inconsequential decisions that are used in laboratory studies. Even after cross-fostering to ensure all parents interacted with equivalent stimuli (broods of a standardized size, begging intensity and size differences), we found that parents in our unsupplemented, high-urgency treatment prioritized accuracy over speed, perhaps because their errors can have larger impacts on both parental and offspring fitness. We also found that individuals made slower decisions when they ultimately fed a non-preferred chick, perhaps because they had to overcome an inhibition against feeding these chicks or because these instances were akin to “slow errors”. We found that the number of options parents had to choose between impacted both their likelihood of moving food and their speed while making a decision; unlike a typical study offering only two options, parents in our naturalistic study faced up to seven options at once that varied dynamically over the course of the feeding visit. We found that execution of real-world parenting decisions is influenced by physical constraints and partially hijacked by offspring, unlike in laboratory studies where subjects usually have complete control over their decisions and actions. We found that parents’ confidence in, detection of errors in, or constraints on their prior decisions shaped how long they spent accumulating evidence in their next decision. We found that individuals varied in how quickly they made decisions, and that females made slower decisions than males and were more likely to change their minds. Males and females may also react differently to changes in the likelihood of offspring starvation and decision complexity. We found these patterns using both GLMMs and SEMs, supporting the robustness of our findings. Finally, we also found evidence that parental decision speed may impact offspring mortality risk. These results, while not yet definitive, highlight new avenues for research on cognition and metacognition in wild animals.

Evolutionary consequences and decision processes

We manipulated biological urgency through treatments where offspring starvation was more or less likely, and thus where each feeding decision had more or less importance to both parental and offspring fitness. We found that urgency influences decision speed, and, to a lesser extent, the likelihood that a parent changes its mind at least once before feeding a chick. In neuroscience models, "urgency gating" comprises modifications of the evidence accumulation rate or of decision thresholds (Cisek et al. 2009; Standage et al. 2011; Thura et al. 2012; Malhotra et al. 2017; Katsimpokis et al. 2020; Kelly et al. 2021). Yet empirical evidence for urgency gating has been inconclusive, and evidence in support of urgency gating can also be explained by standard drift diffusion models (Ratcliff and Smith 2004; Hawkins et al. 2015; Evans et al. 2017). However, we found that the likelihood of offspring starvation—how urgent choosing the correct chick to feed is—shaped how quickly parents made decisions. Under high urgency conditions, parents made slower decisions, suggesting that their decision thresholds had shifted outwards (Katsimpokis et al. 2020). We found that parents made slower decisions and were more likely to change their minds when they ultimately chose to feed non-preferred chicks, again suggesting that decision thresholds may collapse over time as predicted by urgency theory (Cisek et al. 2009; Thura et al. 2012; Malhotra et al. 2017). Parents take longer to choose to feed chicks farther from them, especially when food abundance has been worse. This may indicate that parents from broods where chick starvation was common pay more attention to the outcome of offspring scramble competition than parents that had experienced more benign conditions – indicating that urgency may even shift what evidence they use when making decisions. We also found that the number of begging chicks impacted decision speed and the likelihood a parent moved food before finally feeding a chick. While we primarily used the number of begging chicks as a proxy for the number of options parents had, it may also function as an urgency signal: the more chicks demanding food, the greater the urgency surrounding that feeding decision.

Our findings strongly support a role for urgency signals in the brain. It is possible that urgency effects have rarely shown up in empirical laboratory studies because these studies do not generate urgency in an evolutionarily relevant way that actually impacts how the brain reaches a decision. (Juavinett et al. 2018; Sumner and Sumner 2020). Decisions in our study were literally life or death for offspring since 11% of chicks starved to death in the week before filming. Meanwhile, urgency in laboratory studies is generated by verbally cuing participants or imposing deadlines on decision-making, where the reward is a small amount of food or money. New systems-level insights into decision making likewise support a role for urgency as a top-down mediator of the decision process. For example, an fMRI study in humans found that urgency signals slowing decision-making were based in the caudate nucleus, while evidence accumulation appeared to be situated in the fusiform gyrus (Yau et al. 2020). EEG data likewise supports distinct roles for urgency and evidence accumulation (Yau et al. 2021). Thus, it is probable that the importance of urgency signals will become more apparent with experimental paradigms involving more ecologically relevant and consequential decisions in real-world settings, resulting in a better understanding of the various neural pathways involved in decision-making.

Offspring mortality risk may be affected by parental decision speed. Broods with parents that made slower decisions on average were more likely to experience offspring mortality in the weeks following filming, if those parents had been unsupplemented prior to filming. The opposite was true for parents that had been supplemented: slower decisions led to less offspring mortality. This interaction implies that even small variations in decision speed on the order of one or two seconds could lead to changes in fitness and that optimal decision-making strategies may depend on environmental conditions. Additionally, since post-filming broods consisted of a mix of chicks from supplemented and unsupplemented backgrounds, this effect on mortality is likely driven by differences in parental, not offspring, behavior.

We could not disentangle the effects of previous environmental quality compared to a change in the environment based on our experimental design. Since the treatment stopped after filming, parents from the supplemented treatment would have experienced a decrease in environmental quality since their extra food disappeared in the weeks between filming and fledging, while parents from the unsupplemented treatment would have experienced no change in their environment. We only found an effect of decision speed for offspring mortality after filming and cross-fostering, and not before. This may be because decision speed has different fitness effects at different development stages of a nestling's life. We measured decision speed at the developmental age when great tit offspring require the greatest amount of food, but when offspring are smaller and require less food, decision speed may not matter as much. Our results compare mortality across multiple weeks to decision speed on one day in the middle of the nestling period. Future studies could investigate whether and how decision speed changes over the nestling period, especially as environmental conditions vary and offspring get older.

Theoretical work on the efficiency of parent-offspring signaling has shown that greater decision efficiency can impact whether begging is stable and what information begging can convey (Wild et al. 2017). Faster decisions may allow parents to do more foraging each day. In our study, parents made 31 feeding decisions per hour on average, or a decision every 116 seconds per nest. Assuming parents forage for their brood 8 hours a day and all decisions took an additional three seconds, those three seconds per visit would reduce the total number of feeding visits possible per day from 248 to 242 visits. While the loss of 6 prey items may not seem like much, it approaches the median number of feeds each chick received during the 4 hours of filming (8 feeds, range 0 feeds to 26 feeds per individual chick per hour). If this lost efficiency continued for all 21 days of the nestling period, broods could experience a deficit of 126 prey, which could be the difference between life and death for an individual chick, especially one at the bottom of the feeding hierarchy. Clearly, the biological relevance of the magnitude of changes to decision speed and efficiency warrant further investigation.

Lasting cognitive effects of confidence and/or error detection

Finally, we also found that great tit parents adjust how they accumulate evidence based on their confidence or error detection in their prior decisions. After making a decision in which they changed their mind at least once, birds took longer to reach a decision on their subsequent visit. Furthermore, birds were more likely to continue collecting evidence (by probing their beaks into unchosen chicks' mouths) after making faster decisions where they had spent less time accumulating evidence before executing their choice. This aligns with previous work showing post-error slowing due to individuals shifting their decision threshold outwards or reducing how sensitive they are to sensory inputs (Purcell and Kiani 2016). This implies that parental decisions are not independent of past feeding decisions. Instead animals appear to be reacting to their history and perhaps employing a Bayesian reinforcement-based learning approach to making decisions where options vary in their prior probabilities, rather than simply accumulating sensory evidence for each "trial" (Hanks et al. 2011; Hanks and Summerfield 2017; Mendonça et al. 2020). In the real world, decisions are rarely completely independent of each other, and options rarely have identical prior probabilities of being correct.

Speed-accuracy tradeoffs in the real world

It has often been posited that animals face a tradeoff between speed and accuracy when making decisions; the more time individuals spend accumulating evidence, the more likely they are to choose the correct (or accurate) option (Bogacz et al. 2006; Chittka et al. 2009; Heitz 2014). This tradeoff has been well established through mathematical models, behavioral work in humans and even single-neuron studies in non-human primates (reviewed in (Chittka et al. 2009; Shadlen and Kiani 2013). Essentially, making the correct choice takes time. In our study, there was no correct or incorrect choice on a given feeding visit, but parents did have offspring they did and did not prefer feeding. Our work may therefore be relevant to considerations of speed-accuracy tradeoffs outside the lab, although we do not directly replicate the traditional experimental paradigm for these tradeoffs. For a parent bird, feeding the smallest runts, farther away chicks, and chicks begging less than their nestmates could be perceived as an "error", or as a considered choice in response to environmental decisions (Cotton et al. 1999; Caro et al. 2025*a*). We found that, contrary to what is expected under the speed-accuracy tradeoff framework, great tit parents took more time to make a choice against their typical preference. We also found that the number of options affected decision speed. When parents faced more options, the relationship between speed and decision outcome disappeared; assuming more options yields greater decision difficulty, this seemingly contradicts the inference that it may be hard to detect speed-accuracy tradeoffs for easy decisions (Chittka et al. 2009). Instead, when faced with hard decisions parents may shift to a random allocation strategy, rather than making an informed choice based on a preponderance of evidence, which would remove any speed-accuracy tradeoff (Teichroeb et al. 2023).

These findings enrich our understanding of a simple speed-accuracy tradeoff, and parallels other recent research done on non-humans that likewise did not find the expected pattern that individuals make fast errors and slow correct choices (Heitz et al. 2010; Fetsch et al. 2014; Moiron et al. 2016; Hanks and Summerfield 2017; Shevinsky and Reinagel 2019; Jones et al. 2020). Our findings could be due to the complexity great tit parents experience when making feeding decisions in the wild: they must choose amongst multiple options, varying across multiple parameters including visual (chick size) and auditory (begging calls) information, and stimuli may be constantly changing as offspring behavior changes (Teichroeb et al. 2023). Mathematical models of this tradeoff have typically considered only two options varying in only one dimension (Heitz 2014). New models addressing how more realistic non-binary choices impact speed-accuracy tradeoffs are necessary. Likewise, inconsistent evidence from multiple sensory modalities may disrupt that classical model (Miletić et al. 2021; Lee et al. 2023). Birds could have had to overcome inhibitions against feeding certain chicks, so that decision speed was impacted by the slower process of metacognition and not just sensory perception (Yeung and Summerfield 2012). Great tits could also have experienced collapsing decision thresholds due to urgency (Cisek et al. 2009; Thura et al. 2012; Katsimpokis et al. 2020). Here, the need to make a decision, any decision, increases as time goes on, leading parents to accept feeding non-preferred chicks after enough time had passed. Finally, it is possible that although great tits do not prefer feeding all of their offspring equally, no feeding choice is actually akin to an "error", since parents can gain fitness from any of their offspring surviving. Yet few social choices animals make in nature have definitive correct or incorrect alternatives. The lack of a definitive correct and incorrect choice may be the norm rather than the exception, and so investigations of decision speed should explore this conundrum. It is clear that the relationship between speed and accuracy is complex in the real world, and future studies should investigate how the speed-accuracy tradeoff is impacted by incoherent sensory evidence from multiple sources, more than two choices, and more urgency.

