Wild jackdaws learn social tolerance to exploit new information

Josh J. Arbon[1,2], Noa Truskanov[1,3], Emily Stott[1,4], Guillam E. McIvor[1], Alex Thornton[1]

[1]Centre for Ecology and Evolution, University of Exeter, Cornwall, UK

[2]School of Biological Sciences, University of Bristol, Bristol, UK

[3]School of Zoology, Tel Aviv University, Tel Aviv, Israel

[4]Centre of Evolutionary Biology, School of Biological Sciences, University of Western Australia, Perth, WA, Australia

Abstract

Social tolerance is crucial in facilitating the evolution of cooperation and social cognition, but it is unknown whether animals can optimise their social tolerance through learning. We presented wild jackdaws (*Corvus monedula*) with a novel social information problem using automated feeders: to access food, adults had to inhibit their tendency to displace juveniles and instead show tolerance by occupying an adjacent perch. Adults learned to tolerate juveniles, generalising across juveniles as a cohort and in an unrewarded context, demonstrating learning of a new information-use strategy.

Main

Social tolerance, broadly defined as close proximity to conspecifics with limited aggression[1], is thought to be crucial to the evolution of prosociality[2] and social learning[3] in animals, and underpins distinctive forms of cognition and cooperation in humans[4]. However, tolerating others can entail costs such as foraging competition[5], so individuals may benefit from adjusting their tolerance in response to socio-ecological conditions[6]. Learning to tolerate high-value individuals, or classes of individual, may be beneficial in maximizing access to information[7] or resources[8]. For instance, juveniles are often easily displaced by adults and can be ignored as information sources[9], but as juveniles can be more exploratory and innovative[10] adults could benefit from learning to tolerate and attend to them. In human societies, the digital revolution flips the tendency for youngsters to learn from their elders[11], as older people seek skills from younger "digital natives"[12]. Using learning and generalisation to adjust a social information-use strategy[13] and tolerate individuals with particular

characteristics (e.g. age) may facilitate rapid, adaptive responses in changeable or heterogenous environments where reliable models can change quickly[14]. However, studies have yet to explicitly test whether animals in natural social networks can learn to tolerate others based on their information value.

We tested whether wild jackdaws *(Corvus monedula*) could learn to adjust their social tolerance to maximise rewards by presenting adults with a novel social information-use problem. Foraging adults do not preferentially associate with juveniles other than their own offspring (Supplementary Information: Figure S1) or attend to them as sources of information[9]. However, we simulated a scenario where juveniles became 'knowledgeable' about a new foraging resource by allowing them free access to automated experimental feeders containing high-quality food (mealworms). Feeders remained locked to adults unless there was a juvenile on an adjacent connected feeder, at which point access to adults was granted (hereafter a 'successful cofeeding event'; Figure 1a). As the feeder doors took approximately one second to close after a juvenile departed, adults could scrounge a small reward (max. one beakful) by displacing a juvenile. However, if adults refrained from displacing juveniles and instead tolerated their presence on the adjacent feeder, they gained the far larger reward of feeding for the duration of the cofeeding event (mean ± SE = 12.3 ± 1.5 s). To test whether effects carried over beyond the experimental feeders, we placed pairs of "passive" feeders with low-quality food (grain), freely accessible to all birds, at separate locations (~50 m away). We assigned 30% of adults to a control group, but these adults visited these feeders at low rates, prohibiting analysis (for details see Supplementary Information: Figure S2). Following previous work[15], we analysed data using Relational Event Models (REMs), a form of time-to-event model that accounts for the structure of the social network. Models estimate an Incidence Rate Ratio (IRR), where an IRR of 1.3 means an event is 30% more likely to occur per unit increase in the predictor (see Methods; model outputs in Extended Data Tables 1–6).

