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Corvids can decide if a future exchange is worth waiting for

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Evidence for time-dependent calculations about future rewards is scarce in non-human animals. In non-human primates, only great apes are comparable with humans. Still, some species wait for several minutes to obtain a better reward in delayed exchange tasks. Corvids have been shown to match with non-human primates in some time-related tasks. Here, we investigate a delay of gratification in two corvid species, the carrion crow (*Corvus corone*) and the common raven (*Corvus corax*), in an exchange task. Results show that corvids success decreases quickly as delay increases, with a maximal delay of up to 320 s (more than 5 min). The decision to wait rests both on the quality of the prospective reward and the time required to obtain it. Corvids also apply tactics (placing the reward on the ground or caching it) that probably alleviate costs of waiting and distract their attention during waiting. These findings contrast previous results on delayed gratification in birds and indicate that some species may perform comparably to primates.

Keywords: cognition; corvids; delay of gratification; exchange task

1. INTRODUCTION

Most animals generally neglect long-term benefits for immediate ones, which is often explained by impulsivity [1–4]. Animals appear to value time differently from humans, and this can be expected to affect their capacity to maximize food income or form expectations about future returns in the social domain [1]. Most studies investigating the cognitive determinants involved in the delay of gratification focus on primates owing to their phylogenetic proximity with humans [5,6]. However, accurate maximization of future intakes should be naturally selected in species living in complex social systems like corvids. As food hoarders, time-dependant calculations bear high ecological relevance for them [7–10]. Corvids are used to delaying the consumption of food [11] and to dissociating current from future motivational states [8,10,12]. What is still unclear is how they may integrate the value of a prospective reward according to the time required for obtaining it and if future-oriented decision-making compares with that of other species.

Delay of gratification in animals is generally assessed using classical delay choice tasks [13], where a subject can choose between a small immediate reward and a larger but delayed one. A delay of a few seconds is enough to see animals revert their choice to the immediate option in birds (chicken [14]; pigeons [15,16]) and in monkeys [17–19]. In the delayed exchange task, subjects have to keep food of relatively low value that they can exchange later against one of higher value. Here, primates can sometimes tolerate delays of several minutes according to the value of the expected reward [20–23]. They decide early on whether to wait or not, showing that they anticipate the duration of the delay and whether the reward is worth the cost of waiting. Despite indications that corvids should equate or approach primates' performances in term of impulsivity control, accurate valuation of reward and anticipation of delay duration [10], there is no evidence that this is indeed the case. Here, we investigate this question in two species of corvids, common ravens (*Corvus corax*) and carrion crows (*Corvus corone corone*) using a procedure identical to the one used in primates [20]: subjects are first trained to exchange, then they are given a food item of low value that they can choose to keep or to exchange for a food item of higher quality at the end of a given waiting period. We manipulate two core parameters: (i) the time birds must wait to exchange and (ii) the quality of the food reward obtained (ranging from preferred to highly preferred items). We predict that, similar to primates, birds should exchange more often at short delays and/or for highly preferred food. Additionally, they should give up waiting earlier than expected by chance if the value of the expected reward is not worth waiting for.

2. MATERIAL AND METHODS

The study involves six crows and four ravens held at the Konrad Lorenz Forschungstelle (KLF) in Austria and two ravens tested at Edinburgh Zoo, RZSS, UK. Individuals' species, age, sex, rearing experience and individual food preferences are described in the electronic supplementary material. All birds were first trained to exchange one token for a food reward (see electronic supplementary material, tables S1 and S2). For testing, subjects are voluntarily separated in a familiar compartment. The experimenter stands in front of the cage and gives an initial piece of food to the individual. The experimenter keeps the giving hand closed into a fist while showing in the other hand the exchange reward, of higher quality than the initial item. The reward remains visible during the entire waiting period. After this period elapsed, the experimenter opens the fist presenting the palm up where the subject can return the initial food. If it does so, it receives in exchange the reward. If subjects eat the initial food or give it back too early, the trial ends. Testing is run in a succession of stages corresponding each to a specific waiting period. From one stage to the next, the waiting period increases (starting with 2 s, then 5, 20, 40, 80, 160, 320 and 640 s). Each stage composes of six sessions of eight trials each (electronic supplementary material). Three possible types of reward (low-, medium- and high-quality) are presented 16 times each per stage. Subjects who succeed in waiting at least once at a given stage are tested in the following one.