Individuality in decision-making

Individuals and the sexes differed in how quickly they made decisions and how likely they were to change their minds. This finding aligns with previous studies in non-human animals showing individual variation in speed-accuracy tradeoffs (e.g. great tits (Moiron et al. 2016), archer fish (Jones et al. 2020), zebrafish (Wang et al. 2015), cichlid fish (Wallace and Hofmann 2021), and bumblebees (Wang et al. 2018)). The study of "cognitive styles" in nonhumans, such as fast-deciders vs. slow-deciders and decisive vs. indecisive individuals, has grown in recent years, and has been linked to ecological pressures and to aspects of animal personality (Sih and Del Giudice 2012; Griffin et al. 2015; Liedtke and Fromhage 2019). In budgerigars, for example, bolder birds learn faster compared to less bold birds initially, and are also more likely to interact with and solve novel tasks (Chen et al. 2022). In our study, mean decision speed per individual varied from fast (two seconds) to very slow (ten seconds). The likelihood a parent moved food between chicks before committing to feeding a chick also varied decisive to indecisive: one individual changed their minds on only 5% of their feeding visits, compared to another that changed their mind on 73% of their feeding visits. Individual distributions in decision speed varied between being unimodal and bimodal (fig. 4), and future work could interrogate whether parents with bimodal decision speed distributions are employing different strategies under different contexts (Teichroeb et al. 2023). It would be fascinating to see if these individual differences in parental decision-making relate to other aspects of bird personality and fitness.

We found that females made slower decisions and were more likely to change their minds than males, especially when feeding chicks farther away. When examining only the most scenario, where parents did not move food and fed a chick begging as much or more than its nestmates, we found an interaction between parent sex and urgency (table 4). This pattern could arise via sexual dimorphism in sensory perception or in decision circuits, through different weighting of sensory evidence, decision thresholds, or urgency gating. Because females changed their minds more than males, which may indicate a secondary or metacognitive process, we believe this difference is due to males and females pursuing different decision-making strategies, rather than sensory perception (Fleming et al. 2018; Atiya et al. 2020; Stone et al. 2022). Why the sexes differ in their cognitive processes is unclear, but in many bird species, males and females respond to begging differently based on mating systems (Caro et al. 2025*b*). In great tits, females respond more to begging than males do: across multiple studies, females increase their overall provisioning more than males in response to increases in offspring begging (Caro et al. 2025*b*). Female great tits and male great tits may experience slightly different fitness outcomes based on feeding decisions, but quantifying this effect is outside the scope of this study. Further experiments will have to be conducted both in the field and the laboratory to explain the differences between male and female decision-making.

Social constraints on decisions making

We found that decision-making in the real world is somewhat constrained, which could lead to an over-interpretation of feeding outcomes as completely representative of parental decisions. Offspring have the ability to either beg or not on any given feeding visit, drastically shifting the number of options parents have to contend with from one to seven chicks. The number of begging chicks can affect parental cognition in two ways, by changing decision complexity and by encoding urgency information. If more chicks beg, the overall demand from the brood is higher, indicating higher urgency. Since drift diffusion models of decision-making are binary for choosing option A or B, we do not know what this framework would predict about decision speed and accuracy when individuals are considering option A or B or C or D or E (Lee et al. 2023). The number of begging chicks was associated with both parental confidence and speed, indicating that this change to the decision landscape matters. The number of options individuals are choosing amongst deserves targeted theoretical attention.

Additionally, food allocation patterns might be partially or completely hijacked by chicks, and not be the result of parental decision processes. For example, suppose parents always feed larger offspring. This pattern could arise because parents pay attention to offspring body size information. However, this pattern would also arise if offspring control food distribution and larger offspring outcompete their siblings through “scramble competition” (Royle et al. 2002). This phenomenon may lead to spurious conclusions about what information parents pay attention to and the cognitive processes underlying actions. Our study shows that in great tits at 8 days old, parents definitively control food allocation: parents can remove prey items from the mouth of one chick and place it in another’s mouth (Video S2). While parents have ultimate control, chicks do influence parental decisions through scramble competition for optimal positions close to the parent. Parents from high-urgency broods might pay more attention to the outcome of scramble competition as birds in poorer environments respond to quality rather than need when feeding chicks (Kölliker et al. 1998; Caro et al. 2016). Thus, feeding outcomes and decision processes combine both offspring and parent behaviors. Our study suggests that laboratory studies of social decision-making should explicitly measure and account for actions taken by the stimuli.

Limitations

Because we used wild birds interacting with six or seven live chicks, our data was influenced by many factors that are controlled in laboratory studies but variable in the field. While our study reflects the reality of parental decision-making, our statistical power was limited by the number of interacting factors we had to control for. We had data on 64 individual birds from 32 nests, based on the constraints of field site, which limits the scope of our analyses. Caution should therefore be used in interpreting the interactions in our study. Some of our results could be statistical artefacts. For instance, we found an interaction on parental likelihood of changing their mind between the total number of begging chicks and chick proximity, but this could be explained by the fact that if only one or two chicks were begging, those chicks were almost never farther away than the second closest chick. Furthermore, we were not able to capture information about chick vocalizations or UV signals, both of which can influence parental feeding decisions in great tits (Wright and Leonard 2002). The precision of our data on decision speed was limited to seconds rather than milliseconds, which had some advantages in uncovering secondary cognition, but may have precluded discovering more subtle aspects of the speed-accuracy tradeoff. Our data does not allow us to distinguish whether mind changes in great tit parents are due to a lack of confidence or to detecting an error in how ready chicks were for food, although we can likely rule out errors due to prey not fitting in the mouths of initially chosen chicks because there was no interaction between prey size and the size of the fed chick. Future studies could examine these mind changes at shorter time scales and with more detail on what happens during the movement of food between chicks to better tease these options apart. It is possible that, compared to an undisturbed nest, our experimental manipulations impacted how offspring beg and how parents make decisions, due either to the stress of experimental manipulations or to parents encountering unexpected changes in offspring behavior. However, all of the birds in our study received equivalent disturbance, and so no differences seen within our study can be attributed to this, but future studies could investigate the impact of stress and the unexpected on decision making. Finally, our path analyses are informative but should be interpreted with care, as our data structure was not fully appropriate for this kind of analysis because of our categorical variables and interactions. These limitations notwithstanding, our study highlights the importance of incorporating the context of the natural environment, real-life complexity, and evolutionary consequences into experimental paradigms of decision-making.

Conclusions

When animals make decisions, they must accumulate sensory evidence from multiple sensory modalities and multiple sources, weigh these different stimuli, set decision thresholds that prioritize either speed or accuracy, potentially modulate those thresholds based on the urgency of decisions, and execute their decisions. However, to date, most of what is known about the neural and cognitive mechanisms underlying decision-making has come from laboratory studies—studies that may lack the evolutionary context, complexity, constraints, and consequences that animals experience in the real world. Our study shows that when great tit parents are faced with evolutionarily relevant, complex decisions that have large impacts on fitness, they value accuracy over speed, are influenced by urgency, adjust evidence accumulation to their confidence level, and exhibit individual variation. Some of these findings align with insights from laboratory studies, but others—particularly the importance of urgency signals—do not. Cognitive studies and models of decision-making should better reflect the real world.

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Statement of Authorship

Conceptualization: SMC; Funding acquisition: SMC, CAH, KvO, RMV; Methods development/experimental design: SMC, CAH; Field data collection: SMC, CAH, ACV, TvM; Video scoring: ACV, RMV; Data analysis: SMC; Data validation: SMC; Data visualization: SMC;

Provided additional resources: KvO, CAH; Supervision: CAH, HAH, SMC; Writing original draft: SMC; Writing review & editing: All authors.

Data and Code Availability

All datasets and R code are available in a DataDryad repository (https://doi.org/10.5061/dryad.6hdr7srcf, Caro 2025). This DataDryad repository contains 12 representative videos. The complete collection of videos can be found in two Zenodo repositories: the first (DOI 10.5281/zenodo.15625055) has videos from nests A, AA, B, BB, C, CC, D, DD, E, EE, F, FF, G, H, I, J, K. The second (DOI 10.5281/zenodo.15625465) has videos from nests L, M, N, O P, Q, R, S, T, U, V, W, X, Y, and Z. These files correspond to the variable "Blinded.film.file" which is the file name of the video data where each feeding visit can be found.

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Tables

Table 1: Potential pitfalls of extrapolating insights from laboratory studies on cognition and decision-making to real-world scenarios.