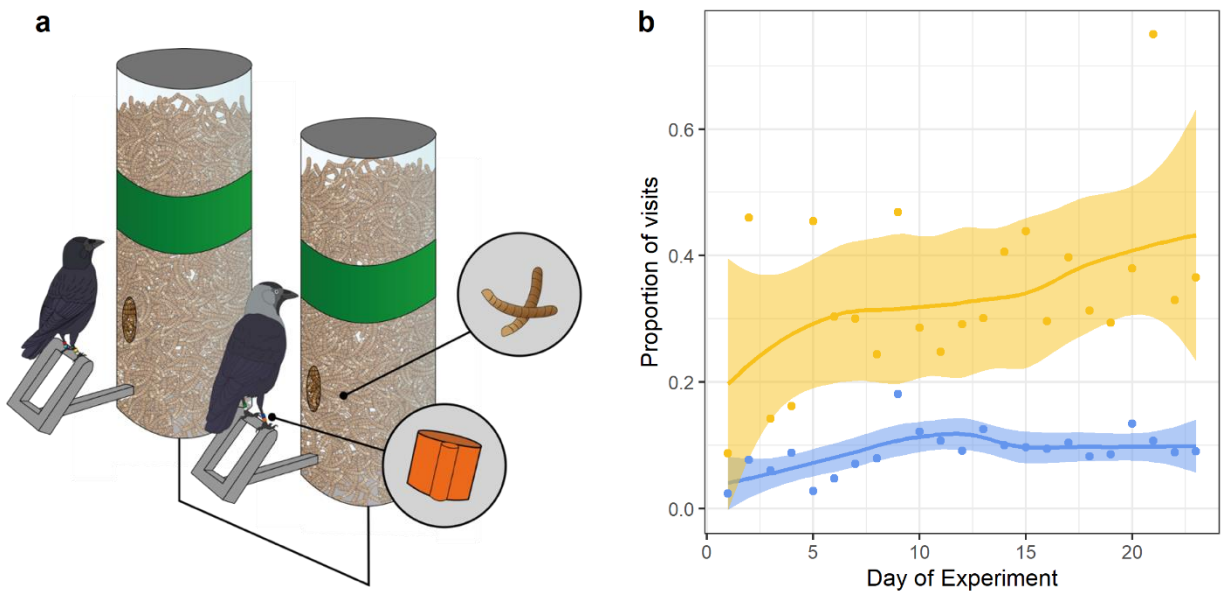

Figure 1. (a) Experimental feeders, showing an adult (right) in a successful cofeed with a juvenile. RFID tags (highlighted), determine access to mealworms by motor-controlled doors. (b) Daily proportion of adult cofeeding events that were successful (yellow) – or initiated by the displacement of juveniles – (blue).

As adult jackdaws gained experience, they increased their tolerant cofeeding with juveniles. Over the experiment, we detected 2431 cofeeding events. Of those, 766 were successful cofeeds between 200 unique adult–juvenile dyads, 176 of which involved adults joining juveniles. Overall, the proportion of adult cofeeding events with juveniles roughly doubled across the course of the experiment (Figure 1b, yellow line). At the individual level, the likelihood an adult joined a juvenile at the feeders (as opposed to joining another adult) increased by 3.5% for each previous successful cofeed the adult had participated in (*IRR* = 1.036, *CI* = 1.024–1.049; Figure 2a). Displacements of juveniles also became slightly more common over the course of the experiment (Figure 1b, blue line) as adults learnt that when displacing juveniles they could scrounge a small reward before the feeder closed (*IRR* = 1.005, *CI* = 1.002–1.007). However, the benefits of tolerant cofeeding with a juvenile (*ad libitum* access) far outweighed the benefits of scrounging. Consequently, the likelihood of displacements of juveniles, relative to that of displacements of other adults, declined by 2.2% per cofeeding success (*IRR* = 0.978, *CI* = 0.969–0.986; Figure 2b), indicating adults learned the rewards of tolerance.