3. RESULTS

As predicted, the number of birds exchanging the initial food for a better quality food as well as the

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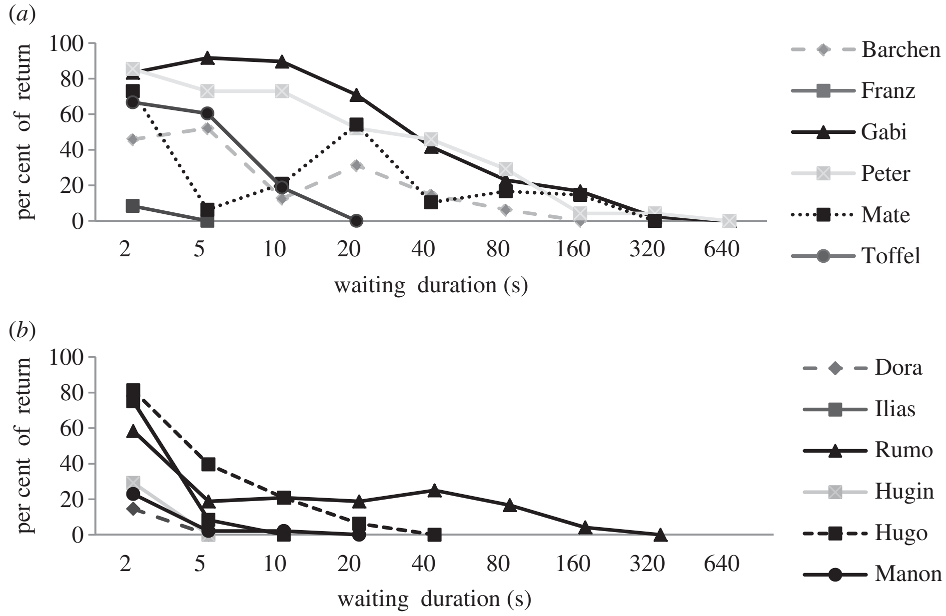

Figure 1. General capacity to wait: percentage of successful exchanges according to the length of waiting period for individual (*a*) crows and (*b*) ravens.

proportion of their successful exchanges gradually decreases as the delay increases (figure 1). Over 40 s, birds succeed in less than 50 per cent of the trials. The maximum delay accepted in this task is 320 s, at which two crows are still exchanging at low rates. No significant difference between species is found when comparing the longest waiting time sustained at least once by each subject of the two species (Mann–Whitney test, $U = 27$; $p = 0.17$, $N_{\text{crows}} = 6$, $N_{\text{ravens}} = 6$). Interestingly, birds can decide early in a trial whether to wait or not. Early renouncement can occur both immediately after and immediately before a success and is not explained by an extinction of the waiting behaviour nor relevant to the hypothesis of a single early attempts followed by multiple renouncement in a given session (figure 2).

Nine subjects renounce waiting significantly earlier than predicted by chance, i.e. in the first seconds rather than randomly in the course of a trial (see electronic supplementary material, figure S1 and table S3). There is also a non-significant trend to give up earlier for the least preferred reward compared with the most preferred one (Wilcoxon, $T^+ = 11$; $n = 4$; $p = 0.06$; in birds giving up earlier for all food qualities). Irrespective of the time to wait, the birds exchange the initial item more frequently when the offered reward is highly preferred (Friedman test, $n = 12$; d.f. $= 2$, $p = 0.003$).

When not exchanging, birds mainly eat the initial food (63.6% of cases), attempt to exchange it too early (19.7%), refuse to pick up the initial item (1.6%) or fail to give it back after the waiting time elapsed (15.1%). Those birds waiting for 20 s or longer routinely drop the food, i.e. placing it on the ground, and/or caching it in nearby crevices, while they visually check or cache repeatedly (see the electronic supplementary material and videos). Successful exchanges at the longest waiting periods (greater than 160 s) are all characterized by the use of placing or a combination of placing and caching.

4. DISCUSSION

Our findings show that two corvid species are capable of controlling their immediate impulse to eat in order to gain a more preferred item in near future (waiting not only for seconds but also for minutes), with a maximal waiting time of up to 5 min. This performance deserves attention considering that previous studies on birds revealed hardly any tolerance to delays (range of few seconds [14–16,24]). However, to our knowledge, this study is also the first report of an exchange task being applied to birds.

The corvids' propensity to exchange low- for high-quality food is affected by both the value of the reward and the time required in obtaining it. This indicates that they integrate the expected reward value and associated time cost when making their decision. The high frequency of eating errors, and the fact that no improvement is observed over a stage confirms that waiting is indeed costly and the motivation to obtain the reward was not strong enough. Giving up earlier than predicted at delays where birds still succeed indicates that they understand something of the duration involved and judge the exchange not worth it. As with impulsivity control and reward value effect, crows and ravens may compare to primates in this respect [25].

In terms of tolerance to long delay, the corvids' maximal response is also comparable to those of monkeys tested in this set-up. Capuchin monkeys (*Cebus apella*), for instance, can wait up to a minute to exchange low-quality against high-quality food [20] although monkeys may wait longer than corvids when allowed to nibble the initial food. Interestingly, birds exchanging at long delays start to place the initial item on the ground and/or cache it to retrieve it later. These behaviours probably alleviate the cost of waiting: not having to hold the food distracts the bird's attention from it. Distractive strategies have been described in delay of gratification tasks in chimpanzees (*Pan troglodytes*)