Laboratory study characteristic	Pitfall for understanding real-world decisions
Forced-choice paradigms with only two options, that vary in only one parameter	Lacks evolutionarily-relevant complexity (Yeung and Summerfield 2012; Heitz 2014; Juavinett et al. 2018; Najafi and Churchland 2018; Sumner and Sumner 2020; Miletić et al. 2021; Lee et al. 2023; Teichroeb et al. 2023)
Stimuli such as whether dots are mostly moving left or right	Lacks evolutionary relevance and/or fitness consequences (Juavinett et al. 2018; Shevinsky and Reinagel 2019; Mendonça et al. 2020; Sumner and Sumner 2020)
Measurements made over milliseconds only	Precludes capturing decisions that require integrating conflicting evidence (Yeung and Summerfield 2012; Waskom and Kiani 2018; Herce Castañón et al. 2019)
Highly invasive methods, such as neural spike recording	Alters behavior (Najafi and Churchland 2018)
Human subjects mostly, followed by rodents and primates less commonly	Not broadly generalizable for insights about cognition in other species (Heitz 2014; Najafi and Churchland 2018; Shevinsky and Reinagel 2019)
Inert or passive stimuli	Only relevant to situations when individuals have complete control over their actions, which may not be the case for social decisions (Royle et al. 2002; Kilner and Hinde 2008; Rodríguez et al. 2008)
Rewards for correct decisions are a small amount of money or food	Lacks evolutionarily relevant fitness consequences, which may preclude observing urgency effects (Juavinett et al. 2018; Sumner and Sumner 2020)
Each decision is made once without the possibility of changing your mind	Precludes potential measures of confidence and error detection in nonverbal animals
There is one definitively correct choice and one wrong choice	Precludes studies on more subtle and realistic decisions, where no one choice is definitively correct or incorrect and where animals do not receive instant feedback on whether they made the right choice or not

Table 2: Impacts on decision speed in great tit parental feeding

Fixed effects	Estimate	SE	Z	P
Intercept	0.99	0.30	3.36	<0.0001***
Number of begging chicks	-0.06	0.04	-1.76	0.079.
Weight rank of fed chick	0.11	0.03	3.47	0.00051***
Fed chick beg rank (not begging the most)	0.35	0.12	2.99	0.0028**
Urgency (supplementation treatment)	-0.10	0.37	-0.26	0.79
Parent sex (male)	-0.14	0.23	-0.62	0.53
Fed chick proximity rank	0.27	0.05	5.99	<0.0001***
Prey size	0.20	0.04	5.19	<0.0001***
Parent sex: fed chick proximity rank	-0.16	0.06	-2.64	0.0084**
Number of begging chicks: weight rank of fed chick	-0.11	0.03	-3.49	0.00048***
Urgency (supplementation) treatment: fed chick proximity rank	-0.14	0.06	-2.48	0.013*
Random effects				
Parent ID	0.125			
Nest ID	0.126			

. p <0.1; * p < 0.05; ** p < 0.01; *** p < 0.001.

Table 3: Factors affecting changes-of-mind in great tit parental feeding decisions

Fixed effects	Estimate	SE	Z	P
Intercept	-1.35	0.29	-4.77	<0.0001***
Number of begging chicks	0.13	0.08	1.75	0.080.
Weight rank of fed chick	0.00	0.07	0.04	0.97
Fed chick beg rank (not begging the most)	0.51	0.29	1.74	0.082.
Urgency treatment	-0.24	0.33	-0.73	0.47
Parent sex (male)	-0.24	0.18	-1.33	0.19
Fed chick proximity rank	0.99	0.10	10.06	<0.0001***
Prey size	0.23	0.08	2.85	0.0044**
Parent sex: fed chick proximity rank	-0.29	0.13	-2.14	0.033*
Number of begging chicks: fed chick proximity rank	-0.32	0.08	-4.04	<0.0001***
Random effects				
Parent ID	0.18			
Nest ID	0.58			

. p <0.1; * p < 0.05; ** p < 0.01; *** p < 0.001.

Table 4: Factors affecting speed of great tit parental feeding decisions in most common feeding visit type: with no movement of food between chicks and where the fed chick was begging the most (n = 1030 feeding visits).

Fixed effects	Estimate	SE	Z	P
Intercept	0.45	0.13	3.48	<0.0001***
Number of begging chicks	-0.23	0.02	10.57	<0.0001***
Weight rank of fed chick	0.18	0.02	8.98	<0.0001***
Urgency treatment	0.13	0.17	0.75	0.46
Parent sex (male)	0.13	0.13	1.01	0.31
Fed chick proximity rank	-0.02	0.03	-0.81	0.40
Prey size	0.22	0.02	8.93	<0.0001***
Parent sex: Urgency treatment	-0.41	0.19	-2.18	0.029*
Random effects				
Parent ID	0.10			
Nest ID	0.09			

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Figure Legends

Figure 1. Decisions are reached when enough evidence accumulates via drift diffusion to reach a decision threshold. Individuals accumulate evidence over time (black line). Colored lines indicate decision thresholds for choosing A or B. Stars indicate decision speed: how long it takes before accumulated evidence drifts to a threshold. There is a speed-accuracy tradeoff. Orange represents an inward-shifted threshold where speed is prioritized. Purple represents an outward-shifted threshold where accuracy is prioritized. Blue represents a collapsing threshold where less evidence is necessary as time goes on (i.e. urgency). Figure adapted from (Zhang and Rowe 2014), best viewed in color.

Alt text: Graph showing time on the X axis and the threshold for making a decision between two choices on the Y axis. Evidence for one choice over the other is shown as a line drifting toward one decision threshold.

Figure 2. Experimental setup. We investigated parental decision-making in the wild by manipulating urgency through providing extra food, standardizing stimuli by cross-fostering chicks, and filming feeding visits at parents' nests. Speed is measured as the time from when a parent entered the nest box to depositing food in the chosen chick's mouth (Video S1). Changes-of-mind are measured as whether the parent placed food in just one chick's mouth or moved food from one chick to another, and likely captures confidence, error detection, or constraints on executing a decision (Video S2). Probing is measured by whether the parent dips its beak into the mouths of chicks after food has been swallowed, and likely captures post-decision evidence collection (n = 32 broods, 62 parents, 1508 feeding visits, Video S3). Cartoon created by SMC.

Alt text: Cartoon showing the three stages of our experimental setup: manipulating urgency through food supplementation, standardizing stimuli through cross-fostering chicks, and filming feeding visits to record decision speed, changes of mind and probing.

Figure 3. Parental decision speed depends on several factors, including which chick is chosen, experimental treatment and parental sex. Lines and data points show predicted decision speeds from the full model. Data points are jittered to better display overlapping values. (A) Parents make faster decisions when choosing to feed chicks begging more ($P = 0.0028$**). (B) Parents in the unsupplemented (urgent, high starvation), treatment made slower decisions, especially when choosing to feed chicks farther away ($P = 0.013$*, low starvation = purple, dashed line, high starvation = light green, solid line). (C) When more chicks begged, the size of the chosen chick did not affect speed, but size did matter when fewer chicks begged ($P = 0.00048$***, few begging chicks = dark green, dashed line, many begging chicks = orange, solid line). (D) Females make slower decisions than males, especially when choosing to feed farther chicks ($P = 0.0084$*, females = red, dashed line, males = blue, solid line).

Alt text: Four panels showing how decision speed is impacted by various factors.

Figure 4. Individuals varied in decision speed even within mated pairs. Panels show the distribution of speed for the female (red) and male (blue) from a nest (nest-ID shown above panel). The fastest deciders were the male from Nest-361 (mean = 1.9 sec, n = 20 decisions), and female from Nest-203 (mean = 2.0 sec, n = 35); while the slowest were the female from Nest-281 (mean = 13.9 sec, n = 57 decisions) and male from Nest-257 (mean = 10.9 sec, n = 25). Three broods are missing one parent because not enough visits from that individual were observed.

Alt text: 32 density plots showing the distribution of decision speeds for the male and female of a nest. Each panel shows one nest.

Figure 5. The likelihood parents move food between chicks before feeding varies with the proximity rank of the chosen chick, the number of options and parental sex. Lines and data points show predictions from the full model. (A) Parents are more likely to move food between chicks if they ultimately choose to feed a chick farther away, particularly if more chicks are begging ($P = < 0.0001$***, few chicks begging = dark green, many chicks begging = orange). (B) Females are more likely to move food than males, especially when choosing farther chicks ($P = 0.033$*, female = red, male = blue).

Alt text: Two panels showing how the likelihood of parents moving food before feeding a chick is impacted by various factors.

Figure 6. Changes-of-mind and speed are both affected by the context of the decision and which decision was made, in addition to a direct effect of changes-of-mind on speed. Each feeding decision has the composite latent variables of urgency (orange: supplementation treatment, number of chicks begging) and which decision was made (blue: the beg rank, weight rank and proximity rank of the fed chick); and other factors (light grey: prey size, parent sex). Thicker lines indicating stronger paths based on standardized coefficients. Dashed lines indicate the fixed factor loadings for latent variables, while solid lines indicate relative factor loadings.

Alt text: Graphic showing the interconnected path between how variables related to the urgency of decision, which decision is made and which parent makes that decision impact whether food is moved or not and how quickly a decision is made.

Figure 7. Prior confidence and/or error detection shapes how long parents spend accumulating evidence on their next visit to the nest. Black lines and data points show predictions from the full model accounting for effects of all variables. Data points are jittered to better display overlapping data points. If parents moved food between chicks on their previous decision, it takes them longer to make their next decision (P = 0.030*, n = 1433 feeding visits). In other words, if a parent is not confident or detects an error on visit 1, they take more time to make a decision on visit 2.

Alt text: Graph showing how the speed of a subsequent decision is impacted by whether the parent moved food on the prior decision.

Figure 8. Decision speeds are associated with changes in the risk of offspring mortality, depending on environmental conditions. When parents had experienced poor environmental conditions in the past (unsupplemented treatment, light green), slower decisions were associated with a higher risk of having at least one offspring starve in the future (P = 0.031*). Conversely, when parents had received supplemental food in the past, slower decisions were associated with less offspring death. N = 32 broods.

Alt text: Figure showing how the risk of offspring mortality is impacted by the interaction between environmental quality and how quickly parents make decisions.