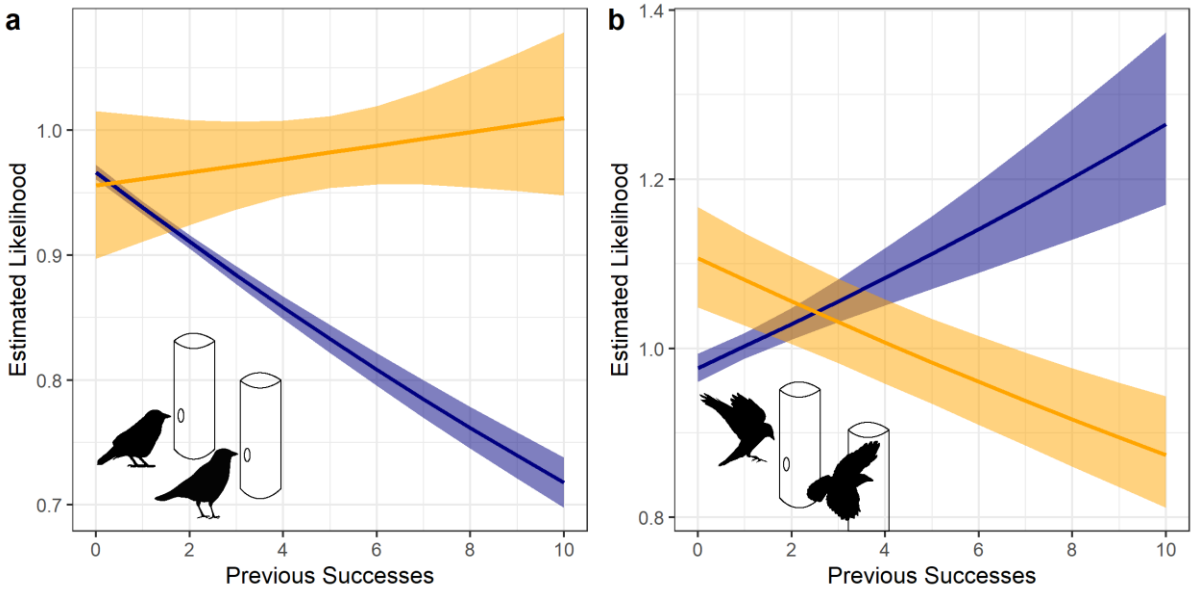

Figure 2. The difference in likelihood of an adult (a) cofeeding with, and (b) displacing a juvenile (yellow) as opposed to another adult (blue) relative to the number of previous successful cofeeding events that adult had previously participated in. Nine adults reached 6 or more previous successes. Lines and shaded area represent median and 95% REM estimates.

Our results also suggest adults generalised across juveniles as a cohort, rather than learning to tolerate specific individuals. In the results above, adults' increases in cofeeding and reductions in displacement were predicted by their total previous successes with any juvenile. By contrast, the number of prior cofeeding events with a specific juvenile did not affect subsequent cofeeding with, or displacement of that juvenile (both estimates span 1: specific individual cofeed *IRR* = 1.000, *CI* = 0.984–1.018; specific individual displacement *IRR* = 0.991, *CI* = 0.983–1.001). Thus, rewarding interactions with juveniles in general were more important in adult decision making than experience with specific juvenile partners. If we exclude one adult that was responsible for a large number of successful joining events (37/176) from analyses, the result that adults generalise to reduce displacements of juveniles is strengthened, though generalisation of cofeeding becomes less clear (Extended Data Tables 5-6). However, we also found that tolerance learnt at the experimental feeders carried over to a non-experimental foraging context, providing further evidence that adults generalised their tolerance of juveniles. Adults increased their association with, and decreased their displacement of, juveniles at passive feeders where no rules were required to access food,

demonstrating a carry-over effect of the experimental rewards (IRR_{Cofeed} = 1.085, CI = 1.075–1.094; $IRR_{Displace}$ = 0.997, CI = 0.996–0.998). The adult previously excluded from analyses never visited these passive feeders.