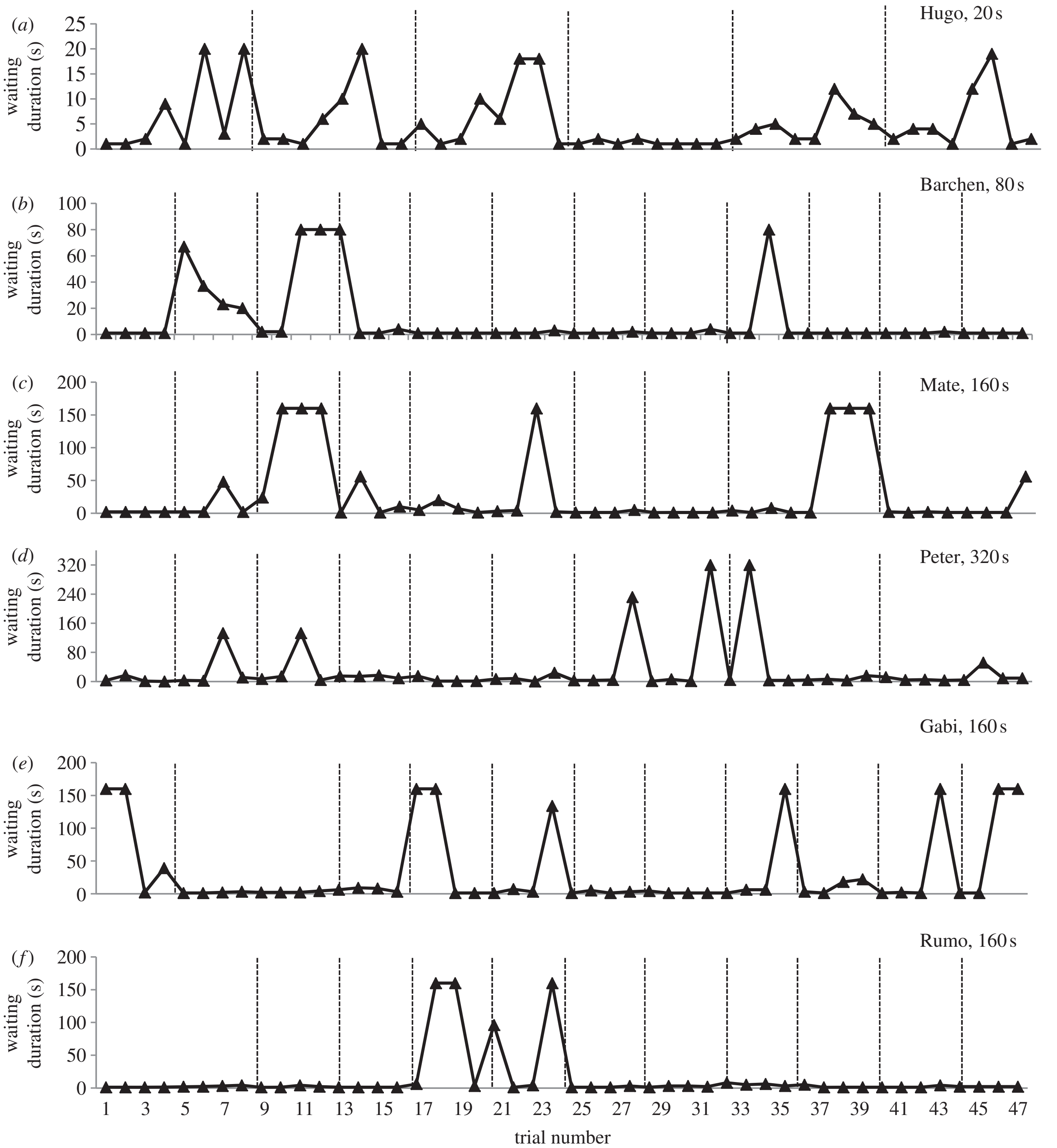

Figure 2. (*a–f*) Waiting duration (including successes) per trial at the last waiting period where birds succeeded at least twice (for the six birds succeeding at waiting for 20 s or more). Vertical lines indicate sessions (eight trials) or half sessions (four trials, see the electronic supplementary material). Attempts to wait and successes neither solely occur in the first tests of the stage nor in the first tests of a session or demi session. Giving up early cannot be explained by progressive extinction of the waiting behaviour. Giving up waiting from the first second of a trial, over several sessions, does not preclude attempting again, and sometimes succeeding, at later sessions for the given waiting period. No improvement is observed across the 48 trials.

[25]. However, letting go of the food and keeping it away from self has yet not been observed in any of the primate species tested with exchange tasks; it certainly improved success rate in the present study.

In humans, children who exert the most patience are also those who attain higher socio-professional positions as adults [5]. It is not known whether good skills at time-related calculation are also correlated with social success in animal societies. Considering the first similarities detected here in performances between social species like corvids and primates, it is worth wondering how early in evolution time-dependent sensitivity might have arisen in animals despite later divergences in the organization of brain structures and tissues [26]. Such sensitivity certainly bears a high ecological relevance in food hoarding and food pilfering species like corvids and could have been selected for specifically. An extensive investigation of other birds and mammal species may bring fresh and much needed insights to this question.

Training and testing comply with Association for the Study of Animal Behaviour guidelines for ethical conduct of research with animals.

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