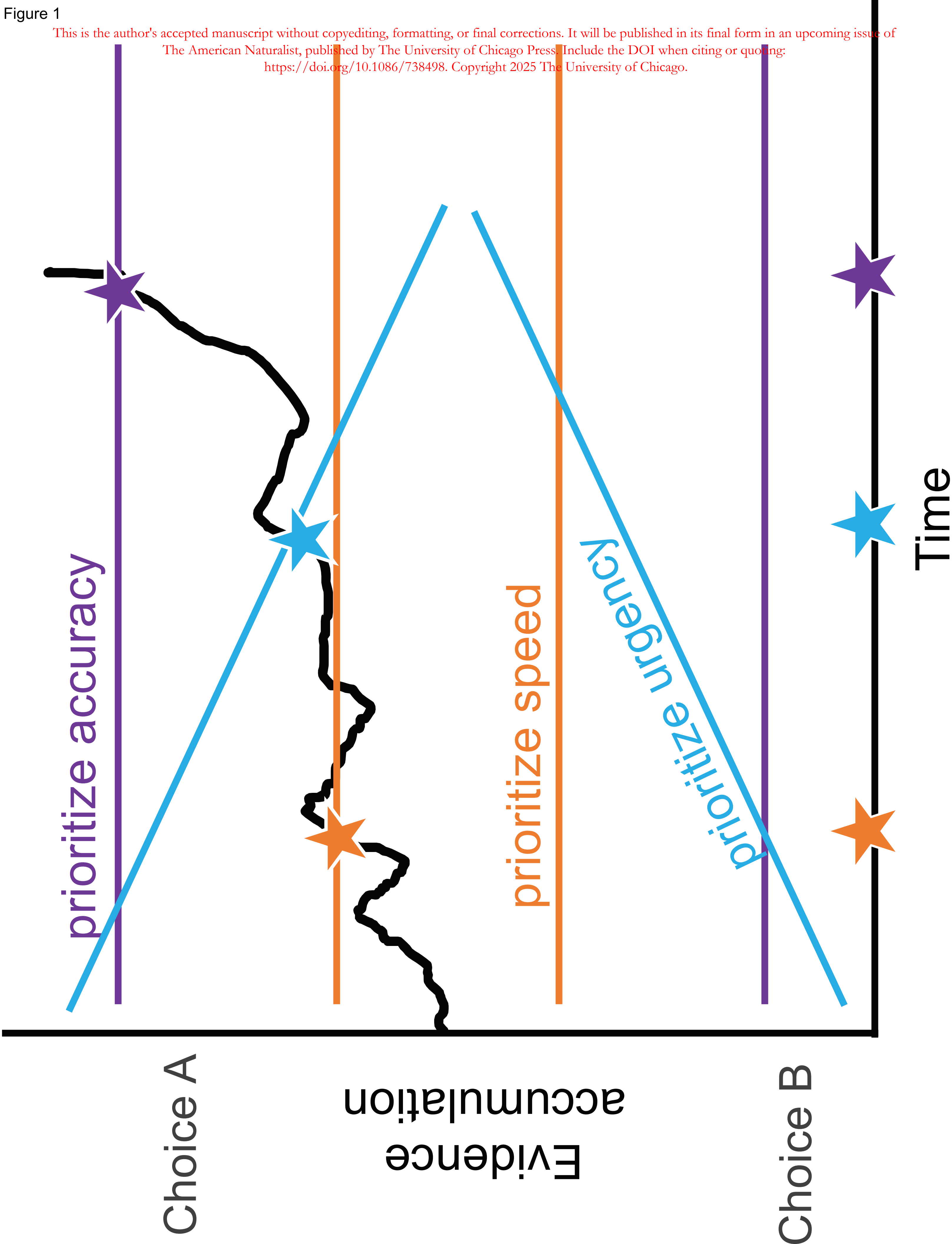
Video S1. Example of a standard feeding visit. Multiple chicks beg and the parent looks around before deciding on a chick to feed.

Alt text: The parent enters the nestbox and chicks immediately begin to beg for food. The parent moves its head in a sweeping pattern across the top of the nest, as it scans the begging chicks before making a decision. Six chicks beg for food during this nest visit. Chicks are individually marked with paint dots. It takes two seconds between the parent's entrance to when a chick is ultimately fed.

Video S2. Example of a feeding visit where the parent can be seen moving food between chicks. **Alt text:** The parent enters the nest and two chicks beg. The parent places the prey in the mouth of the chick at the 12:00 position in the nest, stands up, then goes back to remove the prey from that chicks' mouth. It then places the prey in the mouth of the chick at the 6:00 position in the nest, who eats it. It takes four seconds between the parent's entrance to when a chick is ultimately fed.

Video S3. Example of a feeding visit where the parent can be seen probing chicks after feeding. **Alt text:** The parent enters the nestbox and chicks immediately begin to beg for food. After feeding a chick, the parent continues to dip its beak repeatedly into the mouths of three different chicks. There are seven separate instances of the parent placing its beak inside the mouth of a begging chick, including the actual feed. This nest visit, including post-feeding probing, takes twenty seconds.

Figure 1



prioritize accuracy
prioritize speed
prioritize urgency
Time
Choice A
Evidence accumulation
Choice B

Figure 2

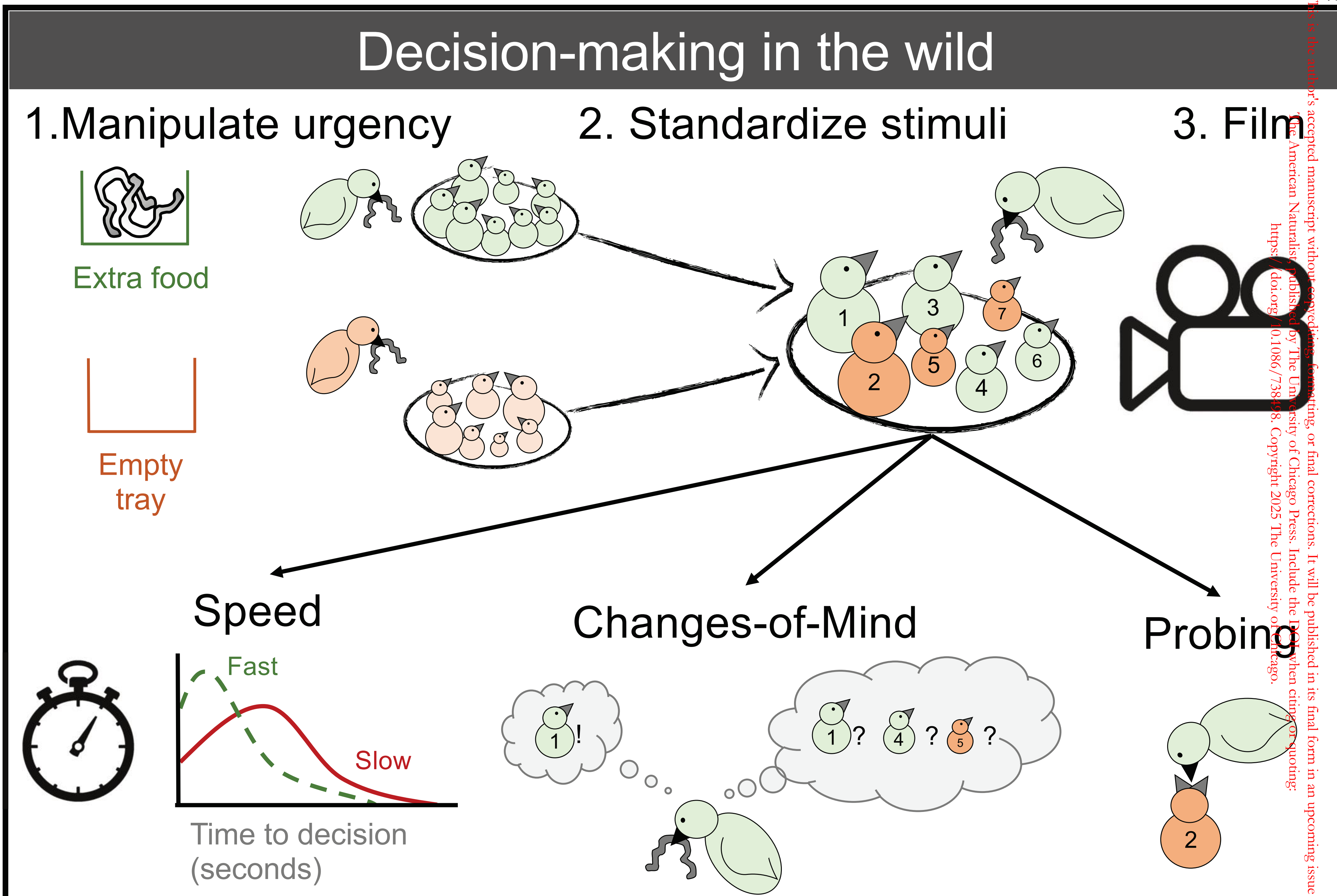

Decision-making in the wild
1.Manipulate urgency
2. Standardize stimuli
3. Film
Extra food
Empty
tray
1
2
3
4
5
6
7
Speed
Changes-of-Mind
Probing
Fast
Slow
Time to decision
(seconds)
1 !
1 ? 4 ? 5 ?
2