Taken together, our findings show that adult jackdaws learn to adjust their social tolerance to access information and rewards from a usually ignored demographic[9]. The results are unlikely to be explained by pre-existing social preferences before the experiment, as performance (proportion of visits that were successful cofeeds) was unrelated to the total number of visits made to the experiment. Similarly, adults' propensity to cofeed with a juvenile when they had no prior experience was unrelated to their overall number of successful cofeeds (Supplementary Information: Figure S3). Instead, adults modified their behaviour by learning the value of tolerating juveniles. Rather than modifying their responses towards the specific juveniles with whom they had successfully co-fed previously, adults appeared to apply a rule across all juveniles, even in an unrewarded context. Thus, jackdaws learned a new social information-use strategy[13,16]: juveniles provide information about the availability of food.

Information-use strategies are known to be influenced by developmental stress[17], but we show that learning can allow strategies to adjust rapidly to novel conditions. This is consistent with suggestions that rather than evolving as fixed, species-typical traits [16], social learning strategies use domain-general associative processes, enabling flexibility in the face of changing payoffs[13]. This flexibility also illustrates the benefits of tracking and responding to others' behaviour in dynamic social environments, a key assumption of the Social Intelligence Hypothesis[18]. However, generalising among similar individuals could facilitate access to valuable new information and opportunities without needing to remember the outcomes of past interactions with many different individuals, reducing cognitive burdens.

Flexibly adjusting social tolerance by learning new information-use strategies could facilitate the flow of information through networks by permitting close observation of a wide range of innovators. Indeed, the ability to capitalise on opportunities generated by innovators through flexible information-use is thought to be a crucial element of human culture[13] and may help to explain how animals like jackdaws can thrive in human-disturbed environments[19]. Our work also provides a rare illustration of the bi-directional interplay between information use and social structure in natural populations; contributing to our understanding of how sociality and decision-making processes coevolve[20].

Methods

Study System

The experiment was conducted on a wild population of colour-ringed jackdaws at two field-sites (Site Y: 50°11'23"N, 5°10'54"W; Site Z: 50°11'55.5"N, 5°10'09.0"W) of the Cornish Jackdaw Project, a long-term field study in Cornwall, UK. The project actively monitors a core nest-box population of ~80 boxes as part of the wider community of birds in the area. Jackdaws are captured at nest-boxes, using walk-in traps and whoosh nets throughout the breeding season, with more than 3000 individuals ringed over a 10-year period. Every individual has a set of uniquely identifiable coloured leg rings, with one ring containing a Radio Frequency Identification (RFID) tag (IB Technologies, Leicester, UK) to enable remote detection via antennae at feeders. Individual age is known from plumage characteristics at ringing. Approximately 150 chicks from nest boxes are ringed each year before fledging, as well as non-nest-box juveniles ringed as part of routine trapping [21].

Experimental Apparatus

Automated feeders were attached to posts approximately 1 m above the ground at prominent locations across the two field sites. Feeders featured a perch with an embedded RFID-detecting antenna that recorded the identity of any visiting bird. Access to the food within the feeder was restricted by a servo-motor controlled perspex door, with the antennae and motor connected by a logger unit (Naturecounters, Maidstone, UK). Feeders were split into two categories, *experimental* and *passive*. *Experimental* feeders were filled with a high-quality food (mealworms)[15], whereas passive feeders were filled with a low-quality food (poultry corn). *Experimental* feeders were placed in pairs 0.5 m apart and directly connected via a networking cable, with access to food within determined by the tag identity and combination of tags across both feeders (see Methods: *Treatments*). Passive feeders opened in response to the reading of any RFID tag, so all tagged jackdaws could access food at all times. *Experimental* and *passive* feeders were identical units running different operational programs, and so were visually distinguished both by food contents and by a green band present on *experimental*, but not passive, feeders (Figure 1). All feeders were closed by default, with a tag read required to trigger door opening.