Figure 3

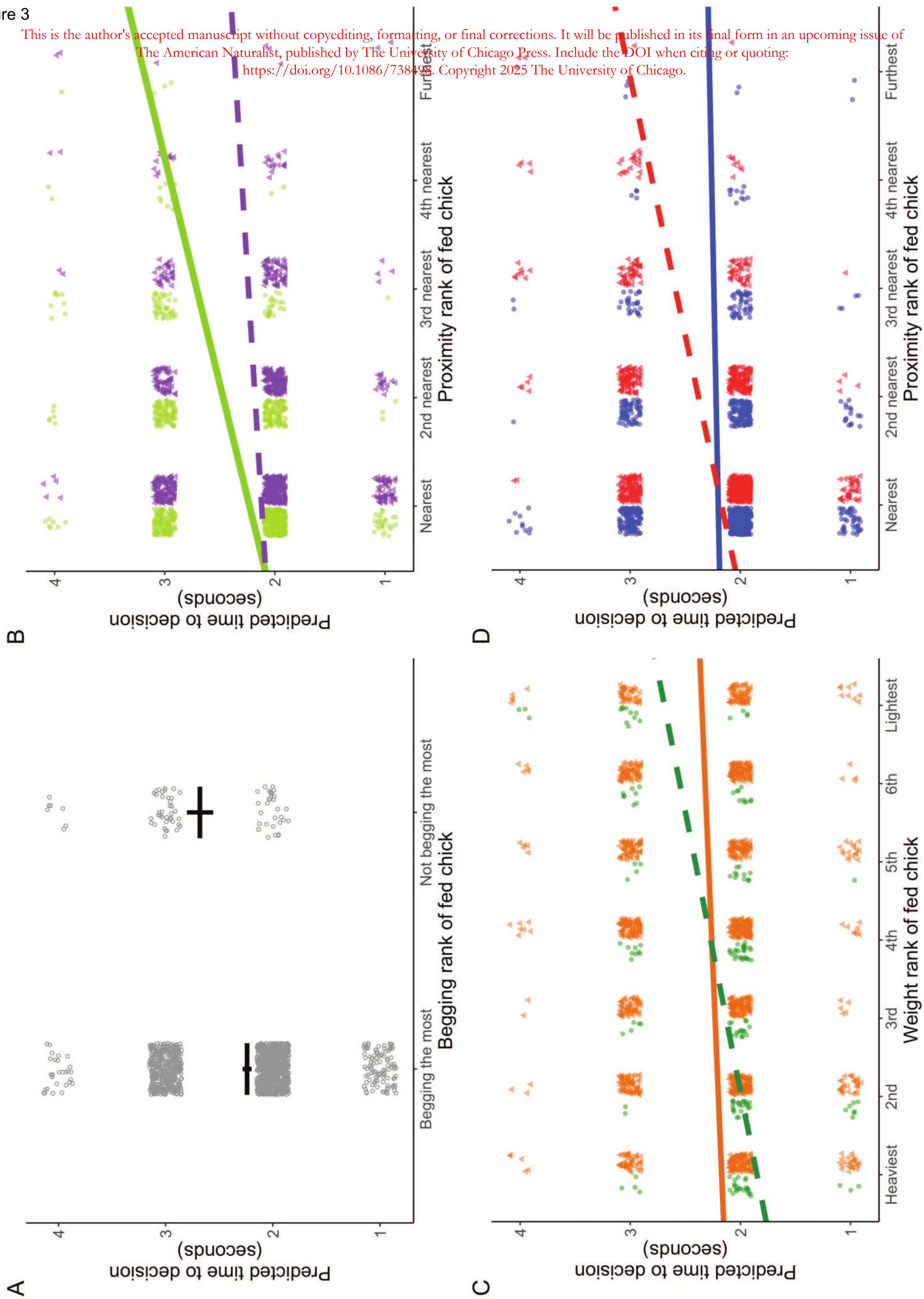

A
Predicted time to decision (seconds)
1
2
3
4
Begging the most
Not begging the most
Begging rank of fed chick
B
Predicted time to decision (seconds)
Nearest
2nd nearest
3rd nearest
4th nearest
Furthest
Proximity rank of fed chick
C
Predicted time to decision (seconds)
Heaviest
2nd
3rd
4th
5th
6th
Lightest
Weight rank of fed chick
D
Predicted time to decision (seconds)
Nearest
2nd nearest
3rd nearest
4th nearest
Furthest
Proximity rank of fed chick

Figure 4

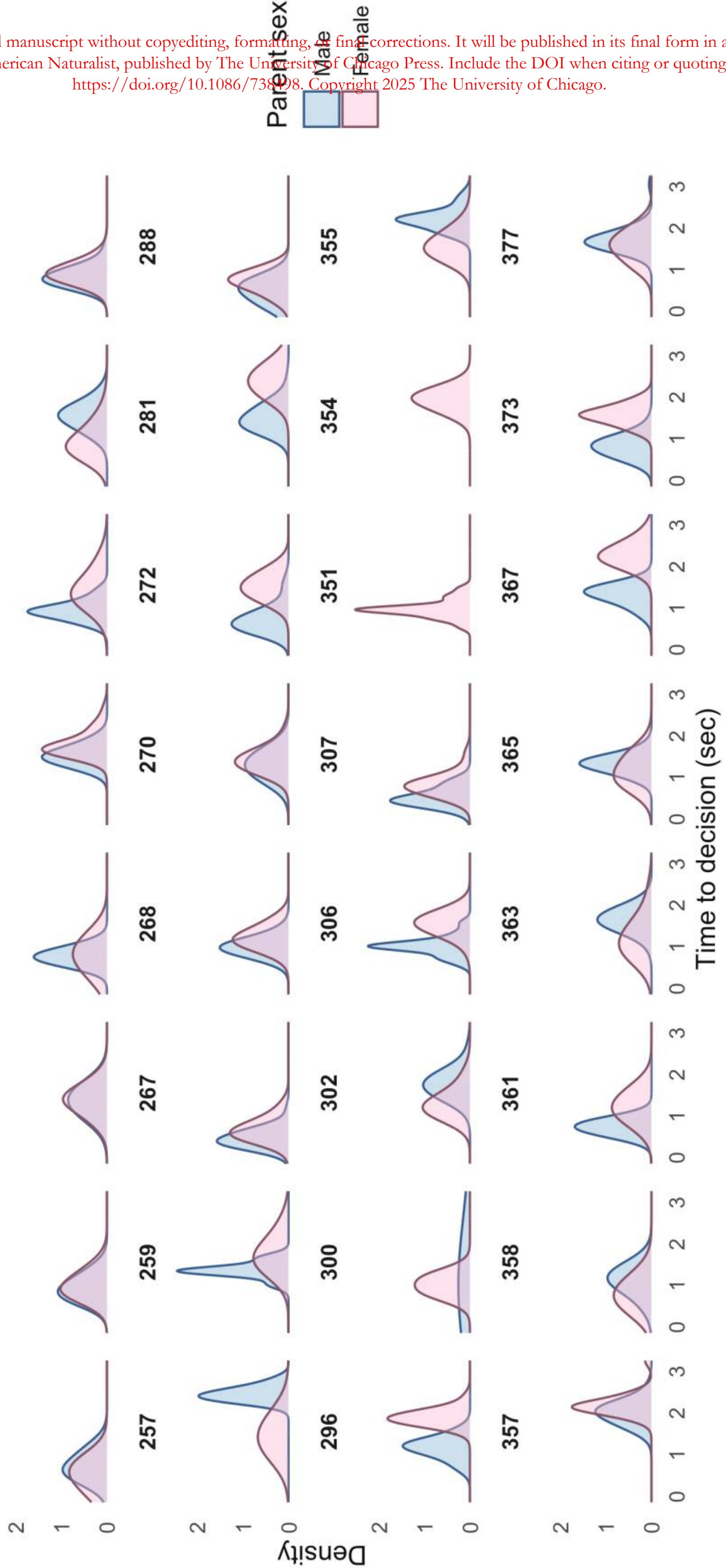

Parent sex
Male
Female
203
207
216
227
240
243
252
253
257
259
267
268
270
272
281
288
296
300
302
306
307
351
354
355
357
358
361
363
365
367
373
377
Density
Time to decision (sec)

Figure 5

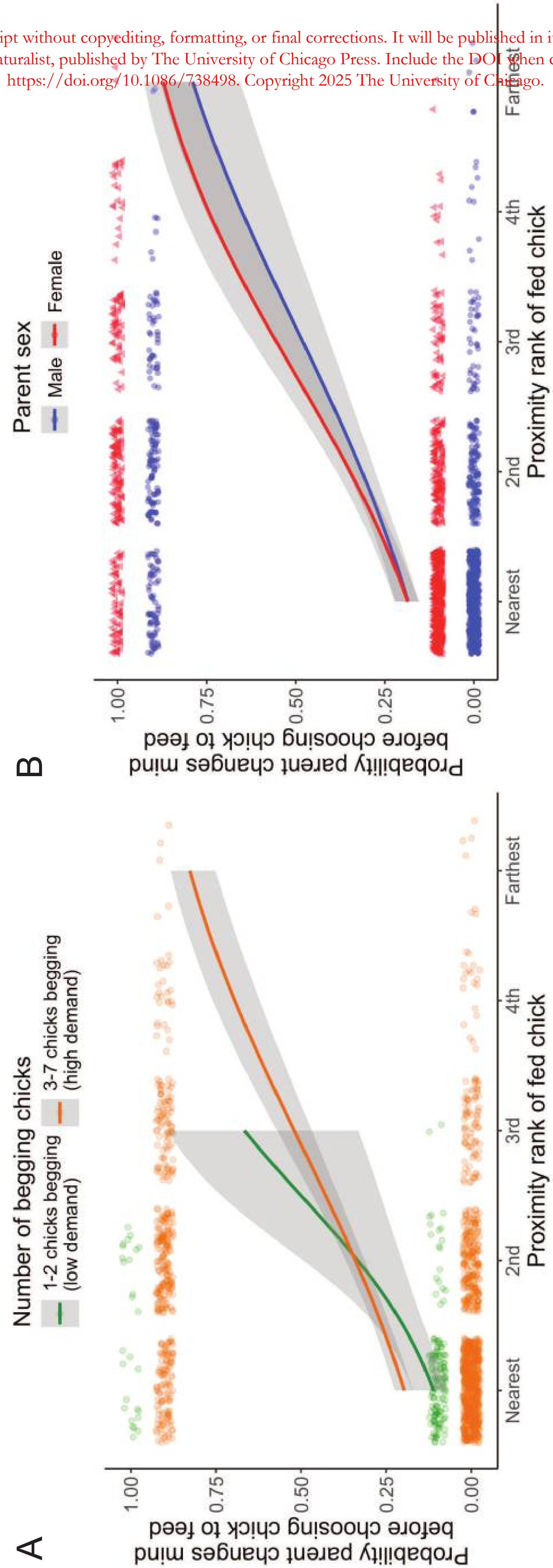

A
Number of begging chicks
1-2 chicks begging (low demand)
3-7 chicks begging (high demand)
Probability parent changes mind before choosing chick to feed
0.00
0.25
0.50
0.75
1.00
Nearest
2nd
3rd
4th
Farthest
Proximity rank of fed chick
B
Parent sex
Male
Female
Probability parent changes mind before choosing chick to feed
0.00
0.25
0.50
0.75
1.00
Nearest
2nd
3rd
4th
Farthest
Proximity rank of fed chick