We placed two pairs of *experimental* feeders at each site, which themselves were flanked by a pair of *passive* feeders to create an experimental array. Together, the four feeders formed a shallow arc, each separated by 0.5 m (setup: *Passive – Experimental – Experimental – Passive*). The passive feeders in *experimental* arrays were primarily designed to attract birds to the array, as well as to provide data on the individuals present in the local area. Data from these *passive* feeders within the experimental array are not presented in this study. For each experimental array, we placed a corresponding pair of *passive* feeders within the same local area which was used to detect associations and displacements outside of the direct context of the experimental setup. These *passive* pairs were placed in the same arrangement as the *experimental* feeders, 0.5 m apart, roughly 50 m from the experimental array. Unfortunately, during the onset of the experiment, a dead jackdaw appeared next to one of the feeder pairs at site Z, resulting in a near-complete abandonment of all feeders at the site. As such, only data from site Y was analysed.

Experimental Trials

Birds were given *ad libitum* access to high-quality food (mealworms) from the feeders for two weeks leading up to the experiment to both facilitate habituation to the new apparatus, as well as ensure that many adults knew that this food was theoretically available from these feeders. The experimental treatment was implemented between the 19th July and 13th August 2021, with experimental sessions conducted in the morning for five hours from ~5:30 am. Outside of these times the experimental feeders were covered in order to prevent access, with passive feeders accessible at all times. All trials were recorded with Sony Handycam (Sony, Tokyo, Japan) camcorders for validation purposes (see Supplementary Material: Displacement Validation).

Treatments

All RFID-tagged juveniles formed the 'knowledgeable' group, giving them unrestricted access to the *experimental* feeders. Treatment adults (70% of adult birds) were able to access the mealworm reward from the *experimental* feeders, but only if a juvenile was present on the connected adjacent *experimental* feeder. Control adults (30% of adult birds) were not able to use the *experimental* feeders under any circumstances. All three groups could access *passive* feeders in an unrestricted manner, including both the two *passive* feeders either side of the

experimental feeders and the *passive* feeder pairs at nearby locations. The control adults were designated to provide baseline data on adult-juvenile interactions with which to compare the learning of the treatment group and this split was chosen to preserve a meaningful comparison between these groups whilst not unnecessarily reducing the sample size of potential treatment adults. However, as seen in the statistical methods, the use of a control group is not necessary for the detection of a change in within-individual behaviour over time. Ultimately, adults in the control group visited experimental arrays at a rate too low to conduct meaningful analyses.

Due to limits in the memory of the microcomputer that controlled the experiment, only adults that had been seen in the habituation phase of the study were split amongst treatments, with adults seen in this phase randomly assigned to either 'treatment' or 'control' at the required 0.7/0.3 probability. Any adults that subsequently interacted with the experiment joined the control treatment by definition as they were able to access the *passive* feeders, but never the *experimental* feeders.

Ethical Note

Research was conducted under ethical permission from the Penryn Campus Ethics Committee (eCORN000406), and in line with Association for the Study of Animal Behaviour ethical guidelines [22]. Birds were ringed under BTO permit (permit nos. C6449, C5752, C6923 and C6079).

Statistical Methods

Relational Event Models (REMs), a type of time to event model for analysing dyadic network data, were run to compare changes in the rates of cofeeding and displacement events based on individual experience (as in [15]). REMs enable analysis to account for the order of events in a network, preventing data aggregation [23–25], and test hypotheses by comparing events against a set of 'non-events', unobserved events that could hypothetically happen between individuals in the network [26]. However, non-events are conventionally evenly sampled from the pool of individuals, which is not a realistic assumption for data of interactions between freely interacting wild animals, where some individuals are more represented in the data-stream than others. In line with conventional social network approaches [27], we used a permutation method to generate null datasets that maintained the structure of the data