Figure 6

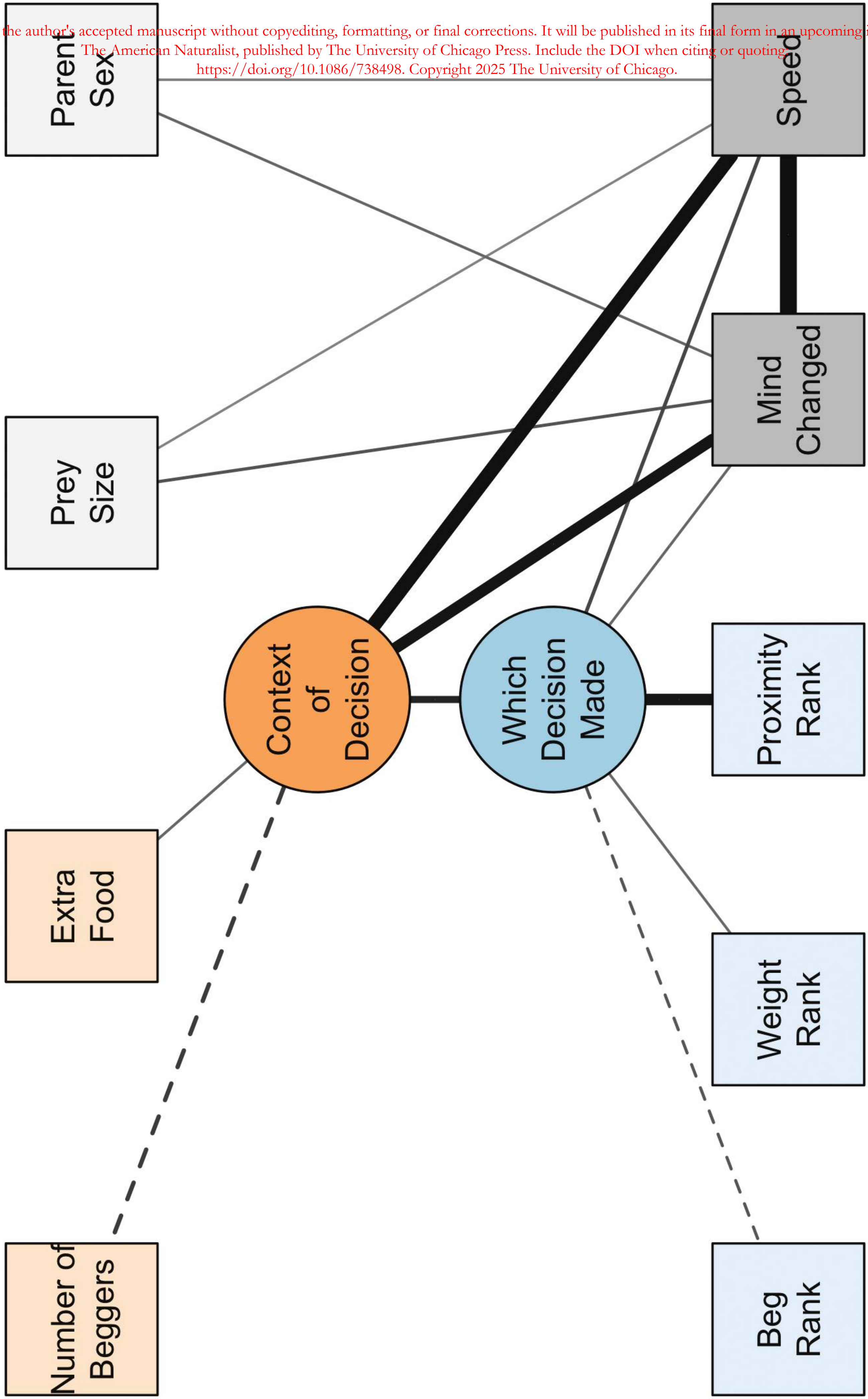

Parent Sex
Prey Size
Extra Food
Number of Beggers
Context of Decision
Which Decision Made
Speed
Mind Changed
Proximity Rank
Weight Rank
Beg Rank

Figure 7

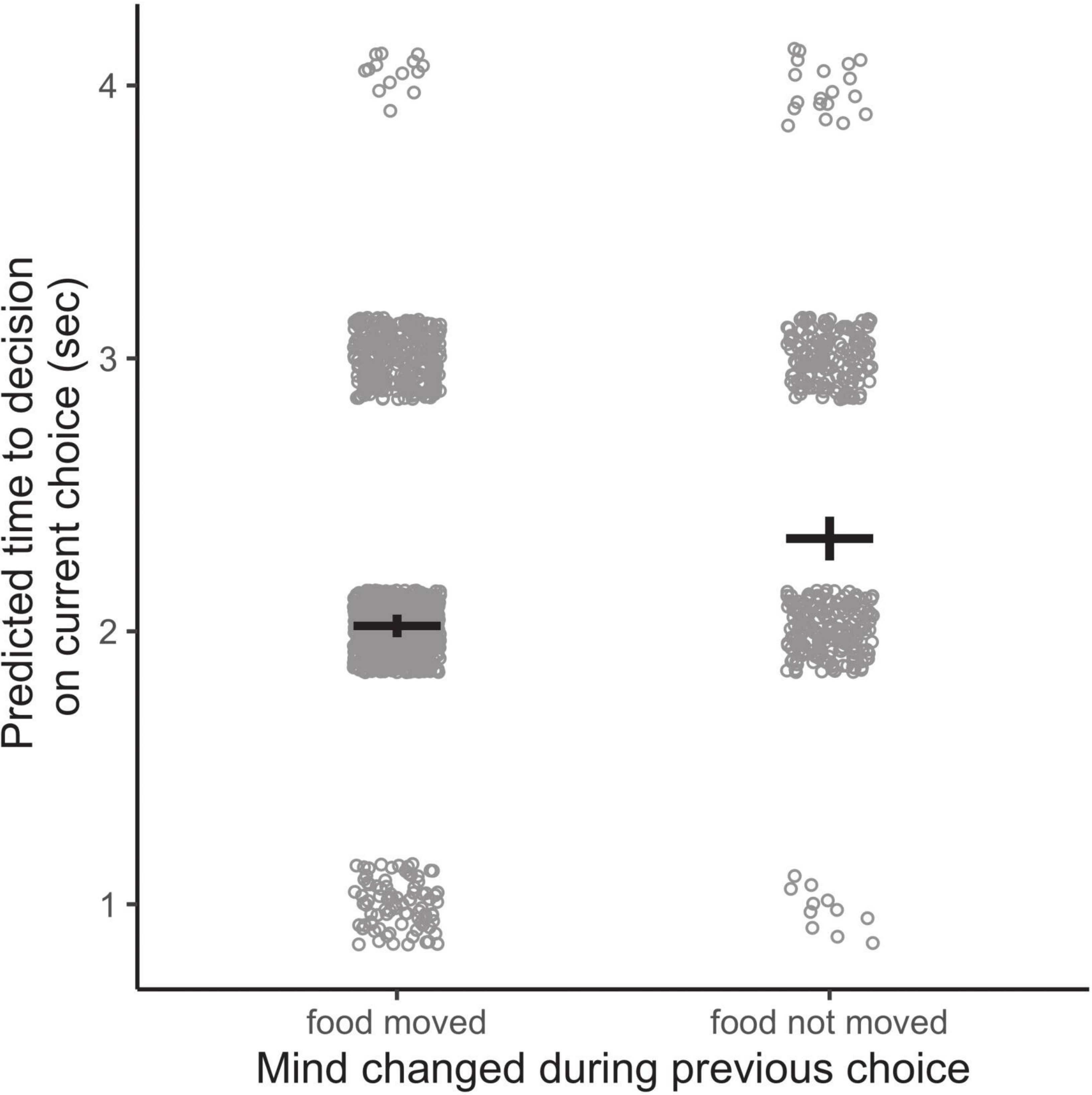
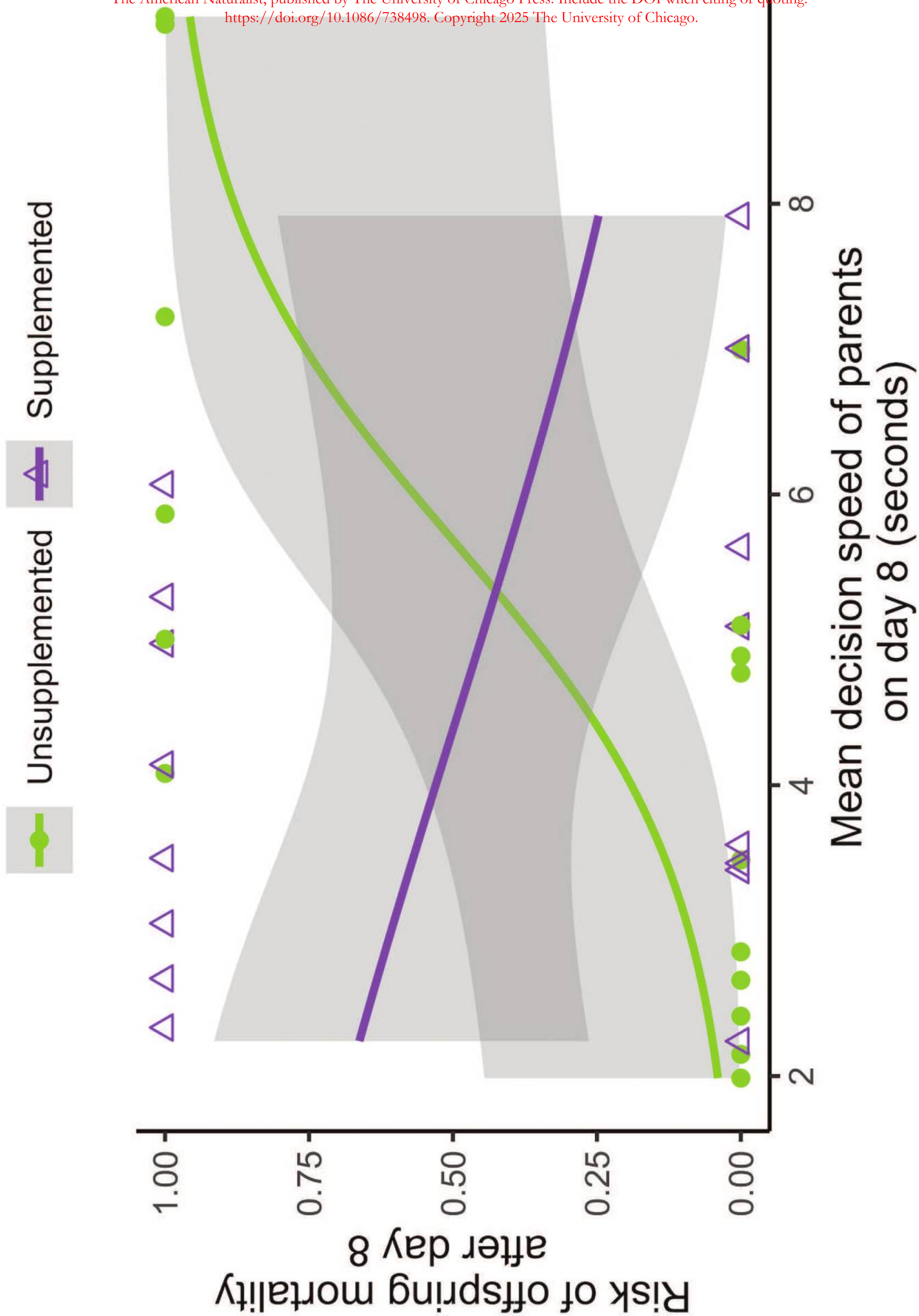

Predicted time to decision
on current choice (sec)
4
3
2
1
food moved
food not moved
Mind changed during previous choice

Figure 8



Unsupplemented
Supplemented
Risk of offspring mortality after day 8
1.00
0.75
0.50
0.25
0.00
2
4
6
8
Mean decision speed of parents on day 8 (seconds)

Supplementary Material for:

Decision-making in the wild: Urgency and complexity drive feeding decision speed and the likelihood of revising a choice in a sex-dependent manner in great tit (*Parus major*) parents

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Supplemental Methods

Details about environmental urgency treatment

Each day for the first week after hatching, we provided approximately 20g of live meal worms (*Tenebrio molitor*) mixed with rehydrated wax worm larvae (*Galleria mellonella*), cut into 0.25 cm pieces (Figure S1). This supplementation represents approximately 20% of the daily nutritional needs of the brood (van Balen 1973; Eeva et al. 2009). We checked how great tits interacted with the food by filming two nests during the supplementation period. Parents took food from the trays and directly fed their offspring (Supplementary Movie 2). Parents also ate the food themselves. Either outcome serves to improve environmental conditions for supplemented families. We placed an empty tray in control (unsupplemented) nest boxes and visited control nests each day so that all nests received comparable human disturbance. We alternated experimental treatments by assigning the first brood of the day that had hatchlings to the supplemented treatment, and then the next brood the unsupplemented treatment. We reversed this order each day. We did not pre-randomize because we wanted to equalize hatch date within each treatment.

Details for cross-fostering treatment to standardize broods

On the 8th day after hatching (filming day), we removed the feeding trays and cross-fostered chicks. To habituate parents, we installed an infrared camera inside the lid of a nest box the day prior to filming. All cross-fostering was done in the morning as soon as possible prior to filming, and all filming occurred between 7:00 and 15:00 (83% of our feeding visits occurred between 9:00 and 13:00). Video of the first 30 minutes after cross-fostering was excluded to give animals time to return to normal behavior. Parents' biological broods were the same age as their filming broods. Parents were not filmed with any of their genetic offspring. Chicks remained in foster broods through fledging.

Hand-feeding protocol:

We ranked chicks by weight in their filming nests. We assigned chicks to be handfed or not handfed in an alternating pattern by weight rank, which was alternated at each nest. For example, the heaviest chick was handfed and the second heaviest was not in filming brood A, while in filming brood B the heaviest chick was not handfed. Immediately prior to filming, we hand-fed selected chicks in an artificial nest containing a cloth wrapped hand-warmer. We fed the chicks with Nutribird A 19 high energy bird food using a 5 mL syringe. We continued feeding until begging ceased and could no longer be induced by whistling or tapping the sides of the bill with a syringe, indicating the chicks were satiated.

Supplemental Figures

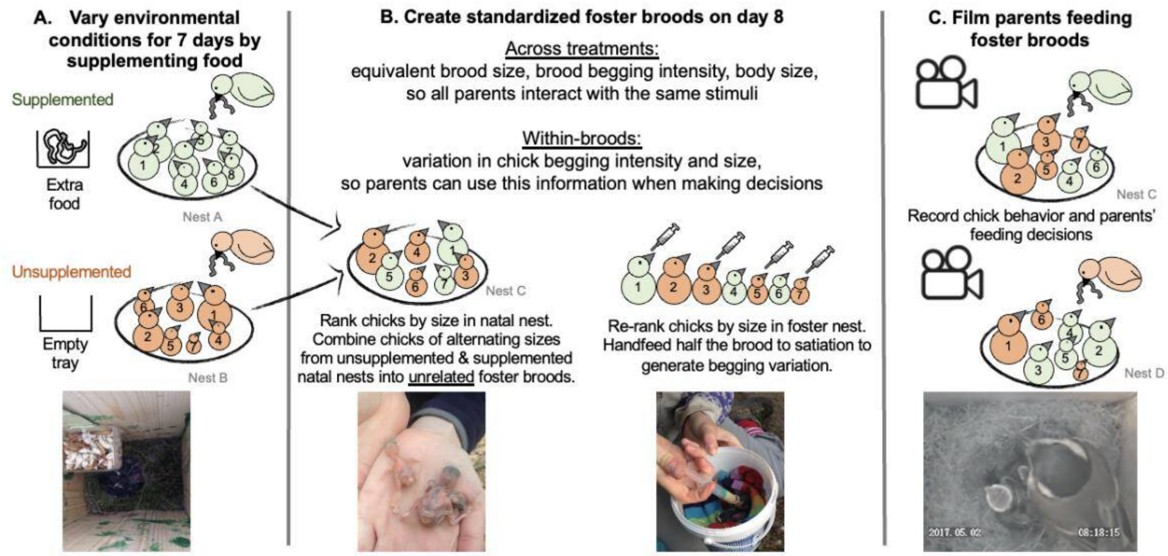

Figure S1. More details on experimental design. (A) On hatching day, nests were randomly assigned to be in a good environment, supplemented (green), or a poor environment, unsupplemented (orange). Supplemented nests received a daily mix of meal worms and wax worms (approximating 20% of the brood's nutritional needs) for the week after hatching. Unsupplemented nests were visited daily to control for human disturbance. **(B)** After 1 week, we ranked chicks by size (weight) within natal nests. We created foster broods with chicks 1, 3, 5 and 7 from natal nest A, and chicks 2, 4, 6 from natal nest B. This accounted for potential differences in chick behavior based on their previous size rank; standardized size differences within broods; and standardized foster brood size to 7 or 6 chicks. We re-ranked chicks by size within foster nests (nest C). We handfed half of each foster brood to satiation in an alternating pattern by size rank; a mix of unsupplemented and supplemented chicks were fed in order to disentangle short-term and long-term need. This standardized brood-level begging intensity at the beginning of filming; ensured begging is variable enough across chicks to be a useable signal; and ensured begging intensity varied across size ranks. **(C)** We filmed adults feeding their fostered broods for 4.5 hours, excluding first 0.5 hours to ensure behavior had normalized (see Videos S1, S2 and S3 as examples). Fostered broods contained only unrelated chicks to ensure adult behavior was not influenced by familiarity to their own chicks. Photos by S. Caro. Figure originally in Caro et al 2025.

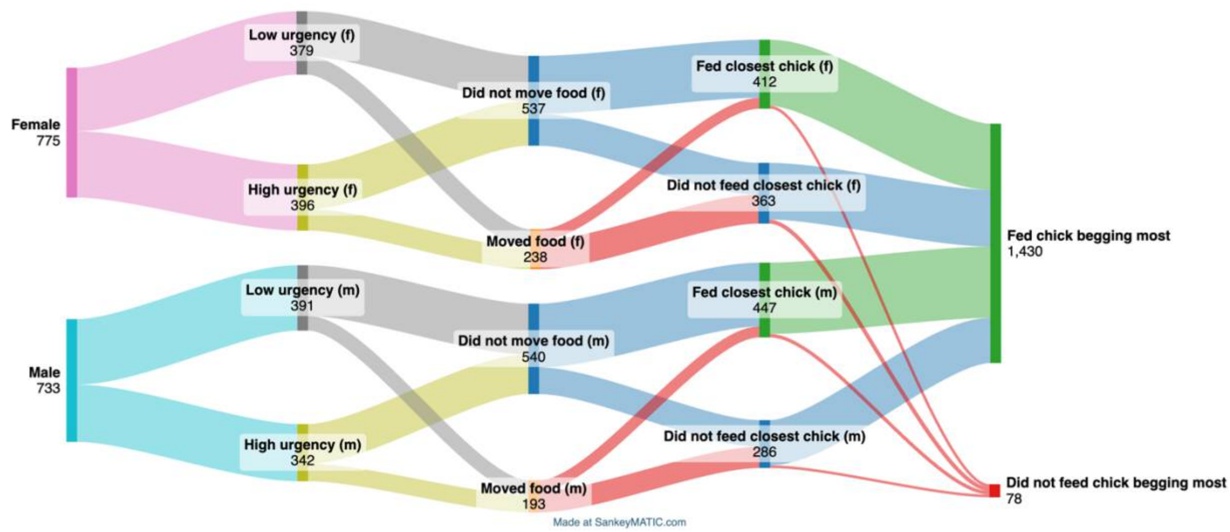

Figure S2. River plot showing how feeding visits progress. This diagram shows how many unique feeding visits comprised various feeding outcomes (n = 1508 visits overall). These decision flows can be represented in multiple ways, given that we recorded data on three traits of the fed chick (begging rank, proximity rank, and size rank) and multiple conditions (parent sex, urgency treatment, prey size), and we have selected a representative flow to highlight how a decision might proceed. For instance, parents typically end up feeding a chick begging as much or more than its nestmates. However, in the instances when they do feed a chick begging less than its nestmates, this could be the result either of moving food away from a chick begging more (n = 31) or of the parent initially choosing a chick begging less than its nestmates (n = 47).

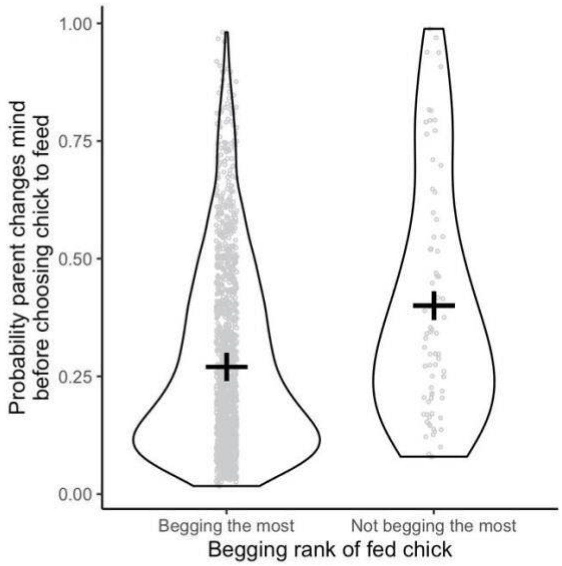

Figure S3. Parents second guess their decisions to feed chicks that are begging less intensely than their nestmates. Parents was less likely to change their minds if they chose to feed a chick begging at least as much as its nestmates ($p = 0.085$.), although this effect is not significant. Chicks were categorized as "begging the most" if they begged more than or as much as other chicks begged on that visit. For example, if the parent chose to feed a chick begging at intensity 2 when another chick was begging at the higher intensity 3, that was classified as "not begging the most". If both chicks were begging at the same intensity level, that was classified as "begging the most". Black lines show predictions and SEs from the full model accounting for effects of all fixed and random variables. Violin plots and data points show the distribution of a parent's predicted probability of changing its mind from the full model.