228 regarding individual activity at the experiment. This method enabled us to account for the
229 varying individual levels of activity seen at the experiment, as well as the opportunities to
230 succeed at the task based on the other individuals present, something we would be unable to
231 incorporate into traditional modelling approaches. We created 10000 permuted datasets to
232 generate predictors of individual experience (number of successful join events by an adult of
233 any juvenile, number of cofeeding events between a specific dyad, number of displacements
234 of any juvenile by an adult). We then ran cox proportional hazard models using the *survival*
235 package [28] in R v4.1.2 [29] between each permuted dataset (non-events) and the observed data,
236 including a strata term for day. We took the median model coefficient of the 10000 models as
237 a point estimate for each parameter, with the 2.5 and 97.5 percentiles of each coefficient taken
238 to generate 95% confidence intervals. All results are reported as Incidence Rate Ratios, which
239 is calculated as the exponential of the cox coefficient.

240 For testing hypotheses about population-level changes over time, we took the
241 observed data-stream of events and separately randomised the identity of both the individual
242 that initiated and joined each event by shuffling (sampling without replacement). For these
243 population-level hypotheses all cofeeding/displacement events were randomised, including
244 those where a juvenile joined or displaced another individual. For testing hypotheses about
245 adult behaviour, all events where an adult was the source of an event (e.g. joined the cofeed
246 or displaced the feeding individual) were randomised, conditioned on the target of the
247 behaviour. This means the identities of the individuals that were joined or displaced were
248 preserved, with the identity of the adult that either joined or displaced them randomised
249 (again by shuffling). This preserved the structure of opportunities to join or displace, enabling
250 us to ask questions about how individual experience influenced who individuals joined and
251 displaced. For testing the hypothesis regarding the duration of successful cofeeding events,
252 the durations of all adult–juvenile cofeeding events were shuffled, with the identities of both
253 the initiator and joiner of the cofeeding event preserved. In all cases, randomisations were
254 constrained within day and feeder pair to preserve the visit structure across the experiment
255 and prevent the generation of scenarios that weren't possible given individual visit history.
256 As such, the estimated differences between permuted and observed datasets are likely to be
257 conservative, producing smaller effects than if using a less constrained permutation
258 procedure.

259 Analyses examined both (a) the number of times an adult joined a cofeed with a
260 juvenile, and (b) total cofeeds including when juveniles joined adults as a predictor (Extended
261 Data Tables 1b, 2b). These were qualitatively equivalent and (a) is presented in the main text.

Acknowledgements

We would like to thank the Gluyas family and Odette Eddy for access to their land to conduct the experiment. Thanks to Andy Young for many valuable discussions and Stephanie King for comments.

Funding

J.J.A. was supported by the Biotechnology and Biological Sciences Research Council-funded South West Biosciences (SWBio) Doctoral Training Partnership [680027356]. A.T. and G.E.M. were supported by a Leverhulme grant [RGP-2020-170] to A.T. and N.T. was supported by an SNSF post-doctoral mobility fellowship [P400PB_194397/1].

References

1. Cronin, K. A. & Sánchez, A. Social dynamics and cooperation: The case of nonhuman primates and its implications for human behavior. *Advances in Complex Systems* **15**, 1250066 (2012).
2. Massen, J. J. M., Ritter, C. & Bugnyar, T. Tolerance and reward equity predict cooperation in ravens (*Corvus corax*). *Scientific Reports* **5**, 1–11 (2015).
3. Coussi-Korbel, S. & Fragaszy, D. M. On the relation between social dynamics and social learning. *Animal Behaviour* **50**, 1441–1453 (1995).
4. Cieri, R. L., Churchill, S. E., Franciscus, R. G., Tan, J. & Hare, B. Craniofacial feminization, social tolerance, and the origins of behavioral modernity. *Current Anthropology* **55**, 419–443 (2014).
5. De la Fuente, M. F. *et al.* Foraging networks and social tolerance in a cooperatively breeding primate (*Callithrix jacchus*). *Journal of Animal Ecology* **91**, 138–153 (2022).

6. Testard, C. *et al.* Ecological disturbance alters the adaptive benefits of social ties. *Science* **384**, 1330–1335 (2024).
7. Van Schaik, C. P. Local traditions in orangutans and chimpanzees: social learning and social tolerance. in *The Biology of Traditions* (eds. Fragaszy, D. M. & Perry, S.) 297–328 (Cambridge University Press, Cambridge, 2003).
8. Miller, R., Schiestl, M., Whiten, A., Schwab, C. & Bugnyar, T. Tolerance and Social Facilitation in the Foraging Behaviour of Free-Ranging Crows (*Corvus corone corone*; *C. c. cornix*). *Ethology* **120**, 1248–1255 (2014).
9. Arbon, J. J., Hahn, L. G., McIvor, G. E. & Thornton, A. Competition and generalization impede cultural formation in wild jackdaws. *Proc. R. Soc. B.* **290**, 20230705 (2023).
10. Morand-Ferron, J., Cole, E. F., Rawles, J. E. C. & Quinn, J. L. Who are the innovators? A field experiment with 2 passerine species. *Behavioral Ecology* **22**, 1241–1248 (2011).
11. Cavalli-Sforza, L. L. & Feldman, M. W. *Cultural Transmission and Evolution: A Quantitative Approach*. (Princeton University Press, 1981).
12. Heyes, C. Blackboxing: social learning strategies and cultural evolution. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* **371**, (2016).
13. Mesoudi, A., Chang, L., Dall, S. R. X. & Thornton, A. The evolution of individual and cultural variation in social learning. *Trends in Ecology and Evolution* **31**, 215–225 (2016).
14. Lee, V. E. & Thornton, A. Animal Cognition in an Urbanised World. *Frontiers in Ecology and Evolution* **9**, 1–20 (2021).
15. Kings, M. *et al.* Wild jackdaws can selectively adjust their social associations while preserving valuable long-term relationships. *Nat Commun* **14**, 5103 (2023).
16. Kendal, R. L. *et al.* Social Learning Strategies: Bridge-Building between Fields. *Trends in Cognitive Sciences* **22**, 651–665 (2018).

17. Farine, D. R., Spencer, K. A. & Boogert, N. J. Early-life stress triggers juvenile zebra finches to switch social learning strategies. *Current Biology* **25**, 2184–2188 (2015).
18. Dunbar, R. I. M. The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews* **6**, 178–190 (1998).
19. Ducatez, S., Sol, D., Sayol, F. & Lefebvre, L. Behavioural plasticity is associated with reduced extinction risk in birds. *Nature Ecology & Evolution* 1–6 (2020) doi:10.1038/s41559-020-1168-8.
20. Kulahci, I. G. & Quinn, J. L. Dynamic Relationships between Information Transmission and Social Connections. *Trends in Ecology and Evolution* **34**, 545–554 (2019).
21. Greggor, A. L., McIvor, G. E., Clayton, N. S. & Thornton, A. Wild jackdaws are wary of objects that violate expectations of animacy. *Royal Society Open Science* **5**, 181070 (2018).
22. ASAB. Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour* **159**, i–xi (2020).
23. Tranmer, M., Marcum, C. S., Morton, F. B., Croft, D. P. & de Kort, S. R. Using the relational event model (REM) to investigate the temporal dynamics of animal social networks. *Animal Behaviour* **101**, 99–105 (2015).
24. Patison, K. P., Quintane, E., Swain, D. L., Robins, G. & Pattison, P. Time is of the essence: an application of a relational event model for animal social networks. *Behavioral Ecology and Sociobiology* **69**, 841–855 (2015).
25. Butts, C. T. A relational event framework for social action. *Sociological Methodology* **38**, 155–200 (2008).
26. Lerner, J. & Lomi, A. Reliability of relational event model estimates under sampling: How to fit a relational event model to 360 million dyadic events. *Network Science* **8**, 97–135 (2020).

27. Farine, D. R. & Whitehead, H. Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology* **84**, 1144–1163 (2015).
28. Therneau, T. M. A package for survival analysis in R. R package version 3.3-0 (2022).
29. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing (2019).