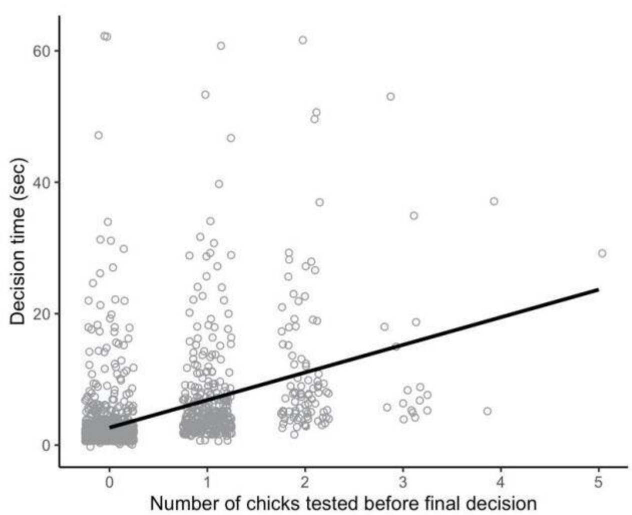

Figure S4. Refeeding affects decision speed. The more times a parent changes its mind before committing to feeding a chick, the longer the decision takes. However, this correlation is $r = 0.42$, indicating that decision speed is not solely determined by the presence or absence of refeeding.

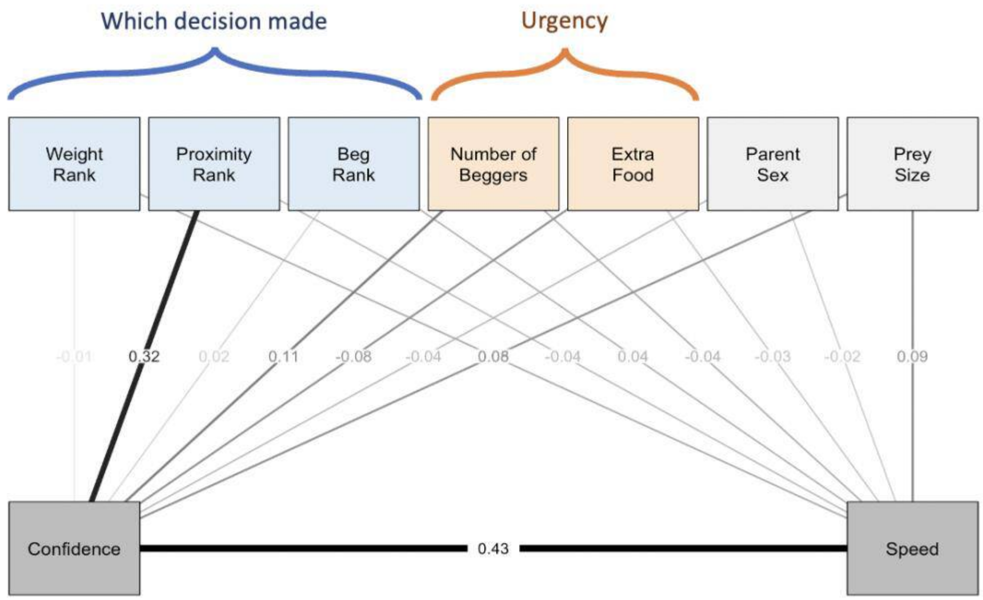

Figure S5. Decision confidence and speed are both affected by the urgency of the decision and which decision was made, in addition to the direct path between confidence (refeeding) and speed. This is a graphical representation of our conception of the pathway best supported by our data, based on AIC values. Each feeding decision has which decision was made (blue: the beg rank, weight rank and proximity rank of the fed chick); the context or urgency of the decision (orange: supplementation treatment, number of chicks begging); and other factors (light grey: prey size, parent sex). The numbers and weights of the paths indicate the standardized coefficients for the path, with thicker lines indicating stronger paths. This model accounts for individual ID and non-normality of the data, though does not allow interactions (n = 1508 feeding visits).

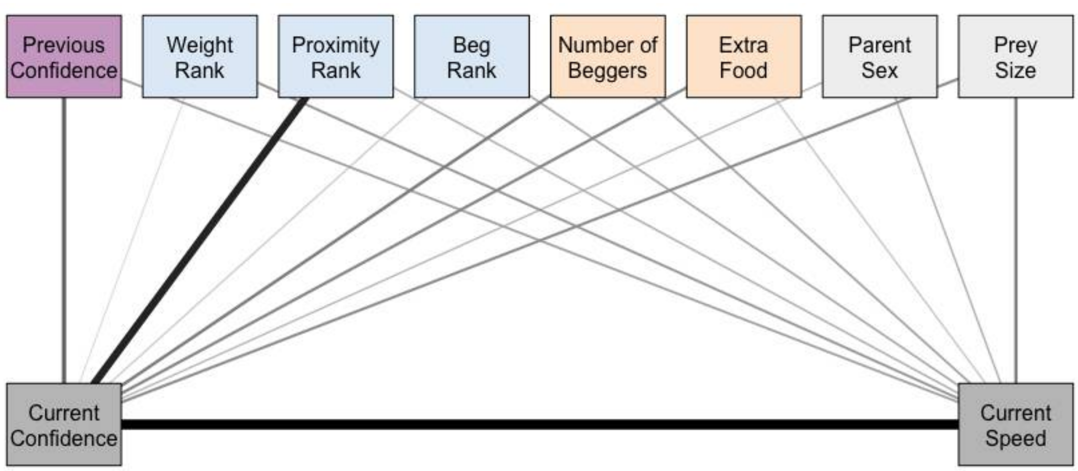

Figure S6. Confidence (refeeding) shapes how long parents spend accumulating evidence on future decisions. The path that best fits our data supports a direct effect of previous confidence on both current confidence and current speed, accounting for all other effects (n = 1433 feeding visits).

Supplemental Tables

Table S1. Impacts on decision speed in great tit parental feeding: Main effects only.

Fixed effects	Estimate	SE	Z	P
Intercept	0.71	0.11	6.26	<0.0001***
Number of begging chicks	-0.04	0.03	-1.30	0.19
Weight rank of fed chick	0.07	0.03	2.92	**0.0035*** **
Fed chick beg rank (not begging the most)	*0.21*	*0.11*	*1.86*	*0.063.*
Urgency (supplementation treatment)	-0.15	0.12	-1.18	0.24
Parent sex (male)	-0.08	0.08	-1.07	0.28
Fed chick proximity rank	0.14	0.03	5.44	**<0.0001*** **
Prey size	0.19	0.03	6.14	**<0.0001*** **
Random effects				
Parent ID	0.05			
Nest ID	0.07			

Table S2. Summaries of PiecewiseSEM comparing different potential pathways.

	Direct paths from…					
Model name	**Path from refeeding to speed**	**Measured variables to refeeding**	**Measured variables to speed**	**Latent composite variables to refeeding**	**Latent composite variables to speed**	**Δ AIC**
Model 3	Yes	Yes	Yes	No	No	Best model (AIC = 11,372)
Model 1	Yes	No	Yes	No	No	+143
Model 2	Yes	Yes	No	No	No	+287
Model 0	No	Yes	Yes	No	No	+1,194
Model 6 (null)	No	No	No	No	No	+1,723
Model 4	Yes	No	No	Yes	No	+4,409
Model 5	Yes	No	No	Yes	Yes	+ 8,669

Models are ranked by AIC values compared to the best model. Models control for individual ID and use a Poisson distribution. Note that Models 4 and 5 contain latent variables, and AIC values for piecewise SEMs were calculated via a work-around using composite variables, and may not be directly comparable.

Table S3. Parental speed, with impact of previous visit.

Fixed effects	Estimate	SE	Z	P
Intercept	0.70	0.11	6.10	**< 0.0001 *****
Parent moved food in previous visit (yes)	0.13	0.06	2.17	**0.030 ***
Total number of begging chicks	-0.02	0.03	-0.87	0.39
Weight rank	0.07	0.03	2.79	**0.0053 ****
Fed chick beg rank (not begging the most)	0.17	0.11	1.54	0.13
Supplemented	-0.14	0.12	-1.14	0.26
Parent sex (male)	-0.10	0.08	-1.26	0.21
Fed chick proximity rank	0.25	0.04	5.70	**< 0.0001 *****
Prey size	0.18	0.03	5.74	**< 0.0001 *****
Total begging chicks: weight rank	-0.06	0.03	-2.34	**0.019 ***
Parent sex: fed chick nearness rank	-0.12	0.05	-2.38	**0.017 ***
Supplemented: fed chick nearness rank	-0.10	0.05	-2.05	**0.040 ***
Random effects				
Parent ID	0.05			
Nest ID	0.07			
Unique row ID	0.54			

We conducted a GLMM with Poisson distribution for decision speed, including confidence in the previous decision. We controlled for parent ID and row ID (to account for overdispersion) as random effects. N=1433 feeding visits, 62 birds.

Table S4. Parent probing after feeding a chick.

Fixed effects	Estimate	SE	Z	P
Intercept	-1.34	0.30	-4.45	< 0.0001 ***
Total begging chicks	**0.24**	**0.08**	**2.95**	**0.0032 ****
Fed chick weight rank	0.12	0.07	1.64	0.10
Fed chick beg rank (not begging the most)	0.06	0.32	0.19	0.85
Supplemented	-0.27	0.33	-0.81	0.42
Parent sex (male)	-0.29	0.18	-1.57	0.12
Fed chick nearness rank	0.03	0.07	0.38	0.71
Parent moved food this visit	**0.83**	**0.17**	**4.80**	**< 0.0001 *****
Parental decision time	**-0.06**	**0.02**	**-3.73**	**0.0002 *****
Prey size	0.05	0.09	0.58	0.56
Random effects				
Parent ID	0.17			
Nest ID	0.56			

We conducted a GLMM, controlled for parent ID and nest ID as random effects. N=1501 feeding visits, 62 birds.